Oecologia (1998) 113:370–376

Dominique Allainé · Laurent Graziani · Jacques Coulon

Postweaning mass gain in juvenile alpine marmots *Marmota marmota*

Received: 9 June 1997 / Accepted: 22 September 1997

Abstract The effects of several environmental factors on the postweaning growth of wild Alpine marmots were investigated. Factors considered were year of birth, sun exposure in the home range, litter size, and sex of young. Components of growth were juvenile mass at emergence from the natal burrow (as a result of preweaning growth) and postweaning growth rate. We also considered the length of the active season during which growth occurs. Mass at emergence and postweaning growth rate varied according to year of birth, were higher in south-facing than in north-facing home ranges, and were higher in small litters. Mass at emergence was higher for males than for females. We suggest that environmental factors affected the juvenile growth pattern through influences on maternal body condition. Our results support Trombulak's hypothesis that mothers maintain as many young as physiologically possible. We suggest that mothers in poor condition sacrificed the mass of their offspring rather than their number. A body mass sexual dimorphism of juveniles occurred at emergence, suggesting that mothers may provide more care for their male than their female offspring.

Key words Alpine marmot · Juvenile growth · Litter size · Body mass · Sexual dimorphism

Introduction

Postnatal growth is an important component of life history. Patterns of growth have been examined in the light of life history theory (Stearns 1976), and as several allometric comparisons across taxonomic groups (Case 1978; Zullinger et al. 1984; Kirkwood 1985; Pontier et al. 1989; Gaillard et al. 1997). Growth reflects adaptation to the environment (Case 1978; Robbins and Robbins 1979). Among ground squirrels, early growth and development can easily be documented. From captive animals, instantaneous growth rates (Brody 1945) have been calculated for several species (Clark and Skryja 1969; Clark 1970; Morton and Tung 1971; Turner et al. 1976; Hirshfield and Bradley 1977; Levenson 1979; Koeppl and Hoffmann 1981). Some descriptions of juvenile growth are also available for the closely related North American species of marmots (Ferron and Ouellet 1991). From interspecific comparisons of growth patterns among the Marmotinae, Clark (1970) suggested that accelerated ontogeny is an adaptive feature of hibernators such as ground squirrels and marmots. Rapid growth allows individuals to store enough fat during the growing season to survive hibernation (Morton and Tung 1971; Hirshfield and Bradley 1977).

A critical factor for juvenile ground squirrel and marmot survival through hibernation is sufficient gain in mass during their first active season (Armitage et al. 1976; Michener 1978). Small juveniles may be unable to survive hibernation (Murie and Boag 1984 for *Spermophilus columbianus*, Lenihan and Van Vuren 1996 for *Marmota flaviventris*). The mass achieved by entrance into hibernation depends on the birth mass, on the growth rates during pre- and postweaning periods, and on the length of the active season. Environmental factors likely affect the mass achieved just before hibernation by acting upon the components of the growing pattern. However, the captive conditions often used in studies of growth patterns in ground squirrels do not allow tests of the effects of environmental factors on the growth of juveniles.

This study examines the effects of several environmental factors on the growth of wild juvenile Alpine marmots *M. marmota*. Components of the growing pattern were the juvenile mass at emergence (as a result of preweaning growth), the postweaning growth rate, and the length of the active season. We tested the following predictions.

D. Allainé (✉) · L. Graziani · J. Coulon
Laboratoire de Biologie des Populations d'Altitude,
UMR 5553, Université Lyon 1, 43 Bd du 11 novembre 1918,
F-69622 Villeurbanne, France
Fax: 04 72 43 14 04; e-mail: allaine@biomserv.univ-lyon1.fr

(1) Year of birth was expected to affect at least two components of the growth pattern (mass at emergence and the length of the growing season) because Alpine marmots faced severe and variable climatic conditions (see also Kiell and Millar 1978; Wroot et al. 1987; Riegger 1996 for other sciurids). Climatic conditions were less variable after juvenile emergence (in July), so the postweaning growth rate was not expected to vary widely among years.

(2) Sun exposure was expected to affect all three components of the growth pattern because exposure affected home range quality (reduced food resources were correlated with late snow melt on north-facing slopes; see also Allainé et al. 1994).

