

Effects of food addition on life history of Yellow-Bellied Marmots

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Abstract. We provided two social groups with supplemental food for several years (River Colony, June 1996–August 2000 and Marmot Meadow, June 1998–August 2000) to examine the effects of food addition on life history characteristics of female Yellow-bellied Marmots (*Marmota flaviventris*). We compared demographic and life history characteristics of supplemented females and reference females living within the same colony but adjacent home ranges. Supplemental food did not increase growth rates during gestation and lactation; however, growth rates of supplemented mothers increased after young were weaned. There was no clear effect of food addition on survival rates, female recruitment, age of first reproduction, or reproductive effort, such as increased litter size or weaning masses of young. Social structure of yellow-bellied marmots is most likely the main factor influencing life-history characteristics and the role of food availability is minor.

Key words: age of first reproduction, growth rates, survival, philopatry, litter size, matriline size

Introduction

Life history theories generally assume that energy resources are finite and must be allocated among reproduction, maintenance, and growth (Boyce 1988). When energy is limiting, reproduction and growth may not occur or be severely reduced. In extreme cases, lack of food resources can increase mortality (Armitage 1994). In marmots, only 2.0–6.4% of available net primary production is consumed (Kilgore and Armitage 1978), suggesting that they are not energy limited. However, individual growth (Lenihan and Van Vuren 1996), reproduction (Armitage and Downhower 1974, Armitage *et al.* 1976, Van Vuren and Armitage 1994a, Schwartz *et al.* 1998), and over-winter survival (Armitage 1994, Lenihan and Van Vuren 1996) are highly variable in natural populations of Yellow-bellied Marmots and these variations may be explained by food availability.

Many researchers have examined the effects of food abundance on vertebrate populations by manipulating food resources, generally food addition (Boutin 1990). Food supplementation strongly affects population densities, home-range size, recruitment, reproduction, and immigration in small mammal populations (Lack 1954, Flowerdew 1972, Sullivan *et al.* 1983, Dobson and Kjelgaard 1985a, Boutin 1990, Klenner and Krebs 1991, O'Donoghue and Krebs 1992, Byrom *et al.* 2000). However, despite the large number of food manipulation studies, the effects of food on populations are poorly understood (Boutin 1990). One problem is the lack of studies that examine the effects of food manipulations at the individual level, specifically effects on life history characteristics. How individuals respond to food addition can provide a better understanding of mammalian life history (Holmes and Sherry 1997). Seasonal variation in food availability is probably the main factor influencing mammalian reproduction and survivorship, especially for small mammals (Bronson 1989).

The purpose of this study was to examine the effects of supplemental food on life history characteristics of female Yellow-bellied Marmots, *Marmota flaviventris*. We address the issue of juveniles in a previous paper (Woods and Armitage 2003) and the data on males are scant. Yellow-bellied Marmots are polygynous and live in colonies composed of a male, one to three independent female groups with non-overlapping territories, known as matriline (see Armitage 1991 for further detail on matriline) and their offspring. Females are capable of reproducing at age 2, but the mean age at first reproduction for these animals is 3 (Schwartz *et al.* 1998). Animals that are 1 year old, known as yearlings, may be present; however, most males disperse because the cost of philopatry is severe (Van Vuren and Armitage 1994b). Female dispersal is facultative and the cost of female philopatry is lower. Female dispersal is mediated by social interactions between adult and yearling females (Brody and Armitage 1985). Yearlings disperse early when adult females are highly antagonistic (Downhower and Armitage 1981). Aggression by adult females may be mediated by their potential reproductive success. Reproductive productivity varies with matriline size (Armitage and Schwartz 2000) and dominant females may adjust their aggression based on the reproductive competition among resident females. Therefore, resident females play a major role in the regulation of population size in these animals.

To determine the effects of food availability on life history, we supplemented the food resources of two social groups of yellow-bellied marmots. These marmots have been studied extensively since 1962 in the East River Valley of Gunnison County and the life history characteristics and demography of these animals under natural conditions have been well documented (e.g., Armitage and Downhower 1974, Armitage 1991, Schwartz *et al.* 1998). We tested the following hypotheses:

1. Supplemented adults will grow faster and reach higher body masses. Growth rates during gestation and lactation will be higher in mothers with supplemental food.
2. Adult female marmots are more likely to survive hibernation with food supplementation.
3. When female recruitment is mediated by food resources, a larger proportion of yearling females will be recruited and matriline size will increase with food addition.
4. A greater proportion of females will reproduce at an earlier age when fed as yearlings and/or juveniles.
5. A greater proportion of adult females will reproduce in food-supplemented groups.
6. Litter size will be higher in supplemented groups.

