Duration of snow cover and its influence on life-history variation in yellow-bellied marmots

DIRK VAN VUREN[1] AND KENNETH B. ARMITAGE

Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, U.S.A

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We evaluated the relationship between growing-season phenology, as indicated by time of snow melt, and intrapopulation variation in reproduction and growth of yellow-bellied marmots. The time of snow melt explained significant proportions of the variation in frequency of reproduction (78%), litter size (79%), and estimated body mass of young of the year (68%), but not growth rate. We suggest that the duration of snow cover, through its effect on the length of the growing season, influences habitat quality; marmots living at localities with prolonged snow cover have a shorter season of access to food. The variation in life-history traits is attributed to phenotypic plasticity and not to local genetic variation.

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Nous avons étudié la relation entre la phénologie au cours de la saison de croissance, telle qu'indiquée par le moment de la fonte des neiges, et la variation intrapopulation de la reproduction et de la croissance chez la marmotte à ventre jaune. Le moment de la fonte des neiges explique une grande partie de la variation dans la fréquence de la reproduction (78%), le nombre de petits par portée (79%) et al masse corporelle estimée des jeunes de 1 an (68%), mais il n'explique pas la variation du taux de croissance. Il est probable que, par ses effets sur la longueur de la saison de croissance, la durée de la couverture de neige influence la qualité de l'habitat; les marmottes qui vivent dans des endroits où la couverture de neige persiste longtemps ont une saison raccourcie d'accès à la nourriture. Il semble que la variation dans les caractéristiques du cycle biologique soit attribuable à la plasticité phénotypique et non à une variation génétique locale.

[Traduit par la rédaction]

Introduction

Growing-season phenology may influence life-history traits of ground-dwelling sciurids in two ways. First, delay in the onset of growth of vegetation during spring may force ground squirrels, newly emerged from hibernation, to subsist on stored fat during mating and gestation, with possible consequences of reproductive failure or reduced litter size (Downhower and Armitage 1971; Knopf and Balph 1977; Murie *et al.* 1980; Murie and Harris 1982). Second, duration of the growing season may limit the time available for ground squirrels to acquire the food resources necessary for growth, reproduction, and accumulation of reserves for overwinter survival (Barash 1974; Andersen *et al.* 1976; Bronson 1980; Kiell and Millar 1980; Armitage 1981; Phillips 1984).

Previous studies of ground squirrels used snow cover or depth of snow as an index of growing-season phenology to explain life-history variation (Downhower and Armitage 1971; Armitage *et al.* 1976; Knopf and Balph 1977; Morton and Sherman 1978; Bronson 1980; Murie *et al.* 1980; Murie and Harris 1982; Phillips 1981, 1984). Most of these studies investigated temporal variation among years in one population or altitudinal variation among two or more populations. Qualitative observations of local geographic variation (Shaw 1925; Svendsen 1974; Andersen *et al.* 1976; Pfeifer 1982; Fagerstone 1988), however, suggest that the approach should be refined further to examine variation among localities within one population.

The yellow-bellied marmot (*Marmota flaviventris*) is a large, hibernating, ground-dwelling squirrel that occupies a variety of habitats throughout much of western North America. The two most important resources required by yellow-bellied marmots are rocks for burrow sites and green herbaceous vegetation for food (Svendsen 1974; Andersen *et al.* 1976; Andersen and Johns 1977; Armitage 1986). In the upper East River valley, near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, marmots live in discrete habitat patches, typically subalpine meadows with rock outcrops or talus, where these two resources co-occur (Svendsen 1974).

Some life-history traits of marmots vary considerably among localities inhabited near RMBL, suggesting that habitat quality varies as well (Armitage 1988). The cause of this variation, however, is uncertain. Overall forage production is an unlikely candidate because dense herbaceous vegetation is present throughout the East River valley for most of the summer; marmots consume less than 4% of aboveground primary production (Kilgore and Armitage 1978). Time of food availability, however, may be important. Marmots often emerge from hibernation by burrowing through the snow and must subsist on stored fat until growth of vegetation begins (Downhower and Armitage 1971). Time of snow melt during spring differs among localities (Svendsen 1974) and seems correlated with time of emergence of marmots from hibernation. Thus, variation in life-history traits among localities may derive, in part, from variation in snow melt patterns and its influence on growing-season phenology. Our objective was to determine if variation in time of snow melt among localities within a population of yellow-bellied marmots explained a significant amount of variation in reproduction and growth of marmots.