(3) Litter size at emergence was expected to affect juvenile mass at emergence from natal burrows. Mothers were faced with limitations on time and resources. They had a limited amount of energy (milk) to invest in their offspring, and a trade-off between size and number of young was expected (Lloyd 1987).

(4) Sex was expected to affect neither mass at emergence nor postweaning growth rates. Because Alpine marmots are monogamous, the fitness return from a male and a female offspring was assumed to be equal. Differential parental care in offspring of either sex was not expected.

Environmental conditions may affect the juvenile growth pattern through influences on the body condition of the mother (Trombulak 1991). We therefore also investigated the effects of year and exposure to sun on mothers' body mass.

Materials and methods

The study site was located at an elevation of 2340 m in the Natural Reserve of La Sassière (Vanoise National Park, French Alps, 45°29′N, 6°59′E). The climate is typical of high mountains with marked snow precipitation. The site is an open meadow characterized by subalpine and alpine vegetation (Gensac and Rothé 1974).

Since 1990, the composition of 16 family groups was determined and 341 Alpine marmots from these groups have been individually marked. Each year since 1991, the litter size at emergence (commonly from two to six) and the date young emerged from their natal burrow were recorded. Young were captured and permanently marked with numbered ear-tags and by the injection of a TROVAN transponder under the skin. Young were weighed and their post-emergence age was calculated from the observed date of emergence. Sex was identified from the anogenital distance (Zélenka 1965). From 1991 to 1996, 247 accurate weights of juvenile marmots of known age and sex were obtained. In several cases, mothers were caught and weighed during the active season. For each family group, the home range was classified according to three categories of sun exposure: south facing, valley, north facing. Snow melt occurred about 1 month earlier on south-facing than on north-facing sites (unpublished data).

Mass of juveniles within 2 days of emergence from their natal burrows was the result of preweaning growth (Payne and Wheeler 1967). The growth rate between juvenile emergence and entry into hibernation reflects postweaning growth. The postweaning growth rate was measured by the slope of the regression of mass on juvenile age from emergence. Assuming all juveniles entered into hibernation at the same time (see Results), the date of juvenile emergence was used as an indicator of the length of the active season (Van Vuren and Armitage 1991, Dobson et al. 1992).

We used four-way analysis of variance to investigate the principal effects of year of birth, sun exposure, litter size, and sex on the mass at emergence of juvenile Alpine marmots. For each factor, we also tested for the homogeneity of slopes (i.e., equal postweaning growth rates). Years considered were 1991 through 1996 for postweaning growth rate and 1993 through 1996 for juvenile mass at emergence. Analyses were run using GLIM software (Baker and Nelder 1978).

Results

The increase in body mass of juvenile Alpine marmots was strongly linear from emergence until just before entry into hibernation (Fig. 1; $r = 0.949$, $P = 0.0001$). The regression equation was body mass = 0.366 + 0.020 age (days). This indicates that, on average, juveniles at emergence weighed about 0.366 kg and their growth rate was 20.0 ± 0.4 (se) g/day.

Mass at emergence

All four factors tested were significant. Mean individual mass of juveniles at emergence was highest in 1993 and lowest in 1995 ($F_{3,70} = 6.49$, $P < 0.05$; Fig. 2a). The difference in mean juvenile mass at emergence between these 2 years was more than 100 g. For a given year, the mass of juveniles at emergence decreased about 60 g from southern to northern exposure ($F_{2,68} = 4.61$, $P < 0.05$; Fig. 2b). Juveniles emerging in the valley had an intermediate mass. Juvenile males (0.380 ± 0.016 kg) were heavier ($F_{1,72} = 6.03$, $P < 0.02$) than females (0.329 ± 0.013 kg) at emergence. Finally, the mass of juveniles at emergence decreased with the litter size at emergence ($F_{5,68} = 8.57$, $P < 0.05$; $r = -0.54$, $n = 74$, $P < 0.001$; Fig. 2c). In litters of six, juvenile marmots were about 140 g lighter than juveniles from litters of two. This reflected a trade-off between size and number.

