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EFFECT OF FOOD SUPPLEMENTATION ON JUVENILE GROWTH AND SURVIVAL IN *MARMOTA FLAVIVENTRIS*

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We provided 2 social groups of yellow-bellied marmots (*Marmota flaviventris*) with 2 types of supplemental feed (high and low protein) to test hypotheses about effects of food abundance and quality on juvenile growth rates and survival. Both supplemented litters and reference litters ceased to gain body mass by 2 weeks before hibernation even though supplemented litters had access to supplemental food. Body mass at weaning did not differ significantly between the 2 groups, but supplemented young had significantly higher growth rates (21.4–48.7 g/day) than reference young (24.1–33.3 g/day) and therefore had higher body mass late in the season. Juveniles that received high-protein supplements grew faster than the low-protein group. The addition of high-protein feed did not increase survival; however, juveniles that received low-protein feed were more likely to survive. Juveniles with higher body mass were not more likely to survive. Marmots must reach a critical body mass to survive hibernation and do not appear to benefit from mass gain beyond the critical body mass.

Key words: body mass, food supplementation, growth, hibernation, juveniles, *Marmota flaviventris*, survival

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Growth, reproduction, and survival are important factors in the evolution of life history in mammals and are assumed to be limited by finite energy resources (Boyce 1988). The availability of energy as a factor limiting population size has been well documented (Boutin 1990; O'Donoghue and Krebs 1992). However, ecological factors may reduce the importance of food quality and quantity and their effects on population dynamics, community structure, and life history traits that are observed in nature (Abdellatif et al. 1982; Arcese and Smith 1988; Castle and Wunder 1995; Hairston et al. 1960; Hubbs and Boonstra 1997; Lack 1954; Ward and Armitage 1981b; White 1993; Wiens 1977).

Food supplementation studies have been conducted to better our understanding of the role of food availability on life-history traits. Most of these studies have focused on small herbivores ≤2 kg body mass (Boutin 1990), so a comparison of how small and large organisms may vary in their responses to food supplementation is difficult (Caughley and Krebs 1983). More information is needed on a wider range of species, including larger herbivores, predators, species living in variable environments, or species that differ widely in life-history traits.

Yellow-bellied marmots (*Marmota flaviventris*) are large (up to 5 kg or more), diurnal, ground-dwelling squirrels that hibernate two-thirds of the year and carry out maintenance, grow, and reproduce in the remaining third (Davis 1976). Unlike other ground squirrels that have been studied, the

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young of all marmot species except *M. monax* delay dispersal until their 2nd summer. The additional summer is necessary to reach a body mass that will increase the probability of successful dispersal (Barash 1989). It has been hypothesized that this delay in dispersal is due to ecological constraints and that it led to the evolution of sociality in marmots (Armitage 1999). However, there are no reported studies of the effects of food supplementation on life-history traits in marmots.

Individual growth (Lenihan and Van Vuren 1996), reproduction (Armitage and Downhower 1974; Armitage et al. 1976; Schwartz and Armitage 1998; Schwartz et al. 1998; Van Vuren and Armitage 1994), and overwinter survival (Armitage 1994; Lenihan and Van Vuren 1996; Schwartz and Armitage 1998) are highly variable in natural populations of yellow-bellied marmots. Marmots generally live in seasonally harsh environments with long severe winters and a short growing season. The importance of food is probably most pronounced for juveniles, which are generally weaned up to 2 months after adults emerge from hibernation and therefore have less time to gain mass before plant senescence. Juvenile ground squirrels and marmots must gain sufficient mass during their 1st active season to survive hibernation (Armitage and Downhower 1974; Lenihan and Van Vuren 1996; Murie and Boag 1984; Slade and Balph 1974). Body mass upon entrance into hibernation is affected by birth weight, length of the active season, and growth rates before and after weaning (Allainé et al. 1998).