Methods

The upper East River flows generally southward through a valley that exhibits the U shape characteristic of past glaciation. Elevation of the valley floor is ca. 2900 m and gradient is gentle, averaging 20 m/km. Eight localities were selected that were part of a long-term study of yellow-bellied marmots that began in 1962 (Armitage 1986). The

greatest distance between localities was 4.8 km, but the greatest difference in elevation was only 165 m. Localities were on either side of the valley or on the valley floor, so slope exposure varied.

Data on patterns of snow melt were collected during May and June from 1983 through 1989. Field work began in early May when most of the upper East River valley remained covered with snow. At intervals of 1 to 5 days, each of the eight localities was surveyed, and percent snow cover within 75 m of the center of the locality was estimated visually. Areal exposure of soil during snow melt progressed according to a negative sigmoidal pattern (Johns and Armitage 1979); thus, we chose the date of 50% snow cover as the independent variable. As snow melted and snow cover at a given locality approached 50%, surveys were increased in frequency to estimate as accurately as possible the date at which one-half of the locality was free of snow. The date of 50% snow cover was estimated for each locality by linear interpolation between estimates made immediately before and after. Estimates were averaged across the 7 years of the study to give one mean date of 50% snow cover, expressed as number of days past 30 April, for each locality.

At each of the eight localities, intensive trapping for marmots was conducted annually for at least 12 years. Each trapped marmot was weighed and affixed with metal ear tags for permanent identification, if not already so marked. Successful reproduction of females was suggested by swollen nipples and subsequently confirmed by emergence of a litter at the female's burrow.

Frequency of reproduction at each locality was calculated by totaling the number of females at least 3 years old present each year, then summing over all years during which trapping was conducted; this sum was divided into the total number of litters observed. Some females first breed when 2 years old (Armitage and Downhower 1974), but only females 3 years or older were considered in order to reduce the confounding effects of socially induced reproductive inhibition (Armitage 1986) on age of first reproduction. Also, because resources for reproduction derive, in part, from fat stored the previous summer (Andersen et al. 1976; Kiell and Millar 1980; Kenagy and Barnes 1988), females that were not resident at a given locality for at least 1 year were excluded.

Litter size was determined by trapping and observation. Growth rates of young of the year were calculated for those individuals for which two or more weights were recorded at least 10 days apart; the difference in body mass between weighings was divided by the number of days elapsed. Body mass of young of the year on 1 August, at age ca. 2 months, was estimated for those young that were weighed within 10 days of 1 August; recorded mass was corrected to estimated mass on 1 August, using the mean daily growth rate calculated for each locality. Too few young were weighed at one locality to estimate mean growth rate, so the grand mean of growth rates for all young was used. Growth rate and estimated body mass on 1 August were calculated only for 1983 through 1989 because data were insufficient for several localities before 1983. Litter size, growth rate, and estimated mass of young on 1 August were averaged across years for each locality.

The relationships between time of 50% snow cover and rate of reproduction (litters per female), mean litter size (young per litter), mean growth rate (g/day) of young, and mean body mass of young were evaluated with simple linear regression. The independent variable was transformed if the relationship appeared curvilinear. Values for rate of reproduction were arc-sine transformed before analysis.

Results

Mean date of 50% snow cover differed among localities by as much as 21 days, from 9 May to 30 May. Frequency of reproduction among localities ranged from 0.53 to 0.68 litters per female and was related to time of 50% snow cover by a negative curvilinear function (arc-sine $Y^{0.5} = 54.09 - 0.00000800X^4$, $F_{1,6} = 21.0$, $P < 0.005$) (Fig. 1). A fourth-power transformation of time of 50% snow cover explained 78% of the variation in frequency of reproduction.