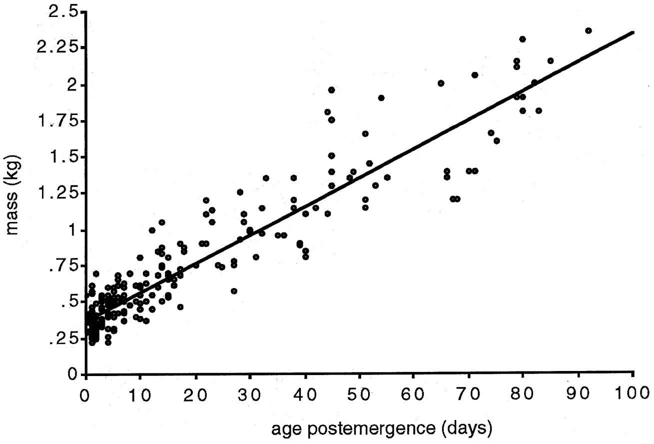

Fig. 1 Body mass as a function of age of juvenile *Marmota marmota*. The age is given from the day of emergence from the natal burrow

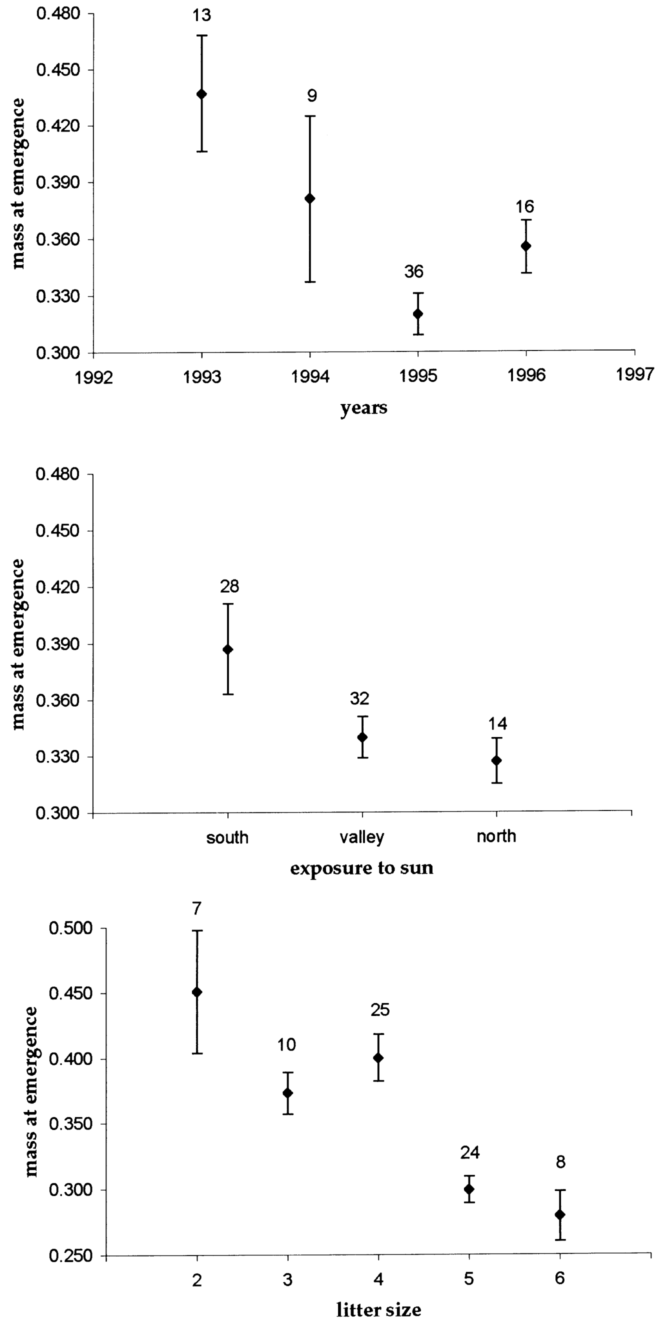

Fig. 2 Effects of environmental factors on juvenile mass at emergence (mean ± SE) in *M. marmota*. Values indicate number of juveniles. **a** Effect of year. **b** Effect of exposure to sun of the home range. **c** Effect of litter size