The persistence of populations of ground squirrels is often determined by the production of yearlings, which is directly related to juvenile survival (Armitage 1986; Dobson 1995). Growth and development have been well documented in several species of ground squirrels (Allainé et al. 1998; Clark 1970; Clark and Skryja 1969; Ferron and Ouellet 1991; Koeppl and Hoffmann 1981; Lenihan and Van Vuren 1996; Levenson 1979; Morton and Tung 1971; Turner et al. 1976). Ground squirrels and marmots have evolved accelerated ontogenies in response to a relatively short growing season and the rapid storage of fat for hibernation (Kiell and Millar 1978; Levenson 1979). Individual development varies, however, and individuals with slow growth rates are adversely affected by the short growing season.

The purpose of this study is to determine whether abundance or quality of food (or both) limit rates of juvenile growth and survival. We provided 2 social groups of yellow-bellied marmots with 2 types of supplemental feed (high and low protein) to test hypotheses about the effects of food abundance and quality on juvenile growth rates and survival. If these marmots are food limited, then survivorship and growth rates should increase with increased food availability. Higher juvenile growth rates should lead to higher body masses at immergence and possibly to increased survival. If growth rates are affected by food quality, growth and survival of juveniles should be greater in groups that receive high-protein supplements. Because the condition of juveniles may be influenced by the condition of their mother (Trombulak 1991) and reproductive females were also provided with supplemental food, we also examined weaning mass of supplemented juveniles. We determined whether supplemented mothers produced larger young and thus subsequently increased their survivorship.

Materials and Methods

We studied yellow-bellied marmots at 2 colony sites about 1.7 km apart in the upper East River Valley near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. The 1st site, Marmot Meadow, is a subalpine meadow at an elevation of 2,930 m with 2 major clumps of rocky outcrops where active burrows are located, bordered by aspen–fir forest and dense willow thickets along the East River. The 2nd is River, a meadow with rolling hills bordered by steep cliffs along the East River at an elevation of 2,867 m (see Armitage 1974, for

photographs of these sites). Burrows in River are located between a small ravine and exposed shale next to and along a cliff face. Marmots move from the cliff burrows to feed within the meadows. The vegetative composition of River and Marmot Meadow habitats is similar to the *Festuca thurberi* community type (Langenheim 1962), dominated by grasses (*Bromus* and *Poa*) 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 2–3 independent female groups with nonoverlapping territories, which produced matrilines (Armitage 1991). We supplemented 1 matriline with either high-protein horse feed, Omolene 300, or low-protein horse feed, Omolene 100 (Purina Mills, LLC, St. Louis, Missouri) at each site and monitored a 2nd matriline for reference ("reference" populations in field experiments are analogous to "controls" in laboratory experiments—Krebs et al. 1976). The only exception occurred during 1996 when the matriline that was supplemented at River was the only group to produce young. We provided 1 matriline at both sites, including 1–2 reproductive females at River, with high-protein feed, which contained at least 16% crude protein and 3.5% fat, during the summers of 1996–2000. The reference group contained 2 reproductive females from 1996 to 1999. The 2 reference females did not survive up to 2000. A lower protein feed, 10% protein and 3.5% fat, was provided to 1 female and her offspring at Marmot Meadow in 1998–1999 and to 2 different females in 2000. The 3 females at Marmot Meadow were littermates, and the only male present was presumed to have fathered all their offspring. At both River and Marmot Meadow, reference and supplemented groups were switched in 2000. The female groups that were used as references were supplemented in 2000 with the same type feed used in previous years. The previous supplemented groups became the reference to confirm that the observed effects during supplementation were not the result of habitat or genetic differences among the animals.

Marmots were livetrapped, weighed, tagged with a numbered metal ear tag (size 1005-3, National Band and Tag Co., Newport, Kentucky), marked distinctively with a black fur dye (Nyanzol-D, J. Belmar, Inc., North Andover, Massachusetts), and sex, age, and reproductive status were 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 using binoculars and 15–60× telescopes. The onset and termination of trapping and observations differed from year to year. In 1996, 1997, and 2000, trapping and observations began the 1st 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 mid-September in 1999. Every year, trapping began before yearling dispersal.