Methods

We studied Yellow-bellied Marmots at two colony sites in the upper East River Valley near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. The first site, Marmot Meadow is a subalpine meadow, bordered by aspen-fir forest and dense willow thickets along the East River at an elevation of 2930 m with two major clumps of rocky outcrops where the active burrows are located. The second, River colony at an elevation of 2867 m, is a meadow with rolling hills bordered by steep cliffs along the East River (See Armitage 1974 for photographs of these sites). Burrows are located between a small ravine and exposed shale next to and along the cliff face. Marmots move from the cliff burrows to feed within the meadows. The vegetative composition of River and Marmot Meadow colonies is similar to the *Festuca thurberi* community type (Langenheim 1962), dominated by grasses (*Bromus* spp. and *Poa* spp.), and common forbs such as cinquefoil (*Potentilla gracilis*), dandelions (*Taraxacum officinale*), yarrow (*Achillea millefolium*), mountain blue bells (*Mertensia ciliata* and *M. fusiformis*) and wild sweet pea (*Lathyrus leucanthus*).

Each colony had a reproductive male and two to three independent female groups or matriline with non-overlapping territories. We supplemented the food for one matriline at each site and monitored the second matriline for reference („reference“ populations in field experiments are analogous to „controls“ in laboratory experiments (Krebs *et al.* 1976)). We provided one matriline at River colony with high protein feed (Omolene 300®), which contained at least 16% crude protein and 3.5% fat, during the summers of 1996–2000. A lower protein feed (Omolene 100®), 10% protein and 3.5% fat, was provided to one female and her offspring at Marmot Meadow colony in 1998–1999 and to two different

females in 2000. The three females at Marmot Meadow colony were littermates and the resident male presumably fathered all their offspring. The female groups that were used as references were supplemented in 2000 with the same feed used in previous years, and the previous supplemented groups became the reference to confirm that the effects of supplementation were not the result of habitat or genetic differences among the animals.

Marmots were live trapped, weighed, tagged with a numbered metal ear tag, marked distinctively with a black fur dye, and sex, age, and reproductive status recorded. Identification and age of all yellow-bellied marmots in the area were known from long-term, continuous studies (Armitage 1991). Methods of trapping, handling, and marking are described elsewhere (Armitage 1974). Offspring groups were determined by trap location and observations made with binoculars and 15-60x telescope. The onset and termination of trapping and observations differed from year to year. In 1996, 1997, and 2000, trapping and observations began the first week of June and ended in late August. In 1998 and 1999, fieldwork began in late May and ended in early October in 1998 and in mid-September in 1999. In every year, trapping began prior to yearling dispersal and emergence of young.

Growth rates were compared by using a general linear model procedure for analysis of covariance (Minitab 1994), which tested for differences between the slopes, with day as the covariate.

The masses of the two groups for each supplemental year were compared using Student's t-test and chi-square analysis was used to determine if marmots were more likely to survive if supplemented. We used Fisher's exact test to determine if survival was independent of supplementation when expected values for chi-square analyses were below 5.

In order to determine if supplementation affected dispersal, we examined female philopatry from data collected from 1966–1995 at the same location.

Results

Changes in Body Mass

Yearlings

Yearlings grow linearly until dispersal (Fig. 1). We compared growth rates of supplemented and reference yearlings only in 1998 because it is the only year in which yearlings survive from both groups. Supplementation did not affect yearling growth ($F_{1,64} = 0.005$, $p = 0.95$). However, yearlings that were supplemented as young the previous year tended to be larger than reference yearlings throughout the summer (Fig. 1). Growth rates and mass of males and females varied widely from year to year. When data were available for comparison, males were larger than females on the first day of trapping at both colonies. Males were significantly larger at River colony in 1997 and 1998 (Student's t-test of y-intercepts, $p = 0.001$ and $p = 0.003$, respectively). Only in 2000 were River colony females larger than males at the start of the summer, although not significantly (Student's t-test of y-intercepts, $p = 0.298$).