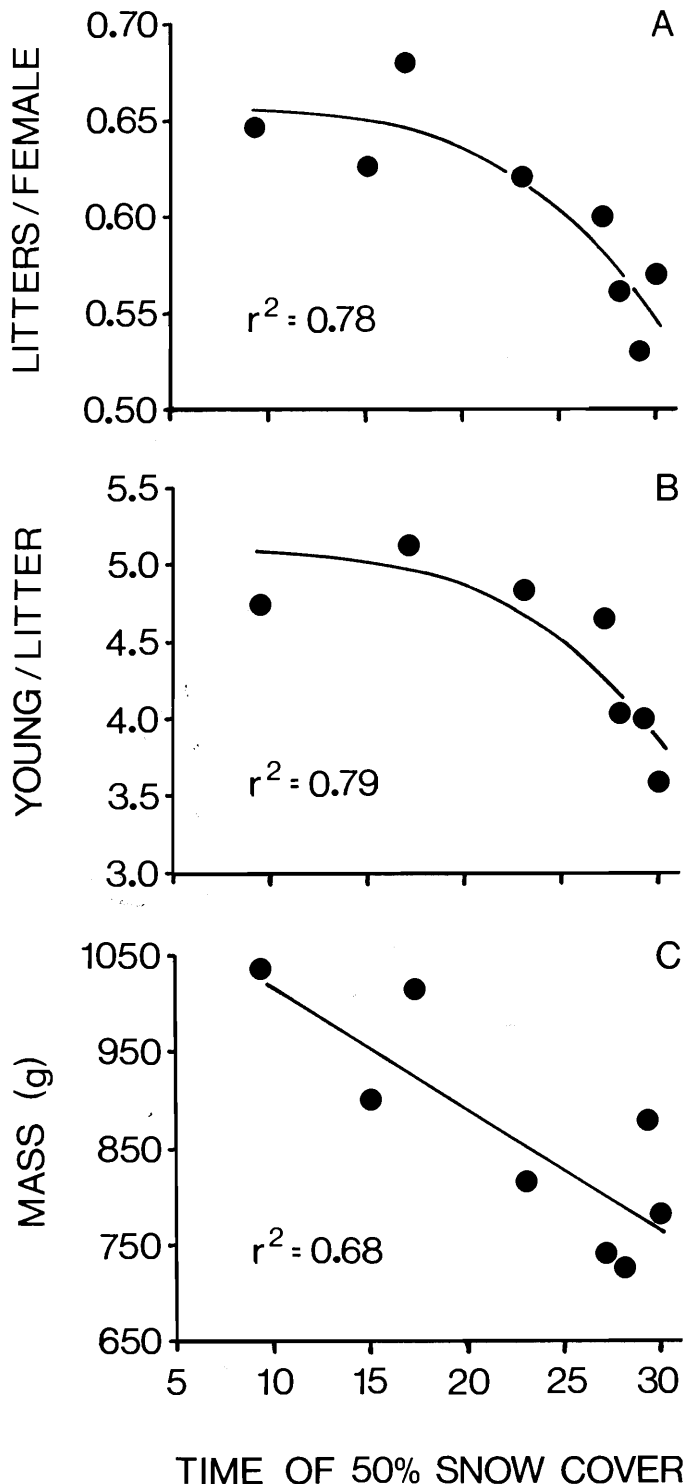Accurate data on litter sizes could not be obtained for one

FIG. 1. Relationship of frequency of reproduction of females (A), mean litter size (B), and mean body mass of young of the year on 1 August (C), to mean date of 50% snow cover (expressed as number of days past 30 April) among localities inhabited by yellow-bellied marmots near RMBL, Colorado.