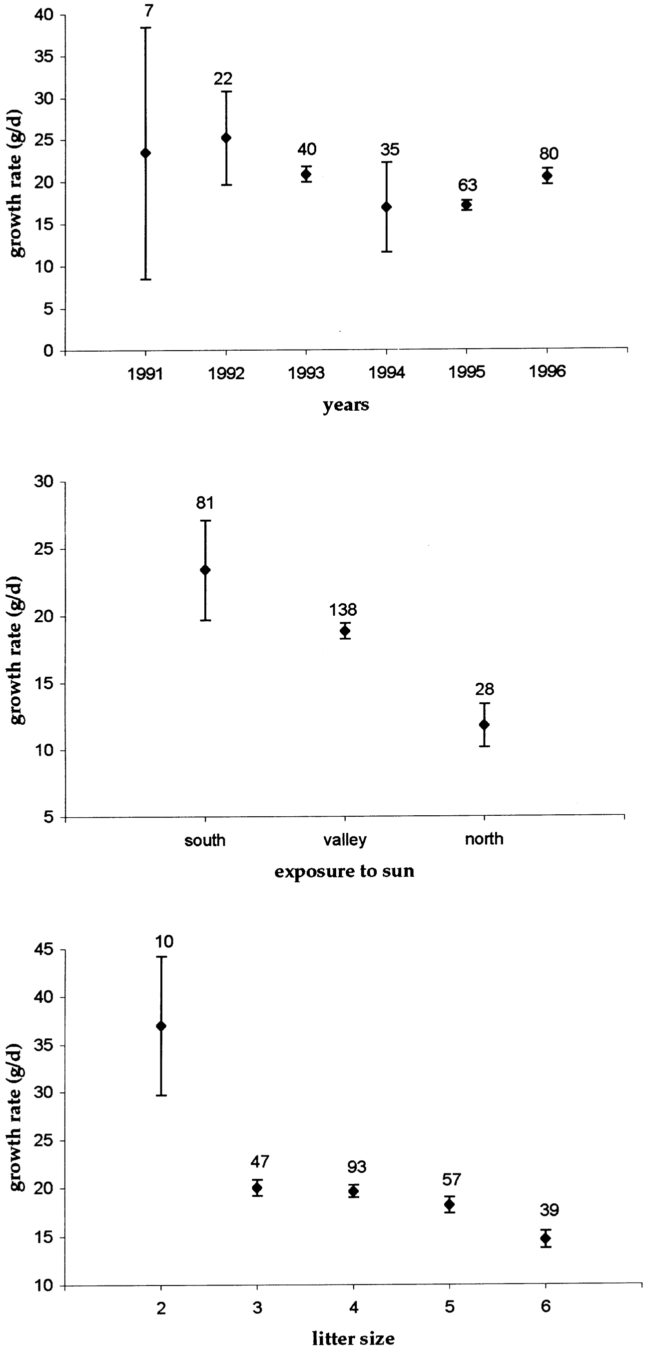

Fig. 3 Effects of environmental factors on juvenile postweaning growth rate (mean ± SE) in *M. marmota*. Values indicate sample size. **a** Effect of year. **b** Effect of exposure to sun of the home range. **c** Effect of litter size

Postweaning growth rate

Slopes of juvenile mass regressed on age differed significantly between years ($F_{5,235} = 3.68$, $P < 0.05$), between exposures to sun (corrected for litter size, $F_{2,241} = 4.54$, $P < 0.05$), and between litter sizes at emergence ($F_{4,235} = 5.89$, $P < 0.05$). Thus, environmental factors such as year of birth (Fig. 3a), and sun exposure (Fig. 3b) affected the growth rate of juvenile marmots during the postweaning period. The postweaning growth rate tended to be negatively correlated with litter size at emergence (Fig. 3c). This was mainly due to high growth rates in litters of twins but the correlation still exists without litters of twins. The same negative trend was observed between litter size and mass at emergence (see above). Consequently, we found a positive relationship between the mass of juveniles at emergence and their postweaning growth rates ($r = 0.403$, $n = 38$, $P = 0.012$). This indicates that small juveniles at emergence in large litters did not experience compensatory growth after weaning. On the contrary, the difference in mass between small and large juveniles at emergence was enhanced during the postweaning period. Slopes did not vary according to sex ($F_{1,243} = 0.88$, $P > 0.05$). The 50-g difference in mass at emergence between males and females should have been maintained at the entry into hibernation.

Litter size at emergence

Litter size at emergence did not vary among years ($F_{6,43} = 0.53$, $P = 0.78$), or with sun exposure ($F_{2,49} = 1.99$, $P = 0.15$). Litter size at emergence was 4.31 ± 0.17 (range 3–6) in the valley and 3.79 ± 0.28 (range 2–6) and 3.57 ± 0.48 (range 2–5) in southern and northern exposures, respectively.