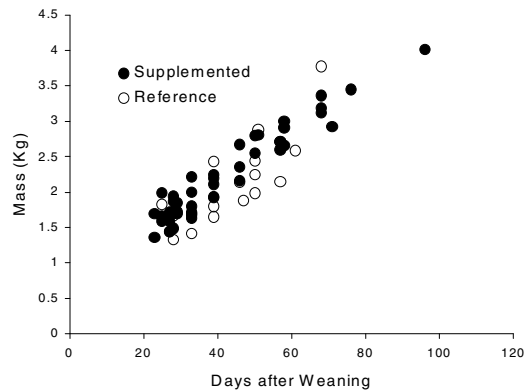


Fig. 1. Growth in mass of supplemented and reference yearling Yellow-bellied Marmots (*Marmota flaviventris*) from River colony, 1998. Yearlings grew linearly and did not have a cessation of growth during the trapping period. Masses of both males and females are used to show growth pattern.

Growth rates varied for both sexes. With few exceptions, males tended to grow faster than females. At River colony, males had higher growth rates than females. The average growth rate for males at River from 1996–2000 was 33.65 g/day (SD=1.96) and was marginally significant when compared to mean female growth rates of 23.0 g/day (SD=10.0; one-tailed t-test, $p=0.07$). Female growth was highly variable and ranged from 16.7–37.9 g/day. Only in 1998, did females grow faster than males, but the difference was not significant. At Marmot Meadow, male and female growth rates did not differ. Average growth rates were 25.8 g/day (SD=5.94) for males and 24.07 g/day (SD=4.33) for females. Masses reached upon entering hibernation could not be determined for both sexes because males disperse earlier than females.

Growth patterns for yearling females are similar to that of juveniles, which have two phases of growth; linear growth followed by slow to zero growth up to two weeks prior to hibernation (Armitage 1996a, Lenihan and Van Vuren 1996, Woods and Armitage 2003). During the course of this study, however, there was no evidence of slowed or ceased growth in yearlings of either sex, regardless of supplementation. It is unclear when or if yearling growth rates would have slowed or stopped prior to hibernation. We trapped only two yearlings as late as August 23, and did not observe a cessation of growth.

Adults

Reproductive two-year-olds were always smaller than older females, and did not have access to the supplemental feed. However, non-reproductive two-year-olds were observed at the feeder and their growth rates and individual masses could not be distinguished from other supplemented adults ($F_{1,21}=0.45$, $p=0.51$; Fig. 2). Growth rates ranged from 19.9–23.8 grams per day for non-reproductive two-year-old females. We were able to determine growth rates for only two of the three reproductive two-year-olds. Female 2114 at River and female 98 at Marmot Meadow had growth rates of 6.40 and 7.42

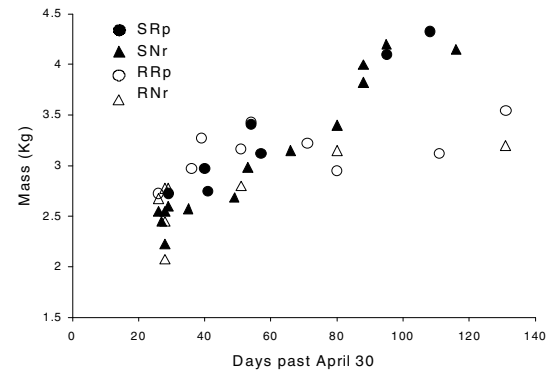


Fig. 2. Growth patterns of supplemented and reference reproductive and non-reproductive females at River colony, 1999. Solid symbols represent supplemented (S) females and open symbols are reference (R) females. Circles represent reproductive (Rp) females and triangles are non-reproductive (Nr).

grams per day, respectively. Growth rates include pre- and postweaning dates, and did not differ over the growth period.