Date of weaning was determined as the date of the 1st observation of young. Juveniles emerge above ground at about the time they are capable of eating solid food (Ferron and Ouellot 1991). All juveniles from the same litter emerged on the same day. Trapping effort was increased upon 1st sighting of juveniles to record mass as close to weaning as possible. Trapping and observations were used to determine litter size and maternity of young. Trapping of juveniles continued daily until the entire litter was captured, then trapping continued weekly for as long as researchers were available. Trapping until entrance into hibernation was not always possible every year.

Because most juveniles were not captured on their weaning day, mass at weaning was determined by regression analysis on mass of juveniles during linear growth. The growth curve of juveniles is linear for several weeks after emergence and then shifts into an asymptotic period of slow or zero growth before hibernation (Armitage 1996; Lenihan and Van Vuren 1996). We compared the growth curves of each group using both linear and nonlinear regression. When marmots were trapped late in the summer and growth shifted into an asymptotic period, we used nonlinear regression to fit the data. A Gompertz nonlinear model was fitted to the data to determine when linear growth ceased. A Gompertz model is a 3-parameter model which determines the maximum mass (α), time at which growth rate is highest (γ), and an equation factor, k, which acts as a scale parameter on day when mass is recorded (x—Seber and Wild

1989:330). We used the Gompertz equation to determine the day at which growth rate is 50% of maximum growth rate. We chose 50% because juvenile marmots maintain their growth rate (linear growth) for a period of time after weaning, and we felt that 50% would be a clear indication when juvenile linear growth ceased. Furthermore, 50% is a value that could be used as a reference point for comparison among groups. The length of the period of growth was defined as the period between weaning and the day at which maximum growth rate decreased by 50%.

We fitted linear regression lines to the defined period of linear growth. From the regression equation, we estimated weaning body mass (y-intercept) and growth rates (slope) for each supplemented and reference group. Maximum body mass of the Gompertz curve is reached as the x-variable approaches infinity and in most cases is biologically impossible. Therefore, we averaged body masses of marmots trapped on the final day to predict body mass upon entry into hibernation for that litter.

The body masses of reference and control groups for each year were then compared using Student's *t*-test. We used standard *t*-tests to compare body mass of each group at weaning (y-intercept) of supplemented juveniles and reference juveniles. Growth rates were compared using a general linear model procedure for analysis of covariance (ANCOVA), which tested for differences between the slopes, with day as the covariate. Data for juveniles of both sexes were pooled because growth rates did not differ between sexes among years (*P*-values ranged from 0.14 to 0.99 using a general linear model for each year and experimental group). We used Mann–Whitney *U*-tests to determine whether there were differences in litter size between supplemented and reference litters. We compared growth rates calculated from regression analyses of supplemented juveniles at River (high-protein feed) with those of supplemented juveniles at Marmot Meadow (low-protein feed) using Mann–Whitney *U*-tests. For reference litters, we used data from 1990 to 2000 to determine whether there was a significant difference in growth rates between the 2 colonies.

Values are presented as means ± *SD*. We present sample sizes (*n*) as number of individuals. In statistical analyses of growth rates, determination of *d.f.* was based on number of data points (body mass and the corresponding day mass was measured) for each regression analysis. Standard deviations of the y-intercepts as calculated by regression analyses were used to calculate *t*. Statistical analyses of estimated hibernation body mass were based on *n* values even though many individuals were litter mates and thus did not represent completely independent samples. Given that the entire colonies were individual matrilines, complete independence of samples was not possible. Lengths of growth periods are reported for litters rather than individuals. Fisher's exact test was used to determine whether survival was independent of supplementation.