Date of emergence

Dates of emergence of adults from hibernation were available only for 1995 and 1996. They did not vary among years (Mann-Whitney U-test: $U = 86$, $P = 0.58$; emergence occurred on average 16 April), but did vary according to sun exposure [Kruskal-Wallis (K-W) test $H = 7.93$, $P = 0.019$]. Emergence of adults from hibernation occurred on average 4 and 11 days earlier in southern (12 April on average) exposures compared to the valley (16 April) and northern (23 April) exposures, respectively.

Dates of emergence of juveniles did not vary significantly among years (K-W test $H = 4.01$, $P = 0.67$; emergence occurred 4 July on average), but varied according to sun exposure (K-W test $H = 20.87$, $P = 0.0001$). Emergence of juveniles occurred on average 6 and 12 days earlier in southern (30 June on average) exposures than in the valley (6 July) and in northern (12 July) exposures, respectively. The differences in dates of emergence of juveniles from south- to north-facing slopes were similar to differences in dates of emergence of adults from hibernation. Assuming an invariant gestation and lactation period equal to 30 and 40 days, respectively (Psenner 1957; Wieser 1983; L. Graziani and D. Allainé, unpublished data), the delay between emergence from hibernation and mating was similar in the three exposures. However, at the time of mating, home ranges on south-facing slopes were usually free of snow; but this was not the case for adults emerging about 10 days later in north-facing slopes, as snow melt occurred about 1 month later (personal observation; see also Van Vuren and Armitage 1991 for *M. flaviventris*). This suggests that females in north-facing slopes had relatively limited access to food resources when starting to reproduce.

Litter size at emergence and mean individual juvenile mass at emergence were not related to the date of young emergence ($r = -0.12$, $P = 0.41$, $n = 49$; $r = -0.29$, $P = 0.20$, $n = 22$; respectively).

Date of entry into hibernation

Dates of entry into hibernation were available only for 1995. Among 20 family groups, hibernation occurred within a week (10–18 October). The last groups entering hibernation were in the valley (2 families) and on a southern exposure (1 family). We thus have no evidence that young entered hibernation significantly later on north-facing exposures. Assuming a mean juvenile active season of 80 days (from mid-July to early October), we suspect that emerging about 12 days later in a home range exposed to the north reduced, on average, the active season for a juvenile by about 15%.

Body mass of the mothers

The overall regression of mothers' body mass on date from April to June was not significant in the valley ($r = 0.006$, $n = 14$, $P = 0.98$) or the north-facing exposures ($r = 0.31$, $n = 4$, $P = 0.68$). The mean body mass of mothers during the breeding period was thus presumed to be constant and equal to 3.58 ± 0.08 kg and 3.13 ± 0.06 kg in the valley and in the northern exposure, respectively. On the other hand, the regression line was significant in the southern exposure ($r = 0.66$, $n = 12$, $P = 0.019$). The mean mothers' mass increased from 3.43 kg at emergence from hibernation to 3.82 kg at the time of juvenile emergence.

Discussion

The increase in body mass of juvenile Alpine marmots was linear from emergence until just before hibernation. Although postnatal increase in mass from birth to adulthood is generally sigmoidal in mammals (Kiell and Millar 1978; Zullinger et al. 1984; but see Gaillard et al. 1997), linear growth just after weaning has been reported for sciurid species (Armitage et al. 1976; Koeppl and Hoffmann 1981; Lenihan and Van Vuren 1996). The overall mass at emergence of juvenile Alpine marmots was 0.366 kg. Body mass at emergence was higher than that observed by Ferron and Ouellet (1991) for the woodchuck *M. monax* (249 g) but lower than that of the yellow-bellied marmot *M. flaviventris* (about 500 g; Armitage et al. 1976), two marmot species of the same adult size as the Alpine marmot. If we consider a mean adult female mass of 3.58 kg during reproduction, mean juvenile mass at emergence represents 10.2% of adult body mass. This percentage appears to be low compared to North American ground squirrel species (see Armitage 1981). The postweaning growth rate for juvenile

Alpine marmots in natural conditions is probably close to 20 g/day. This is in agreement with growth rates of juvenile yellow-bellied marmots which varied from 11 to 26 g/day (Armitage et al. 1976).

