Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*)

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Abstract: We compared patterns of growth in juvenile yellow-bellied marmots (*Marmota flaviventris*) between 2 years in which precipitation differed, and we determined if mass at entry into hibernation affects over-winter survival. Juveniles exhibited an asymptotic growth pattern with mass gain for a mean of 60.8 days, followed by stable mass until entry into hibernation. Growth ceased in early September, shortly after the end of the plant growing season. Juveniles born in 1991, a year of late snowmelt and low summer precipitation, entered into hibernation at significantly lower mass than juveniles born in 1992. Juveniles born in 1992 survived better despite experiencing a long winter during which they spent more days in hibernation and lost more mass. Overall, heavier juveniles were more likely to survive hibernation. Further, mass at entry into hibernation apparently had a greater effect on over-winter survival than did winter severity.

Résumé : Nous avons comparé la croissance chez des Marmottes à ventre jaune (*Marmota flaviventris*) juvéniles au cours de 2 années où les précipitations ont été différentes et nous avons tenté de déterminer si la masse au début de l'hibernation affecte la survie au cours de l'hiver. Les jeunes marmottes ont une croissance asymptotique et leur masse augmente pendant 60,8 jours en moyenne, puis reste stable jusqu'au début de l'hibernation. La croissance cesse en septembre, peu après la fin de la saison de croissance de la végétation. La masse de juvéniles nés en 1991, année où la neige a fondu tard et où les précipitations au cours de l'été ont été faibles, s'est avérée beaucoup plus faible au moment de l'entrée en hibernation que celle des juvéniles nés en 1992. Les juvéniles nés en 1992 ont survécu mieux, en dépit de l'hiver long qui les a forcés à rester en hibernation plus longtemps et au cours duquel ils ont subi des pertes de masse plus importantes. Dans l'ensemble, les juvéniles plus lourds ont de meilleures chances de survie à l'hibernation. De plus, la masse au moment de l'entrée en hibernation semble avoir plus d'effet sur la survie au cours de l'hiver que la rigueur même de l'hiver.
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Introduction

Juvenile growth and survival are important demographic traits among hibernating ground-dwelling squirrels. For example, these two traits may be particularly sensitive to changes in resource availability, indicating substantial phenotypic plasticity in life-history variation (Dobson 1988). In addition, slow growth of juveniles among large-bodied species is considered a major factor in the evolution of sociality in ground squirrels (Armitage 1981). Furthermore, production of yearlings, which is influenced by juvenile survival, can be the primary determinant of population size (Dobson 1995).

The importance of juvenile growth and survival derives, in part, from the environmental constraints faced by ground-dwelling squirrels, which often live in environments that are seasonally severe. The annual cycle of a hibernating squirrel entails a short active season in which it must reproduce and gain sufficient mass to survive the upcoming months of winter hibernation. Juvenile squirrels initiate their first annual cycle upon weaning, well after the rest of the population has

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emerged from hibernation; thus, juveniles may experience a severely constrained initial active season (Murie and Boag 1984; Dobson et al. 1992). Juvenile growth and development are rapid, allowing acquisition of fat stores for hibernation (Neal 1965; Clark 1970; Morton and Tung 1971; Kiell and Millar 1978). Still, juvenile ground-dwelling squirrels may suffer high mortality during the first year of life (King 1955; Davis et al. 1964; Barash 1973; Armitage and Downhower 1974; Slade and Balph 1974; Sheppard and Swanson 1976; Michener and Michener 1971, 1977; Holmes 1979; Murie and Boag 1984). Over-winter survival may depend on accumulated fat reserves, which are thought to be reflected by body mass at the time of hibernation (Michener 1974; Morton 1975; Armitage et al. 1976; Michener 1978; Murie and Boag 1984), leading to the expectation that juveniles entering hibernation at higher body masses have a greater probability of surviving hibernation.

The yellow-bellied marmot (*Marmota flaviventris*) is a large ground-dwelling squirrel that inhabits seasonally harsh environments and hibernates during more than half of the year. Juveniles are weaned about 2 months after adults emerge from hibernation, so the time available for growth is limited. Mass gain is believed to be important for over-winter survival of juvenile marmots (Armitage et al. 1976). Juveniles might increase their mass gain either through higher growth rates or through a longer active season, and both variables might be influenced by environmental factors. Early snowmelt during spring may stimulate early reproduction, resulting in early weaning (Armitage et al. 1976;

Van Vuren and Armitage 1991) and consequently a longer active season. Low rainfall during summer may reduce the quality of food available, thus reducing juvenile growth rates (Armitage 1994). Juveniles might extend their active season into the fall (Van Vuren and Armitage 1991), but the nutritive value of late-season vegetation is low (Frase and Armitage 1989).