The growth rates of the supplemented female at River colony were significantly higher than adult (3 or older) females that were not fed in 1996 and 1997 (Table 1). Adults were caught too infrequently in 1998 for statistical analysis. In 1999, reproductive females that were fed had higher growth rates than unfed females, but only when growth rates were compared after weaning. Prior to weaning (July 10) growth rates of two-year-olds, reproductive, and

River Colony				
Year	Treatment	Growth Rate (slope)	R ²	n
1996	Supplemented	34.4 ∇ 6.0	0.97 (3)	1
	Reference	15.2 ∇ 1.8	0.90 (10)	2
	P	0.01		
1997	Supplemented	21.8 ∇ 1.4	0.99 (4)	1
	Reference	11.9 ∇ 2.6	0.95 (3)	1
	P	0.03		
1999	Supplemented	21.7 ∇ 1.4	0.93 (21)	6
	Reference			
	Before Weaning	22.4 ∇ 8.8	0.45 (10)	3
	P	0.92		
	Reference			
	After Weaning	6.23 ∇ 4.7	0.47 (4)	1
	P	0.01		

Table 1. Growth rates (g/day) of adult Yellow-bellied Marmots. Supplemented marmots represented in this table are reproductive, with the exception of 1999 which includes non-reproductive females, but their growth rates did not differ from reproductive females. Growth rates were determined by regression analysis on mass determined by trapping. The number of mass values used in the regression analysis is written in parentheses. n = number of adults in treatment group. Values are given as mean ∇ standard deviation. P values of growth rate comparisons are from general linear model procedure for analysis of covariance.

non-reproductive females do not differ significantly ($F_{4,14}=0.44$, $p=0.78$). Several unfed adults decreased growth after weaning, which contrasts with other observations (Andersen *et al.* 1976, Armitage *et al.* 1976). The reason for the differences is unknown. Female 279 reproduced in 1999 and accumulated mass at a rate of 20.7 g/day before weaning, but 6.23 g/day after weaning. Reproductive female 1399 was supplemented and had growth rates of 21.1 g/day throughout the summer. The growth rate of non-reproductive female 2114 was 20.3 g/day prior to August 1 and she did not have access to supplemental food. When trapped one month later, her weight had not changed, she was the only non-reproductive female that ceased growth late in the summer and she did not survive the winter of 1999–2000. Adult marmots were caught too infrequently in 2000 for statistical analysis.

At Marmot Meadow, all females trapped at the age of two or older were reproductive. Supplementation did not occur during the first two years, 1996 and 1997. Growth rates for each individual varied from year to year. In 1996, all three females raised their young at Main Talus. Female 2009 was dominant to her sisters (2007 and 2019; Brady and Armitage 1999), and the two females moved to a nearby site (Aspen Burrow) within the colony by June 1997, where they stayed for the remainder of the study.

During the first year, growth rates did not differ between females 2009 and 2019, 41.8 g/day and 44.7 g/day, respectively. Growth rates are based on only three data points so should be treated with caution. Growth rate of female 2007 was 6.9 g/day and significantly lower than that of her sisters ($F_{1,5}=8.49$, $p=0.03$). In 1997, female 2019 grew significantly faster (27.7 g/day) than female 2009 (9.42 g/day; $F_{1,7}=24.55$, $p<0.001$). Female 2007 was only trapped twice, but weighed 2800 grams on July 1 and was approximately 600 grams lighter than female 2009. In both 1996 and 1997, female 2007 was the smallest female, followed by 2009 and female 2019 was the largest female.

In 1998 supplemental food was provided to female 2009 at Main Talus. She grew linearly at the rate of 22.0 g/day, which was significantly higher than that of both reference females (10.1 g/day and 3.59 g/day for females 2019 and 2007, respectively) when the entire summer was considered ($F_{2,20}=30.23$, $p<0.001$). However, when only growth rates prior to weaning were considered, the differences among the females disappeared ($F_{2,10}=0.63$, $p=0.55$). By the end of the summer, 2009 was the largest female and 2007 remained the smallest. Female 2009 was trapped on September 19 and weighed 5.090 kilograms, the largest female caught on record. Growth rates did not differ significantly among the three marmots in 1999 ($F_{2,27}=0.33$, $p=0.72$). Growth rates were 13.5, 14.5, and 16.1 g/day for females 2007, 2019 and 2009, respectively. Female 2007 remained the smallest female and 2009, the largest.

The two females at Aspen burrow were provided with supplemental feed in 2000, and female 2009 at main talus was not supplemented. Growth rates changed after weaning for all three marmots. Female 2009 at Main Talus lost mass during gestation and lactation without the added food (-9.56 g/day), but had an increased growth rate of 27.8 g/day post-weaning. In contrast, females 2019 and 2007 gained

mass (14.8 and 17.8 g/day) during gestation and lactation with food addition, but growth rates changed dramatically after weaning. Female 2007 lost mass at a rate of -3.5 g/day and female 2019 had a reduced growth rate of 3.7 g/day. The order of mass of the three females returned to its original order with female 2019 being the largest of the three. Increased food availability did not increase the mass of female 2007 beyond that of 2009 and she remained the smallest marmot.