Year of birth affected both the mass at emergence and the postweaning growth rate of juveniles, but we were unable to test for year effects on the length of the postweaning active season. Thus, our first prediction was partly supported. This cohort effect could be related to variations in climatic conditions, in population density or in habitat quality. Our observations indicated that home range size and quality (food resources) were relatively stable in time (Perrin et al. 1993, unpublished data) suggesting that juvenile growth pattern may not vary as a result of variations in density or habitat quality. Although we have no test for this, the cohort effect seems to be better explained by climatic variations. Indeed, the mass at emergence and the postweaning growth rate of juveniles may be indirectly affected by the snow cover during hibernation and at the time of adult emergence (via an effect on mother condition) and directly affected by rain or snow falls and dry periods (K.B. Armitage, personal communication) during the active season.

Exposure to sun affected both the mass at emergence, the postweaning growth rate, and the length of the postweaning active season. Thus, our second prediction was supported. Juveniles born on southern exposures emerged heavier, grew faster, and benefitted from a longer time to gain weight before hibernation than juveniles born on northern exposures. We suggest that exposure and year effects produced great variability in the quality of juveniles born in our population. This was also the case in the yellow-bellied marmot, for which weight of young during the 1st week postemergence ranged from 340 to 910 g for males and from 230 to 790 g for females (Armitage et al. 1976).

Trombulak (1991) has shown that juvenile Belding's ground squirrels *S. beldingi* born to mothers who received supplemented food were heavier at emergence from natal burrows than were the offspring of control females. This suggests that maternal condition directly influences juvenile growth rate during lactation. Because the timing of reproduction was the same among years, we assume that some constraints (a short active season) may preclude mothers from delaying their reproductive activities (i.e., to improve their body condition; Rowe et al. 1994). Mothers may begin reproduction in poor body condition during bad years. Because mothers on southern exposures accumulated mass due to early access to food resources during the breeding period, whereas mothers in the valley and on northern exposures did not (see also Rayor 1985 for *Cynomys gunnisoni*; but see Michener 1978 for *S. richardsonii*), we assume that mothers were in better condition in southern than in northern exposures (see also Dobson et al. 1992 for variation with altitude in *S. columbianus*). Thus, the two environmental factors considered here may directly affect the body condition of the mothers. Females in unfavorable environmental conditions (i.e., northern exposures) entered into reproduction in poor body condition, reproduced less often (Allainé et al. 1994), and were unable to ensure a high preweaning growth rate for their offspring. Consequently, the mass of their juveniles at emergence was low. The positive relationship between mass at weaning and postweaning growth rate indicates that light juveniles did not compensate for their mass handicap. We conclude that year of birth and exposure to sun likely affect the juvenile growth pattern by acting upon the maternal condition.

Juvenile mass at emergence and postweaning growth rate tended to decrease with litter size, as already observed for other sciurid species (Belding's ground squirrel, Trombulak 1991; Uinta ground squirrel, *S. armatus*, Riegger 1991; black-tailed prairie dog, *C. ludovicianus*, Hoogland 1995). Thus, our third prediction was supported. Rowe et al. (1994) presented a model to explain the seasonal decline in clutch size as a result of a conflict between advantages of early breeding and advantages of delay. As an alternative trade-off hypothesis to the Rowe et al. (1994) model, Dobson and Michener (1995) suggested that mothers may compensate late emergence (short active season) with an increased energy investment (high mass at emergence but small litter size) so that late and early young have similar body mass at entry into hibernation. The fitness cost of breeding late in Richardson's ground squirrels would be the reduced number of offspring produced. We did not observe that litter size decreased as the breeding season progressed, contrary to a basic assumption of the Rowe et al. (1994) model. Moreover, young emerging late (in northern exposures) were lighter than young emerging early (in southern exposures). Dobson and Michener's (1995) hypothesis that late-breeding females produce few but heavy juveniles was thus not supported by our results.