Associations between mass gain and over-winter mortality among juvenile marmots have been reported (Armitage et al. 1976; Armitage 1994), but mass at hibernation was estimated from masses recorded several weeks or more prior to hibernation. Little is known about late-season growth of juvenile marmots, but there is some evidence that growth may cease well before hibernation begins (Andersen et al. 1976; Armitage 1994). Given the presumed importance of maximum mass gain to over-winter survival, evidence that growth ceases is perplexing.

Our objective was to determine patterns of growth in juvenile yellow-bellied marmots during their first year of life, compare those patterns between 2 years that differed markedly in precipitation, and determine if mass at entry into hibernation affects over-winter survival.

Methods

Research was conducted from June 1991 through May 1993 in the upper East River valley near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. The study area was 4.8 km in length and ranged in elevation from 2850 to 3050 m. Local habitats included spruce forest (*Picea* spp.), aspen woodlands (*Populus tremuloides*), and subalpine meadows dominated by tall forbs and grasses.

The distribution of marmots in the study area was clumped, corresponding to the patchy distribution of suitable habitat, typically rock outcrops or talus adjacent to meadows (Svendsen 1974). Yellow-bellied marmots in this area have been the subject of ongoing study since 1962 (Armitage 1991). Marmots emerged from hibernation in early May and were typically active into September. Juvenile marmots first appeared above ground at the natal burrow in late June or early July.

Locations inhabited by pregnant females were observed to determine first appearance of a litter of juveniles above ground. Juveniles first emerge from the natal burrow at about the time they begin eating solid food (Ferron and Ouellet 1991). Thus, time of weaning is approximately coincident with first emergence from the natal burrow (Grizzel 1951), and date of weaning was assigned as the day on which a litter of juveniles was first observed above ground. All juveniles in a litter first emerged on the same day. Three litters were excluded from particular analyses because of uncertainty of date of weaning. Litter size and composition were determined by observation and live-trapping. Juveniles were live-trapped, weighed to the nearest gram, sexed, ear-tagged and dye-marked for individual recognition, and then released. Juveniles were retrapped and reweighed regularly from weaning until entry into hibernation.

Weaning masses and growth rates were calculated for each litter by combining mass data for all juveniles within the litter because the number of masses recorded for an individual juvenile was often small. For each litter, the masses of individual juveniles were plotted as a function of days after weaning. These plots revealed two separate phases of growth. Juveniles gained mass linearly for several weeks, then mass stabilized until entry into hibernation. Thus, we analyzed growth rates by fitting a regression to masses recorded for each litter from weaning until growth ceased; the time of cessation of growth was determined by visual inspection of the

plotted data. The regression equation provided estimates of growth rate (slope) and mass at weaning (y intercept). Three litters were eliminated from the growth-rate analyses because of small sample sizes ($n \leq 10$ masses).

Date of entry into hibernation was determined by observation, live-trapping, and radiotelemetry. Thirty-eight juveniles from 16 litters were surgically implanted with transmitters (Van Vuren 1989) to facilitate location of littermates. Juveniles with transmitters within the same litter entered hibernation together.

To determine mass at entry into hibernation, we trapped intensively late in the active season. Mass at entry into hibernation was determined for each juvenile and was calculated as the mean of masses after growth ceased. Juveniles that were not recaptured after growth ceased but had entered hibernation were assigned the mean mass for that litter or were excluded from analysis if no such data were available.

To accurately determine time of emergence from hibernation during spring, trapping and observation were initiated in May prior to emergence of yearlings. Transmitters implanted the previous summer facilitated the location of emerging yearlings; radio-equipped littermates always emerged within a few days of each other. Thus, date of spring emergence was assigned for yearling littermates as the first observation or capture of one member of that litter.