Survival

Although growth rates increased, and therefore body mass upon entering hibernation, adult survivorship was unaffected by food supplementation. The reference group at River Colony had two adult females in 1996. Reference female 281 was killed by a badger in 1999 at 10 years of age. The second female, 279, died the following winter during hibernation, also at the age of 10. The supplemented social group contained two females in 1996, females 431 and 1399, the offspring of 431. Female 431 died after summer 1998 during hibernation at the age of 11. Five three-year-old supplemented adult females died overwinter between 1998 and 2000. At Marmot Meadow, the only two-year-old, recruited in 1999, was not captured or observed during the subsequent summer and is assumed to have died during hibernation.

Female Philopatry and Matriline Size

Individuals that remain in their natal colony throughout their yearling year are considered to be recruits (Brody and Armitage 1985) and add to the resident population. Females were not more likely to remain in their natal areas when supplemented. In 1998, one of the two reference females at River colony produced one female yearling, which dispersed. Supplemented females produced 15 female yearlings from 1996–1999, and 60% (9) remained as two-year-olds. Over half (5) were recruited in 1999, the first year that old female 431 did not return. Forty-four female yearlings were produced from 1966–1995 at River Colony. Only 50% (22) of these yearlings were caught the following summer as 2-year-olds. The likelihood that a female would disperse did not differ significantly between the supplemental years and previous years ($c^2 = 0.45$, $p = 0.50$).

In 1999, at Marmot Meadow, one two-year-old female remained at a location peripheral to her natal area. She was the offspring of one of the two reference females. She was the only two-year-old ever caught at Marmot Meadow between 1996 and 2000. The supplemented female remained aggressive to all yearlings during the course of this study and actively chased her offspring from previous years from the feeder.

In several instances, females were considered residents of the colony, but peripheral to their natal area. Peripheral females remained within the home range of their mothers, and either did not associate or had limited home range overlap with other adult females. Peripheral females were considered a separate matriline. At River, matriline size (2) did not change for reference females from 1996–1999. In contrast, matriline size varied from 2–6 females in

the supplemented group. The summer following the death of female 431, the supplemented matriline at River colony consisted of six females, the largest matriline on record. Two other females moved to adjacent sites to form matriline of one. Five of the six females returned in 2000, but split into two matriline with a matriline of four occupying both South Mound and Spruce Mound of River colony. The fifth female moved to an adjacent site north of the main colony.

Matriline size varied little at Marmot Meadow. In 1996, the three females raised their litter at Main Talus forming a matriline of 3. The subsequent years, the matriline split into two groups, one at Main Talus and two females at Aspen Burrow. Only in 1999 did a third matriline of one form in an area peripheral to Aspen burrow.

Age of First Reproduction

Supplementation did not affect age of first reproduction. No marmot at any site reproduced as a yearling. Of the two two-year-olds that reproduced at River, one was supplemented as a juvenile and yearling, and the other, as a yearling only. Neither female had access to the feeder as a two-year-old. Only 2 of 9 (22%) resident two-year-olds from the supplemented groups reproduced as two-year-olds. Six of 18 (33%) recruited two-year-olds produced litters at River colony from 1966–1995. The proportion of reproductive two-year-olds did not differ significantly between supplemented groups and proportion of reproductive two-year-olds from 1966–1995 (one-tailed test, Fisher exact test, $p=0.45$). Three females at Marmot Meadow reproduced for the first time in 1996 at the age of 2 and all subsequent years of the study. A two-year-old was recruited in 1999 and weaned a litter of five, but never had access to supplemental food.

Litter Size

Over the course of this study, seven females had access to supplemental feed while caring for their young. We treated each litter produced as an independent sample. Although the sample size is small, mean litter-size of supplemented females was 4.92 ($n=13$, $SD=1.19$) and ranged from 3–7. The average litter size for reference females was 5.00 ($n=9$, $SD=1.32$), ranging from 2–6. Litter size is not correlated with body size in these animals (Schwartz *et al.* 1998) and varies per individual from year to year, so we were not concerned about pseudoreplication. There was no statistical difference between supplemented and reference litter-size (Mann-Whitney U-test, $p=0.70$). Juveniles of supplemented females were not significantly larger at weaning than reference juveniles (Woods and Armitage 2003), and therefore supplemented mothers did not invest greater amounts of energy into offspring size.