Alpine marmot mothers in northern exposures bred late, were in poor condition and were perhaps unable to increase their energy investment in juveniles. Thus, they may have been unable to compensate for late breeding. Although there is probably a survival advantage for young that are weaned as large as possible, our data support Trombulak's (1991) conclusion for Belding's ground squirrels that mothers maintain as many young as possible, with juvenile size at weaning depending on the body condition of the mother. Mothers in poor condition sacrificed investment in individual juvenile mass at weaning, rather than reducing the number of their offspring. The fitness cost of breeding late (breeding in poor condition) in Alpine marmots would be the reduced mass and perhaps survival of offspring produced. Data on juvenile survival to yearling age are clearly needed to test if light juveniles born late in the season exhibit low survival, although Murie and Boag (1984) present some preliminary support for this idea in *S. columbianus*.

Social thermoregulation during hibernation may decrease the importance of body mass before hibernation in juvenile Alpine marmots (Arnold 1990). Maintenance of large litters is also in agreement with the absence of a cost of reproduction associated with such large litters for *S. columbianus* (Hare and Murie 1992; Risch et al. 1995). We suggest that two types of species exist among the Marmotini: species for which variation in juvenile mass is an important aspect of female reproductive success and species for which such variation does not affect female reproductive success. Species belonging to the first type (such as Richardon's ground squirrels, Dobson and Michener 1995; Columbian ground squirrels, Murie and Boag 1984; yellow-bellied marmots, Lenihan and Van Vuren 1996) may follow the basic assumption of the Rowe et al. (1994) model (seasonal decline in litter size) and may support the Dobson and Michener (1995) hypothesis (increased energy investment to compensate late emergence). Species belonging to the second type (such as black-tailed prairie dogs, Hoogland 1995; Belding's ground squirrels, Trombulak 1991; Alpine marmots, this study) may support neither the basic assumption of the Rowe et al. (1994) model (no seasonal decline in litter size) nor the Dobson and Michener (1995) hypothesis (no increased energy investment to compensate late emergence).

Sexual dimorphism in body mass at weaning was observed, but postweaning growth rates were the same for males and females. Our fourth prediction was thus only partly supported. This indicates that the growth rate prior to weaning was higher for male than for female juvenile Alpine marmots. This contradicts the absence of sexual dimorphism reported for the woodchuck (Ferron and Ouellet 1991). Energy expenditure of the mother might thus depend on the sex of the juveniles produced.

Acknowledgements This work was supported by the French CNRS and the Région Rhone-Alpes (XI plan Etat-Région). We thank the Vanoise National Park for allowing us to work in the Natural Reserve of La Sassière. We thank J.M. Gaillard, F.S. Dobson, and W. King for their constructive comments on early drafts. W. King also edited our English. We thank N.G. Yoccoz for his statistical assistance, and E. Farand, M.C. Bel and S. Magnolon for their help in the field and for the discussions we had.

References

Allainé D, Rodrigue I, Le Berre M, Ramousse R (1994) Habitat preferences of Alpine marmots *Marmota marmota*. Can J Zool 72:2193–2198

Armitage KB (1981) Sociality as a life-history tactic of ground squirrels. Oecologia 48:36–49

Armitage KB, Downhower JF, Svensen GE (1976) Seasonal changes in weights of marmots. Am Midl Nat 96:36–51

Arnold W (1990) The evolution of marmot sociality. II. Costs and benefits of joint hibernation. Behav Ecol Sociobiol 27:239–246

Baker RJ, Nelder JA (1978) The GLIM system. Release 3: generalized linear interactive modelling. Numerical Algorithm Group, Oxford

Brody S (1945) Bioenergetics and growth. Reinhold, New York

Case TJ (1978) On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q Rev Biol 53:243–282

Clark TW (1970) Early growth, development, and behavior of the Richardson ground squirrel (*Spermophilus richardsoni elegans*). Am Midl Nat 83:197–205

Clark TW, Skryja DD (1969) Postnatal development and growth of the golden-mantled ground squirrel, *Spermophilus lateralis lateralis*. J Mammal 50:627–629

Dobson FS, Brady MJ, Geddes C (1992) Seasonal activity and body mass of Columbian ground squirrels. Can J Zool 70:1364–1368

Dobson FS, Michener GR (1995) Maternal traits and reproduction in Richardson's ground squirrels. Ecology 76:851–862

Ferron J, Ouellet JP (1991) Physical and behavioral postnatal development of woodchucks (*Marmota monax*). Can J Zool 69:1040–1047

Gaillard JM, Pontier D, Allainé D, Loison A, Hervé JC, Heizmann A (1997) Variation in growth form and precocity at birth in eutherian mammals. Proc R Soc Lond B 264:859–868