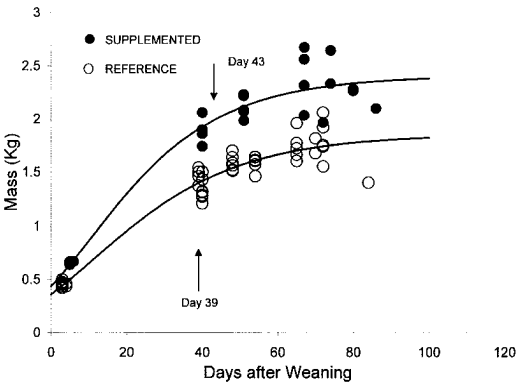


FIG. 1.—Growth in body mass of food-supplemented and reference litters of juvenile yellow-bellied marmots (*Marmota flaviventris*) from Marmot Meadow, Gunnison County, Colorado, 2,930 m elevation, in 1998. Pattern of growth is fit with a Gompertz curve. Juvenile growth rates decrease to 50% of maximum growth rate at day 43 and 39 days after weaning for supplemented and reference groups, respectively, and are followed by a period of stable body mass. Juvenile marmots did not enter traps between day 6 and day 39 (probably due to weather and perhaps other factors). Both examples represent typical growth patterns for all litters whether food-supplemented or not.

RESULTS

Length of growth period.—Trapping did not always take place late into the summer; therefore, length of the growth period before the plateau could be determined for only a few years. Plateaus occurred in both supplemented and reference groups (Fig. 1),

TABLE 1.—Comparison of body mass at weaning and growth rates of juvenile yellow-bellied marmots between colony with food supplements and reference colony in Gunnison County, Colorado. Body mass at weaning estimated from regression of data from juveniles pooled within a treatment group. The number of individuals in each treatment group is *n*. The coefficient of determination for growth rate regression equation is r^2. *P* values for weaning masses based on 2-tailed Student's *t*-test, *P* values for growth rates based on analyses of covariance using general linear models. Supplemented and reference groups were interchanged in 2000. River colony is not represented for 1998 due to insufficient trapping data.

	Treatment	Weaning date	Weaning mass (g)		Growth rate (g/day)		r^2	*n*
			$\bar{X}$	*SD*	$\bar{X}$	*SD*		
River colony								
1997	Supplemented	26 June	345	34.0	36.1	1.3	0.96	11
	Reference	6 July	410	40.0	33.3	1.4	0.96	8
	P		<0.001		0.15			
1999	Supplemented	3 July	676	45.5	43.6	1.9	0.95	4
	Reference	5 July	494	39.3	26.3	1.4	0.93	5
	P		<0.001		<0.001			
2000	Supplemented	8 July	592	15.2	47.9	2.0	0.99	3
	Reference	14 July	592	28.7	31.4	3.0	0.93	4
	P		0.50		<0.001			
Marmot Meadow colony								
1998	Supplemented	9 July	468	38.7	35.5	1.5	0.99	5
	Reference	11 July	373	35.9	25.4	1.2	0.96	12
	P		<0.001		<0.001			
1999	Supplemented	9 July	450	52.4	29.4	2.2	0.85	6
	Reference	13 July	470	33.3	23.3	1.5	0.86	11
	P		0.03		0.02			
2000	Supplemented	8 July	374	22.2	21.4	0.9	0.94	12
	Reference	10 July	362	49.7	24.1	2.3	0.86	6
	P		0.15		0.28			

and there was no clear effect of supplementation on the onset of the plateau period.

Supplemented litters at River (in 1999) and Marmot Meadow (in 1998 and 2000) had growth periods of 47.3, 38.9, and 58.1 days, respectively, compared with growth periods for reference litters of 47.8, 42.9, and 38.9 days. Overall, supplementation does not appear to affect the growth period. However, the growth period for the supplemented group appears to be longer at Marmot Meadow in 2000, but the small number of litters precludes statistical testing of the difference.