Duration of hibernation was calculated for those yearlings for which date of entry into hibernation and date of spring emergence were known. Total over-winter mass loss and mass loss per day were calculated for each yearling for which hibernation duration was known and pre- and post-hibernation masses were available. Hibernating juveniles that were not recaptured after spring emergence as yearlings were considered over-winter mortalities.
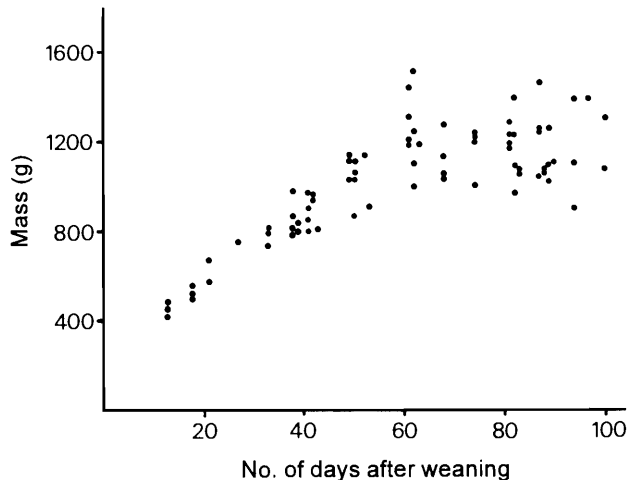
Precipitation patterns differed markedly during the 2 years of the study, as indicated by measurements recorded at Rocky Mountain Biological Laboratory (B. Barr, personal communication). During the winter of 1990–1991, 1.5 times as much snow fell, almost 6 times as much snow remained on 30 April, and the last snow melted 19 days later compared with the winter of 1991–1992. Summer precipitation patterns also differed markedly between years; 1991 was a drought year, precipitation being below average compared with the average rainfall in 1992.

Means were compared by Student's t test. When an F test indicated unequal variances, means were compared by Student's t test for unequal variances (Sokal and Rohlf 1969).

Results

Eleven litters of juveniles were monitored in each year of the study, for a total of 113 juveniles (54 female, 59 male) in 22 litters. For the 2 years combined, the mean date of weaning among litters was 5 July (SD = 8.0 days, range = 22 June − 24 July; n = 19) and the mean mass at weaning was 442 g (SD = 138.2 g; n = 18). Litter size ranged from two to eight and was negatively correlated with mean mass at weaning (r = −0.491, df = 14, P = 0.05). After weaning, juveniles exhibited positive linear growth ($\bar{x}$ = 19.7 g/day, SD = 5.51 g/day; n = 19). Growth rates among litters ranged from 13.2 to 34.4 g/day, and r^2 values of growth-rate regressions ranged from 0.82 to 0.98. Growth rate showed no relationship to litter size (r = −0.097, df = 15, P > 0.50). Positive linear growth, however, eventually stopped (Fig. 1). Of 17 litters for which late-season masses were available, all showed evidence of cessation of growth, after which masses remained stable until hibernation ("plateau" period; Phillips 1981, 1984). The mean date of cessation of growth was 4 September (range = 26 August −

Fig. 1. Growth in mass of a representative litter of juvenile yellow-bellied marmots (*Marmota flaviventris*) from weaning until entry into hibernation. Note that the shape of the curve shows two separate phases of growth: (*i*) juveniles within the litter initially exhibit positive linear growth, and (*ii*) growth of juveniles within the litter ceased around 60 days after weaning, and masses were maintained during the "plateau phase" until entry into hibernation.

Table 1. Growth of juvenile yellow-bellied marmots during a 2 year period near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado.

	1991	1992	P
Weaning date			
Mean	8 July	2 July	0.14
SD (days)	5.15	9.4	
n	9	10	
Weaning mass (g)			
Mean	433	450	0.81
SD	170.5	106.4	
n	9	9	
Growth rate (g/day)			
Mean	18.5	21.0	0.36
SD	3.93	6.87	
n	10	9	
Date of cessation of growth			
Mean	5 Sept.	2 Sept.	0.25
SD (days)	4.8	6.2	
n	9	8	
Hibernation date			
Mean	29 Sept.	26 Sept.	0.20
SD (days)	6.7	2.9	
n	11	10	
Hibernation mass (g)			
Mean	1470	1662	0.04
SD	279.9	482.1	
n	37	35	
Over-winter mass loss (g)			
Mean	420	625	0.001
SD	188.3	198.4	
n	20	23	
Over-winter mass loss per day (g/day)			
Mean	1.8	2.6	0.003
SD	0.83	0.84	
n	20	23	
Hibernation duration (days)			
Mean	225.9	233.0	0.003
SD	10.02	3.49	
n	24	26	

Note: Weaning dates, weaning masses, growth rates, dates of cessation of growth, and dates of hibernation are based on litters. Hibernation masses, mass loss, mass loss per day, and duration are based on individuals.

13 September, SD = 6.4 days; n = 17). The duration of positive growth among litters ($\bar{x}$ = 60.8 days, SD = 6.36 days; n = 16) was negatively correlated with time of weaning (r = −0.724, df = 14, P < 0.01); late-weaned juveniles gained mass for a shorter period of time than did early-weaned juveniles. Littermates almost always entered hibernation within a 1- to 2-day period and into the same hibernaculum; only one juvenile hibernated away from its littermates and at a different date. The mean date of entry into hibernation was 27 September (range = 17 September − 13 October, SD = 5.4 days; n = 21).