Gensac P, Rothé B (1974) Carte de la végétation de la Réserve de la Grande Sassière. Trav Sci Parc Nat Vanoise 5:77–104

Hare JF, Murie JO (1992) Manipulation of litter size reveals no cost of reproduction in Columbian ground squirrels. J Mammal 73:449–454

Hirshfield JR, Bradley WG (1977) Growth and development of two species of chipmunks: *Eutamias panamintinus* and *E. palmeri*. J Mammal 58:44–52

Hoogland JL (1995) The black-tailed prairie dog: social life of a borrowing mammal. Univ. Chicago Press, Chicago, Illinois, USA

Kiell DJ, Millar JS (1978) Growth of juvenile arctic ground squirrels (*Spermophilus parryii*) at McConnell River, N.W.T. Can J Zool 56:1475–1478

Kirkwood JK (1985) Patterns of growth in primates. J Zool 205:123–136

Koeppl JW, Hoffmann RS (1981) Comparative postnatal growth of four ground squirrel species. J Mammal 62:41–57

Lenihan C, Van Vuren D (1996) Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). Can J Zool 74:297–302

Levenson H (1979) Sciurid growth rates: some corrections and additions. J Mammal 60:232–235

Lloyd DG (1987) Selection of offspring size at independence and other size-versus-number strategies. Am Nat 129:800–817

Michener GR (1978) Effect of age and parity on weight gain and entry into hibernation in Richardson's ground squirrels. Can J Zool 56:2573–2577

Morton ML, Tung H-CL (1971) Growth and development in the Belding ground squirrel (*Spermophilus beldingi beldingi*). J Mammal 52:611–616

Murie JO, Boag DA (1984) The relationship of body weight to overwinter survival in Columbian ground squirrels. J Mammal 65:688–690

Payne PR, Wheeler EF (1967) Growth of the foetus. Nature 215:849–850

Perrin C, Allainé D, Le Berre M (1993) Socio-spatial organization and activity distribution of *M. marmota*: preliminary results. Ethology 93:21–30

Pontier D, Gaillard JM, Allainé D, Trouvilliez J, Gordon I, Duncan P (1989) Postnatal growth rate and adult body weight in mammals: a new approach. Oecologia 80:390–394

Psenner H (1957) Neues vom Murmeltier. Säugetierkd Mitt 5:4–10

Rayor LS (1985) Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (*Cynomys gunnisoni*). Can J Zool 63:2835–2840

Riegger JF (1991) Female investment strategies and reproductive success in the Uinta ground squirrel, *Spermophilus armatus*. PhD thesis, University of Michigan, Ann Arbor

Riegger JF (1996) Body size, litter size, timing of reproduction, and juvenile survival in the Uinta ground squirrel, *Spermophilus armatus*. Oecologia 107:463–468

Risch TS, Dobson FS, Murie JO (1995) Is mean litter size the most productive? A test in Columbian ground squirrels. Ecology 76:1643–1654

Robbins CT, Robbins BL (1979) Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. Am Nat 114:101–116

Rowe L, Ludwig D, Schulter D (1994) Time, condition, and the seasonal decline of avian clutch size. Am Nat 143:698–722

Stearns SC (1976) Life-history tactics: a review of ideas. Q Rev Biol 51:3–47

Trombulak SC (1991) Maternal influence on juvenile growth rates in Belding's ground squirrel (*Spermophilus beldingi*). Can J Zool 69:2140–2145

Turner BN, Iverson SL, Severson KL (1976) Postnatal growth and development of captive Franklin's ground squirrels (*Spermophilus franklinii*). Am Midl Nat 95:93–102

Van Vuren D, Armitage KB (1991) Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Can J Zool 69:1755–1758

Wieser R (1983) Les marmottes. Payot, Lausanne

Wroot AJ, Wroot SA, Murie JO (1987) Intraspecific variation in postnatal growth of Columbian ground squirrels (*Spermophilus columbianus*). J Mammal 68:395–398

Zélenka G (1965) Observations sur l'écologie de la marmotte des Alpes. Terre Vie 19:238–256

Zullinger EM, Ricklefs RE, Redford KH, Mace GM (1984) Fitting sigmoidal equations to mammalian growth curves. J Mammal 65:607–636