In most cases, growth in body mass of juveniles stabilizes after an initial period of linear growth. We examined trapping records dating back to 1969 where there was sufficient information to determine growth rates, and only 7 of 48 juveniles at River and Marmot Meadow lost body mass after their maximum body mass was reached. Of the 7, only 2 juveniles lost >100 g after reaching their maximum body mass.

Weaning body mass.—We compared the body mass (g) at weaning of 35 juveniles (18 high-protein supplement, 17 reference) at River over 3 summers (1997, 1999, and 2000). Fifty-two juveniles (23 low-protein supplement, 29 reference) were compared at Marmot Meadow during the summers of 1998–2000 (Table 1). Supplemented juveniles were weaned at significantly larger body masses than reference juveniles in 1999 ($t = 16.15$, $d.f. = 53$, $P < 0.001$) at River and in 1998 ($t = 5.95$, $d.f. = 23$, $P < 0.001$) at Marmot Meadow. Body mass at weaning of supplemented juveniles did

not differ significantly from that of reference juveniles in 2000 at Marmot Meadow ($t = 1.05$, $d.f. = 55$, $P = 0.15$) or at River ($t = 0.004$, $d.f. = 14$, $P = 0.50$; Table 1). Reference juveniles were significantly heavier at weaning than supplemented juveniles in 1997 at River ($t = 6.72$, $d.f. = 60$, $P < 0.001$) and in 1999 at Marmot Meadow ($t = 1.94$, $d.f. = 73$, $P = 0.03$). For all supplemented litters combined, mean litter size was 4.92 ± 1.19 and ranged from 3 to 7. The average reference litter size was 5.00 ± 1.32, ranging from 2 to 6. There was no statistical difference in sizes between supplemented and reference litters (Mann–Whitney $U = 110$, $d.f. = 9, 13$, $P = 0.70$).

Growth rate and hibernation body mass.—Growth rates varied from year to year for both experimental groups in both colonies (Table 1). The slopes of regression lines differed significantly among groups at River in 1999 ($F = 83.6$, $d.f. = 1, 51$, $P < 0.001$) and 2000 ($F = 22.7$, $d.f. = 1, 14$, $P < 0.001$) but not in 1997 ($F = 2.1$, $d.f. = 1, 60$, $P = 0.15$). Growth rates of supplemented and reference groups differed at Marmot Meadow in 1998 ($F = 23.8$, $d.f. = 1, 36$, $P < 0.001$) and 1999 ($F = 5.6$, $d.f. = 1, 73$, $P = 0.02$) but not in 2000 ($F = 0.001$, $d.f. = 1, 49$, $P = 0.28$). When all years were combined, grand mean growth rates (42.53 ± 5.97 g/day) at River for marmots that were fed high-protein feed were significantly higher than growth rates (28.77 ± 7.07 g/day) for marmots that were fed low-protein feed at Marmot Meadow, (1-tailed Mann–Whitney $U = 15$, $d.f. = 3, 3$, $P = 0.04$). We compared reference juvenile growth rates from 1990 to 2000 between River and Marmot Meadow. Mean growth rates between River (23.7 ± 5.35 g/day) and Marmot Meadow (22.80 ± 2.44 g/day) did not differ statistically ($P = 0.68$).

Juveniles with supplemental food reached higher body masses at hibernation than juveniles in reference groups in all years except 1997 at River (Table 2). The final masses of juveniles for each year varied, partly as a result of time that trapping was terminated. However, within years, trapping was consistent, and supplemented juveniles entered hibernation at higher masses than reference juveniles. When trapping continued until hibernation (1999 River, 1998 and 2000 Marmot Meadow), supplemented juveniles averaged 2.216 ± 0.69 kg, compared with 1.488 ± 0.27 kg for reference juveniles.