The mean mass of individual juveniles was 1563 g (SD = 400.5 g; n = 72) when they entered hibernation; thus, hibernating juveniles had more than tripled their mass since weaning. Mass at weaning was positively correlated with hibernation mass (r = 0.632, df = 63, P < 0.01). Juveniles that survived over winter ($\bar{x}$ = 1654 g, SD = 411.3 g; n = 53) entered hibernation at significantly higher masses (t = 4.52, df = 58, P < 0.001) than did juveniles that died over winter ($\bar{x}$ = 1308 g, SD = 225.5 g; n = 19). Hibernation lasted a mean of 229.6 days (SD = 8.14 days; n = 50). Yearlings that survived hibernation lost 32% of their body mass (total mass loss, $\bar{x}$ = 530 g, SD = 217.6 g; n = 43) and lost mass during hibernation at a mean rate of 2.3 g/day (SD = 0.92 g/day; n = 43).

Although the differences were not statistically significant, during 1991, a year of persistent snow cover, juveniles showed somewhat later weaning dates, lighter weaning masses, slower growth rates, later dates of cessation of growth, and later hibernation dates than did juveniles in 1992 (Table 1). Mass at entry into hibernation, however, was significantly lower (P = 0.04) in juveniles born in 1991 than in those born in 1992 (Table 1). Hibernation mass loss and duration also differed significantly between years; juveniles born in 1992 hibernated longer (P = 0.003), lost more mass

(P = 0.001), and lost mass at a faster rate (P = 0.003) than did juveniles born in 1991 (Table 1). Further, despite entering hibernation at a significantly higher mass, juveniles born in 1992 lost 38% of their body mass during hibernation compared with a 28% loss for juveniles born in 1991. Over-winter survival of juveniles was higher (χ^2 = 5.44, df = 1, 0.025 > P > 0.01) for those born in 1992 (86%; n = 73) than for those born in 1991 (66%; n = 38).

Discussion

Growth of juvenile yellow-bellied marmots prior to weaning is expected to be primarily influenced by maternal condition and available resources. Allocation of these resources,

through lactation, during the postnatal or dependent period (Phillips 1981) should be reflected in mass at weaning. Mean mass at weaning (442 g) was consistent with Andersen et al.'s (1976) estimate of 446 g for juvenile marmots living 16 km north at a higher elevation (3380 m). Juvenile Columbian ground squirrels also showed no significant difference in mass at weaning between low- and high-elevation populations (Dobson et al. 1992). The similarity of mass at weaning at different elevations among populations implies that mass at weaning is not determined primarily by environmental factors; instead it appears to be determined developmentally by maternal investment, which remains constant among populations (Phillips 1981, 1984; Pontier et al. 1989).

If mass at weaning is in fact dependent on maternal allocation, one would expect that litter size might affect weaning mass (Pontier et al. 1989). Mass at weaning and litter size are negatively correlated in a variety of rodent species (Krohne 1981; Myers and Master 1983; Dobson and Myers 1989) including ground squirrels (Turner et al. 1976; Michener 1989). In yellow-bellied marmots, litter size and mass at weaning were negatively correlated, suggesting that maternal allocation is limited in this species and must be partitioned among individuals within a litter.

The negative effect of litter size on mass at weaning may have future consequences for juvenile marmots if this initial variation in mass holds for the duration of the active season. From studies of Franklin's ground squirrel (*Spermophilus franklinii*) (Turner et al. 1976) and deer mice (*Peromyscus maniculatus*) (Myers and Master 1983), it is evident that size differences at weaning persist well after weaning and even into adulthood. Among marmots, juveniles that were heavier at weaning were also heavier when they entered hibernation.

Preweaning growth rates, being dependent on a restricted food source via lactation, are negatively related to litter size in some ground squirrels (Koeppl and Hoffmann 1981; Phillips 1981). The effect of litter size on postweaning growth rates, when juveniles are independent and have access to a more abundant food source, is less clear. After weaning, growth rates are affected more by environmental conditions (Phillips 1981; Pontier et al. 1989) and may show a positive relationship to litter size that partially mediates the earlier effect (Koeppl and Hoffmann 1981), or a negative relationship favoring smaller litters (Phillips 1981), or may be highly variable among individuals (Wroot et al. 1987). Growth rates of marmots generally increase with elevation, compensating for the shorter active seasons experienced at higher altitudes (Andersen et al. 1976; Webb 1980). In the present study, growth rates of juvenile marmots were highly variable among litters and showed no relationship to litter size.