The smallest litter was produced by one of the two-year-olds at River colony. However, the age of the female was probably not the main cause for the small litter size. Mean litter size does not differ between age classes of Yellow-bellied Marmots (Schwartz *et al.* 1998) and the small litter was probably the result of individual variation or loss of young prior to weaning.

Discussion

Population densities increased dramatically in most terrestrial vertebrates when food supplemented (Boutin 1990). In two species of ground squirrels, population densities more than tripled in the presence of added food (*Spermophilus parryii plesius*: Hubbs and Boonstra 1997, Byrom *et al.* 2000, *S. columbianus*: Dobson and Kjelgaards 1985b). In other mammalian species, food addition increased juvenile recruitment in *Peromyscus mexicanus* (Duquette and Millar 1995), increased overlap of home ranges in two species of voles (*Microtus californicus*: Ostfeld 1986, *Clethrionomys rufocanus*: Ims 1987), and in most mammals studied, increased proportion of females breeding, decreased age at first reproduction and increased litter sizes (Boutin 1990). In contrast to these studies, yellow-bellied marmots did not respond to food addition as did other vertebrates. Yellow-bellied Marmots responded similarly to other studies only in their increased growth in response to food addition, however, other parameters did not differ significantly. Unlike the other mammals studied, marmots are highly social and the importance of the matriline is probably more important than environmental factors such as food availability.

Changes in Body Mass and Survival

Growth in marmots is clearly limited by food supply. Adults grow faster when supplemented and are capable of reaching higher masses. Marmots entering hibernation at larger masses, however, were not more likely to survive compared to reference adults. Most marmots were larger at the end of the summer compared to the beginning, regardless of their reproductive condition or feeding regime. Marmots must accumulate sufficient amounts of fat to survive hibernation. The amount of fat necessary or „critical mass“ needed to survive hibernation is probably gained under natural conditions, and mass above the critical mass does not impart added survivorship benefits to the individual (Woods and Armitage 2003).

Female Philopatry and Recruitment

Surviving marmots that are larger as a result of food addition are not more likely to remain in their natal area. The number of resident females is stable when considered over a long period (Armitage 1991). Matriline size increases when recruitment of daughters occurs (Armitage 1996b); recruitment is affected by both agonistic and amicable behavior between residents and recruits (Armitage 1986, 1989, 1996b). If a habitat is „full“, recruitment does not occur and there is no immigration into these colonies (Armitage 1984, 1991).

Determining what defines a habitat as full remains unclear. In this study, adult females were provided an abundant and quality food resource, but recruitment did not increase significantly. As a matter of fact, in most cases, matriline size did not change in the presence of food addition. Matriline size doubled in 1999 in the supplemented group at River, but only after the death of the dominant

female. It is unclear how the added food supply and the change in the social system may have interacted to produce the large matriline. However, the social system probably had a greater effect on matriline size.

The space made available by the death of the two reference females at South Mound became occupied by Spruce females in 2000. Five females were present, however, one female moved to another burrow location. The remaining four shared both sites, three females lived at South Mound and one female lived at Spruce, indicating that matrilineal fission may be occurring. The location of the supplemental food was switched in 2000, but all females had access to it. If the matriline splits in 2001, it would indicate that interactions among adult females are more important than food resources in determining matriline size.

Therefore, matriline size may not be affected by increased food availability, but may be mediated by other factors, such as number and quality of hibernacula (Andersen *et al.* 1976), individual variation in female aggression (Svendsen and Armitage 1973) and current matriline size (Armitage 1998). In the latter case, females may make recruitment decisions based on potential future reproductive success and survivorship. Survivorship and net reproductive rate increase as matriline size increases, but net reproductive rate decreases when matriline size is greater than three (Armitage and Schwartz 2000). Females can increase their fitness by recruiting daughters when the matriline is small because larger matriline have a competitive advantage over conspecifics (Armitage 1998). However, recruitment should only occur if the habitat can sustain an increased number of females.