Survival.—The effect of supplementation on survival was not consistent in all groups (Table 2). In 1997 and 1998, supplemented juveniles at River did not survive better than reference juveniles (1-tailed test, Fisher's exact test, $P = 0.234$ and $P = 0.96$ for 1997 and 1998, respectively). However, in 1999, reference juveniles survived better than supplemented young (1-tailed test, Fisher's exact test, $P = 0.04$). In contrast, supplementation increased juvenile survival at Marmot Meadow in 1998 ($P = 0.004$) and had a marginally positive effect in 1999 (1-tailed test, Fisher's exact test, $P = 0.075$).

Discussion

Juvenile marmots and ground squirrels must attain a sufficient body mass to survive hibernation (Armitage 1994; Armitage and Downhower 1974; Lenihan and Van Vuren 1996; Murie and Boag 1984; Slade and Balph 1974), and juveniles that are weaned late in the summer are less likely to survive hibernation (Armitage et al. 1976; Neuhaus 2000). However, in our study, providing marmots with horse feed as a supplemental food source increased growth rates and thus body mass upon entrance into hibernation but in most cases did not significantly increase overwinter survival. Environmental factors such as food quality and availability clearly affect growth (White 1993); but internal factors such as an endogenous rhythm may be a greater influence on the date of cessation of growth and thus length of the growth period.

Length of growth period.—Yellow-bel-

TABLE 2.—Comparison of survival and estimated body mass at hibernation of juvenile yellow-bellied marmots between colony with food supplements and reference colony in Gunnison County, Colorado. Body mass at time of hibernation estimated from late-season individual body masses. Body mass given as mean ± *SD*. *P* values of body masses are based on 2-tailed Student's *t*-test; *P* values for survival are from 1-tailed Fisher's exact tests. Supplemented and reference groups were interchanged in 2000.

		Supplemented	Reference	*P*
River colony				
1997	Survived	9	3	0.234
	Died	2	5	
	Mass at hibernation (estimated)	1,793 ± 87.5	1,833 ± 14.8	0.600
1998	Survived	5	2	0.576
	Died	3	2	
	Mass at hibernation (estimated)	2,456 ± 36.9	1,518 ± 16.8	0.006
1999	Survived	0	4	0.040
	Died	4	1	
	Mass at hibernation (estimated)	2,490 ± 22.4	1,464 ± 28.0	<0.001
2000	Survived	2	1	0.371
	Died	1	3	
	Mass at hibernation (estimated)	1,708 ± 17.1	1,406 ± 14.3	0.019
Marmot Meadow colony				
1998	Survived	4	0	0.004
	Died	1	12	
	Mass at hibernation (estimated)	2,325 ± 19.7	1,736 ± 26.8	0.006
1999	Survived	6	6	0.075
	Died	0	5	
	Mass at hibernation (estimated)	1,668 ± 22.5	1,314 ± 15.3	0.012
2000	Survived	6	4	0.437
	Died	6	2	
	Mass at hibernation (estimated)	1,433 ± 11.6	1,204 ± 10.1	0.004

lied marmots reduce feeding rates about 2 weeks before hibernation (Couch 1930). Plants begin to senesce in mid-August (Frase and Armitage 1989; Kilgore and Armitage 1978; Langenheim 1962) and become dry, decreasing in nutritive value (Armitage 1994; Armitage et al. 1976; Webb 1980). Thus, poor forage quality may prevent adequate marmot growth late in the summer and eventually cue the onset of hibernation. In our study and others (Armitage 1996; Lenihan and Van Vuren 1996), juveniles entered hibernation more than 2 weeks after their growth ceased. Growth periods of marmots during our study fall within the range of growth periods of previous years (Armitage 1996; Lenihan and Van Vuren 1996), and juvenile growth stops even in the presence of food supplementation. The length of the marmot growth period appears to be independent of environmental factors, at least food availability.