Previous studies have shown evidence of asymptotic growth curves in juvenile ground-dwelling squirrels (Snyder et al. 1961; Blake 1972; Michener 1974; Morton et al. 1974; Morrison and Galster 1975; Dolman 1980; Koeppl and Hoffmann 1981; Phillips 1981), including yellow-bellied marmots (Andersen et al. 1976). Various explanations for this growth pattern have been suggested; heavier juveniles entered hibernation first, creating a false plateau, or unusually dry weather caused mass gain to stop (Michener 1974). In marmots, cessation of growth coincided with the first fall snowstorm, suggesting that late-season snowstorms may

cause termination of growth (Andersen et al. 1976). None of these explanations are consistent with our findings, for the following reasons. Growth was determined for each litter, and littermates hibernated within 1−2 days of each other, so the plateau was not the result of early hibernation by heavier littermates. Summer precipitation differed between the 2 years of the study, yet juvenile masses reached a plateau in both years. Further, no snowstorms coincided with cessation of growth.

The time available for juvenile growth before hibernation is substantially shorter than the active season. Seasonal energy intake is determined not by the length of the marmot's active season but rather by that of the plant growing season. The plant growing season within the East River valley is initiated by snowmelt (Van Vuren and Armitage 1991) and typically extends from early June to mid-August (Barrell 1969), at which time plants begin to senesce, owing to frost, lack of precipitation, or both (Langenheim 1962; Kilgore and Armitage 1978; Frase and Armitage 1989). The nutritive quality of forage decreases as vegetation dries out (Armitage et al. 1976; Webb 1980; Bintz 1984; Armitage 1994), well before juveniles enter hibernation. Juvenile growth is thus limited by the number of days during which the plant growing season and juvenile active season overlap. Early-weaned litters had more days for gaining mass before the onset of plant senescence than did those weaned later, supporting previous findings of higher survival in early-weaned litters (Armitage et al. 1976). Because mass gain is important to over-winter survival, the reason why juveniles remain active after mass gain has ceased remains uncertain. Evidently the nutritive quality of vegetation is sufficient to maintain body mass for some time after plant senescence has occurred. Consequently, juveniles may remain active, despite no further mass gain, in order to shorten the time of hibernation and its accompanying energy deficit.

Studies of *Spermophilus* spp. have shown that juveniles with low body mass may extend their active season under favorable environmental conditions (Morton et al. 1974; Morrison and Galster 1975; Boag and Murie 1981). Whether marmots employ this strategy remains unknown. The latest litter of juveniles to enter into hibernation, on 13 October 1991, also had very low mass at hibernation. None of these juveniles survived over winter, indicating that they had insufficient fat stores to survive hibernation (Phillips 1981). Marmots (Armitage et al. 1976) as well as other ground-dwelling squirrels (Mrosovsky 1971) will enter hibernation despite poor condition, suggesting that the benefits of hibernation outweigh the costs of continued activity as winter approaches.

Juvenile marmots that survived over winter entered hibernation at significantly higher mass than those that died, confirming that heavier juveniles are more likely to survive their first hibernation. Juveniles that died over winter entered hibernation at a mean mass 346 g less (21%) than those that survived.

Our study addressed growth and survival during 2 years; thus, between-year comparisons lack replication and should be interpreted with caution. Nonetheless, precipitation differed substantially between years in ways that might have influenced growth and survival. Snow cover during spring persisted 19 days longer in 1991 than in 1992; additionally,

summer rainfall was especially low during 1991. Early snowmelt leads to higher juvenile masses in August (Van Vuren and Armitage 1991). Further, rainfall during the growth season is positively correlated ($r = 0.62$) with juvenile survivorship (Armitage 1994). Thus, we expected to find negative effects on growth of juveniles during 1991. A trend toward such effects was evident, but differences were small and not significant statistically until juveniles entered hibernation (Table 1). Apparently, marmots are able to compensate for late initiation of the growing season and low summer rainfall.

Juveniles hibernated longer and lost more mass during the winter of 1992–1993 than during the winter of 1991–1992. The cause may be especially heavy snowfall during the winter of 1992–1993, which was more than twice as heavy and persisted 33 days longer than the winter of 1991–1992. Previous studies found that few yearlings survived when snow cover persisted well into spring (Armitage and Downhower 1974). Surprisingly, however, over-winter survival was higher for juveniles born in 1992. These results suggest that mass at entry into hibernation might have a greater effect on over-winter survival than does winter severity.

Acknowledgements

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