A female may fail to recruit a daughter when the habitat is unable to support a larger matriline and risks being replaced by an unrelated immigrant (Armitage 1991). Thus, one might expect older females to recruit daughters who would inherit the matrilineal resources. However, older marmots, especially those living singly are less likely to recruit daughters than younger females living in a matriline (Armitage 1987). Older marmots may not be present to assist their daughters and they may be left in small matriline, susceptible to conspecifics (Armitage 1998), mortality (Van Vuren and Armitage 1994a) or immigrants (Armitage 1991). Clearly, abundant food supply did not increase recruitment, and the recruitment of daughters is influenced more by social constructs, then by food availability.

Age of First Reproduction and Litter Size

Schwartz *et al.* (1998) suggested that age at first reproduction may be determined by energy (i.e., food) availability in yellow-bellied marmots. In most ground-dwelling sciurids, yearlings either do not reproduce or reproduce at a lower frequency than adults. For example, yearling females are more likely to reproduce in supplemented populations of Columbian ground squirrels (Dobson and Kjelgaard 1985a). Among marmots, only woodchucks, *Marmota monax*, are known to reproduce as yearlings (Armitage 2000, Snyder 1962). Yearling woodchucks are probably capable of reproducing for a variety of

reasons. First, woodchucks are weaned at a larger mass. Female juvenile woodchucks weigh on average 690 grams (Snyder *et al.* 1961) compared to 550 grams for juvenile Yellow-bellied marmots (Armitage *et al.* 1976). Second, the growing season of about 5 months for juvenile woodchucks is double that of juvenile yellow-bellied marmots (Armitage 1981). Juvenile yellow-bellied marmots have higher growth rates (23–33 grams per day; Woods and Armitage 2003) than juvenile woodchucks (16–20 g/day; Snyder *et al.* 1961). Therefore, woodchucks are capable of reproducing as yearlings because they initiate growth at a larger size and have a longer growing season, which compensates for their slower growth rates. Even when juvenile marmots are supplemented and grow at rates of 24–49 g/day (Woods and Armitage 2003), the growing season of yellow-bellied marmots is too short to enable yearling reproduction.

Supplemented juveniles are capable of reaching masses of 2300–2700 grams upon entrance into hibernation. Despite large emergence masses, juveniles caught as yearlings never weighed more than 1600 grams by the end of May. Juveniles lost up to a third of their body mass during hibernation. We examined all yearlings at all colonies trapped in the East River Valley from 1966–2000. The largest female yearling caught at any colony at the end of May was 1700 grams, which is less than the smallest reproducing two-year-old (1850 g) recorded from 1966–2000. The growing season for yellow-bellied marmots (and the other 12 species) is too short (Armitage 1999, 2000) and juveniles do not have time to gain sufficient mass to reproduce as yearlings.

Reproductive suppression is probably the main cause of why most 2-year-olds do not reproduce. Reproduction is inhibited by dominant females (Armitage 1986, 1998) and two-year-old females are more likely to reproduce in the absence of adult females, including their mothers (Armitage 1998). During the course of this study, females that reproduced at the age of two only did so if they moved away from their natal site, but remained within the boundaries of the colony. Litter size did not vary with age, and marmots can reproduce in successive years from age two, i.e., females at Marmot Meadow reproduced every year from 1996–2000 with or without food addition. Therefore, lifetime reproductive success can increase when reproduction begins as soon as possible.

Conclusions

There is evidence to partially support only two of our original six hypotheses. Hypothesis #1 was partially supported. Food supplementation did increase growth rates, but only after weaning in reproductive females. In hypothesis #3, we proposed that food addition would increase matriline size. In 1999, we observed a record matriline size, but it appears that the death of the dominant female is most responsible for the change in the social structure, and was probably mitigated by the added food supply. Furthermore, we did not observe any change in matriline size in the other colony. There was no evidence from this

study to support our remaining hypotheses.

Food supplementation did not increase survival, decrease age of first reproduction, increase the proportion of females reproducing, nor did litter size increase in food supplemented mothers. Although food restriction is beyond the scope of this study, the addition of food did not greatly affect life history characteristics. Mothers increase the survival of their young simply by allowing their daughters to remain in their natal area and decrease mortality as a result of dispersal (Van Vuren and Armitage 1994b). Reproductive suppression, aggression towards conspecifics, and the influence of matriline size and relatedness are the most important factors influencing population dynamics and life-history characteristics. Social structure is more important than food resources in its influence on the life history of Yellow-bellied Marmots.

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