Laboratory evidence suggests that food intake by marmots and ground squirrels (Concannon et al. 1992; Davis 1976; Ward and Armitage 1981a) and many species of birds and mammals (Gwinner 1986) is controlled by an endogenous circannual rhythm, independent of external cues. Ward and Armitage (1981a) observed a 25-fold difference in food consumption between summer and winter (excluding torpor during hibernation) by yellow-bellied marmots housed under constant conditions (12L:12D photoperiod, 20°C; food available ad lib). Thus, in the absence of environmental cues, marmots increased their food intake in summer and decreased their intake in winter. Ground squirrels and woodchucks housed under constant conditions exhibit a circan-

nual cycle for 1–2 years before asynchrony (Concannon et al. 1992; Davis 1967, 1970; Pengelley and Asmundson 1969). Our study shows that providing supplemental food in the field probably does not alter the endogenous circannual rhythm of food intake in yellow-bellied marmots. Because virtually all growth occurs before the plateau stage, the most important factors in determining mass upon entrance into hibernation are weaning mass, growth rate, and length of the period of linear growth.

Weaning body mass, growth rate, and hibernation body mass.—Our data provide no clear indication that supplementation increased body mass at weaning. Supplemented juveniles were weaned at a significantly greater body mass only twice, in 1999 at River and 1998 at Marmot Meadow. In the remaining years, reference juveniles were weaned at a greater body mass or there was no significant difference between the 2 groups (Table 1). Litter sizes did not differ between groups; therefore, litter size was not a factor in determining individual body mass at weaning.

Growth rate appears to be the most important factor determining mass upon immergence into hibernation. In most cases, supplementation significantly increased juvenile growth rates at both colonies. However, at River in 1997, reference juveniles successfully crossed territorial boundaries and were caught and observed at the supplemental feed, and their growth rates were not different from supplemented juveniles. At Marmot Meadow in 2000, average growth rates did not differ between the 2 groups. Deer and cattle frequently visited that supplemental food cache and may have reduced the amount of supplemental food available to marmots, possibly explaining the similarity of growth rates.

Body mass late in the active season was significantly higher in food-supplemented groups, except at River Colony in 1997 (Table 2). Those marmots were weaned at significantly higher body mass than were supplemented juveniles, but they were not significantly heavier at immergence into hibernation due to slightly higher growth rates of juveniles in the supplemented group.

Generally, growth rate has the greatest impact on body mass at the time of entry into hibernation; higher growth rates in supplemented groups led to greater body mass at the time of entry into hibernation (Tables 1 and 2). However, in 2000, at Marmot Meadow, a greater body mass at entry into hibernation was achieved in a supplemented group without a significantly greater growth rate. This supplemented group had a body mass at weaning and a growth rate that were statistically indistinguishable from those of the reference group. However, the supplemented group experienced a growth period that was nearly 20 days longer than that of the reference group (58.1 days compared with 38.9 days), and it eventually entered hibernation at a significantly higher body mass as a result.

It remains unclear why there was such a large difference in growth period between the 2 groups of juveniles at Marmot Meadow in 2000. Although there was an apparent effect of cattle and deer on the feeding station during this year, it is possible that later in the summer, their impact was reduced because both cattle and deer migrate down the valley. There were no other apparent effects of supplementation on the termination of the growth period.

Survival.—Juvenile marmots must enter hibernation at sufficient body mass to survive hibernation (Armitage and Downhower 1974; Lenihan and Van Vuren 1996). Body mass upon entrance into hibernation is mainly influenced by birth weight, length of the active season, and growth rates before and after weaning (Allainé et al. 1998). As a result, availability and quality of food should be an important factor affecting mass upon hibernation. However, at River, there was no evidence that increased food, and therefore higher body mass, affects overwinter survival of juvenile marmots, and at Marmot Meadow increased food

availability significantly enhanced survival only in 1998. There was only a marginally significant effect on survival at Marmot Meadow in 1999. It may be that slight differences in hibernation environments at the 2 sites or genetic differences between the 2 groups contributed to the apparent difference in survival independent of supplementation.

At River and at Marmot Meadow, supplementation may not have had a greater effect on survival because most marmots (supplemented and reference) may have been able to reach some "critical" hibernation body mass even without supplemental food. Marmots do not store food and must rely on accumulated body fat to survive hibernation. We consider the critical body mass for hibernation to be that which includes the minimum amount of stored fat required to survive hibernation. Body mass is clearly important for hibernating animals, and yellow-bellied marmots may generally attain sufficient body mass under natural conditions. Based on our laboratory data for hibernating marmots, loss of body mass for juvenile yellow-bellied marmots varied from 1.23 to 3.53 g/day ($\bar{X} = 2.34 \pm 0.684$ g/day). Lenihan and Van Vuren (1996) reported that yellow-bellied marmots lost 1.8–2.69 g/day over a 230-day hibernation in the field, a rate of loss of body mass similar to our laboratory studies. Thus, if a 1,300-g juvenile marmot loses 2.6 g/day for 230 days it would weigh about 700 g when hibernation was terminated, more than 200 g heavier than the smallest yearling we have ever caught. In 1992, mean immergence mass of 7 juveniles was 1,333 ± 103 g. Six of the 7 juveniles survived hibernation and were caught as yearlings with a mean mass of 490 ± 35 g. The loss of body mass was more than 800 g, and survival was high. This example supports a proposed critical body mass of about 1,300 g, a mass that is generally attained by juvenile marmots before hibernation. The body mass necessary to survive hibernation will depend on many factors such as temperature of the hibernaculum, length of the hibernation season, and even availability of food upon emergence from hibernation. Unlike adult marmots, when juveniles leave their hibernaculum for the first time in spring, if food is not available, they will reenter hibernation and will terminate their hibernation period only when food becomes available (French 1990). Critical hibernation body mass will likely vary with different winter conditions. Regardless of the body mass necessary to ensure overwinter survival, we suggest that insufficient body mass occurs only under extreme summer conditions such as drought and is generally not the leading cause of overwinter mortality in this population of juvenile yellow-bellied marmots.

Food supplementation has increased survival in populations of *Microtus pennsylvanicus* (Desy and Thompson 1983), *M. californicus* (Ford and Pitelka 1984), *Peromyscus leucopus* (Hansen and Batzli 1979), *Apodemus sylvaticus* (Flowerdew 1972), *Tamias townsendii* (Sullivan et al. 1983), and *Spermophilus columbianus* (Dobson and Kjelgaard 1985a, 1985b). In contrast, food addition did not have an effect on juveniles at River. Although we observed some significant effects of supplementation on survival at Marmot Meadow (Table 2), most juveniles exceeded the body mass we predicted would be necessary for surviving hibernation, and survival was most likely influenced by factors other than body mass upon entering hibernation. None of the 12 reference juveniles survived hibernation in 1998 despite having larger emmergence masses than all juveniles in either group in subsequent years. Food addition may have a greater effect on survival during years in which the growing season is shortened by environmental factors (Armitage 1994; Armitage et al. 1976; Inouye et al. 2000) or when juveniles fail to gain sufficient mass as a result of other factors such as birth defects, wounds inflicted by predators, or parasites (Arnold and Lichtenstein 1993; Van Vuren 1996).

There is relatively little information on effects of parasites on growth, but this may be important in survival of juveniles. Parasite communities in the digestive tract have been examined in several species of marmots—*Marmota marmota* (Callait 2000), *M. monax* (Fleming et al. 1979), *M. sibirica* (Zhaltsanova and Shalaeva 1990). Although helminths are generally expelled from the marmot host when the intestinal tract atrophies before hibernation (Callait 2000), 2 marmots housed in our facilities failed to gain weight until treated with a vermifuge and they passed ascarid worms; thereafter, they gained mass. The possible role of parasites in this study is unknown.

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