locality. Among the other seven, mean litter size ranged from 3.64 to 5.13 young. Like frequency of reproduction, litter size was related to time of 50% snow cover by a negative curvilinear function ($Y = 5.10 - 0.00000154X^4$, $F_{1,5} = 18.8$, $P < 0.01$) (Fig. 1); a fourth-power transformation of time of 50% snow cover explained 79% of the variation in litter size. Frequency
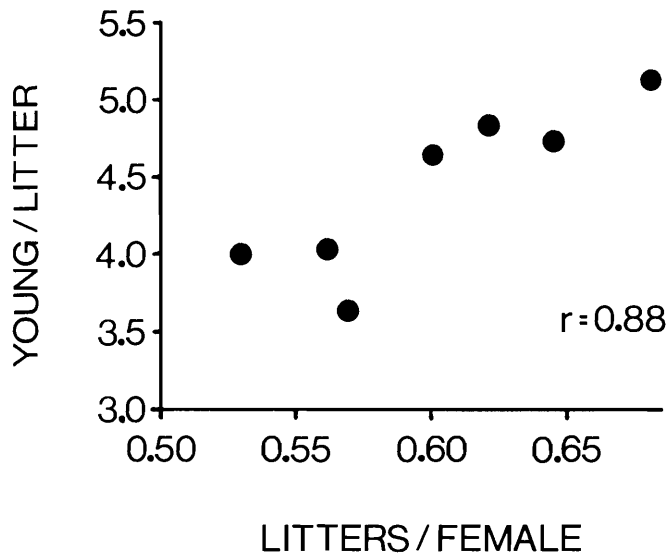
FIG. 2. Relationship between mean litter size and frequency of reproduction of female yellow-bellied marmots among localities near RMBL, Colorado.

of reproduction and mean litter size were positively correlated ($P < 0.01$) among the seven localities (Fig. 2).

Mean growth rate of young among seven localities ranged from 16.7 to 23.6 g/day but was not significantly related to time of 50% snow cover ($r^2 = 0.14$, $F_{1,5} = 0.81$, $P > 0.75$). The grand mean of growth rates for all young was 20.4 g/day ($n = 211$, SD = 6.50). Mean body mass among localities ranged from 725 to 1036 g and was negatively related to time of 50% snow cover ($Y = 1145.5 - 12.72X$, $F_{1,6} = 12.6$, $P < 0.025$) (Fig. 1). Time of 50% snow cover explained 68% of the variation in estimated mass of young on 1 August.

Discussion

Some of the variation among localities in mean date of 50% snow cover resulted from slope exposure, degree of shading by trees, and spring avalanches that redistributed snow. Most of the variation, however, resulted from asymmetrical snow deposition during winter; snowfall is consistently greater toward the head of the valley, apparently because of an interaction between storm path and local topography (W. Barr personal communication). Snowpack in early May was always 0.5 to 1.0 m deeper at the northernmost locality than at the southernmost.

Plant growth began as soon as the soil was exposed by melting snow, a relationship typical of plants in subalpine (Svendsen 1974) and alpine (Billings and Bliss 1959) environments. Thus, the date of 50% snow cover approximated the time at which an appreciable amount of green herbaceous vegetation became available to marmots. Correspondingly, marmots near RMBL foraged infrequently when snow cover was extensive, but increased their foraging activity markedly when snow cover shrank below ca. 50% (Johns and Armitage 1979). Plant senescence appeared to be caused by cessation of the summer monsoon season, onset of hard freezes, or both. Both factors acted consistently over the entire study area, and plant senescence, as indicated by pronounced yellowing, occurred generally simultaneously throughout the valley. Thus, time of 50% snow cover was also an indicator of duration of the growing season.

The active season of high-elevation ground squirrels should be timed to maximize growth and reproduction (Armitage et al. 1976; Morton and Sherman 1978; Michener 1979; Bronson

1980). Translocated yellow-bellied marmots in Oregon shifted their active season to coincide with local phenology in just 2 years (Thompson 1979), suggesting that marmots near RMBL that live at localities with persistent snow cover could time their active season accordingly. We observed that marmots at such localities initiated their active season consistently later in May than did marmots at localities where snow melted early, although we were unable to quantify these observations. Because the growing season ends more or less simultaneously throughout the upper East River valley, a consistently delayed active season probably means a shorter time of access to growing vegetation for food.

We suggest that a lower frequency of reproduction at localities where snow cover persisted (Fig. 1) was a physiological response to reduced annual food intake. Individual female marmots near RMBL sometimes breed in consecutive years, demonstrating a capacity for annual breeding, but this capacity often is not realized. One explanation is reproductive inhibition (Armitage 1986), but we suggest the principal reason is that food resources are not available for a sufficient length of time during the short growing season to satisfy annual needs for both maintenance and reproduction. Females probably breed whenever they have accumulated fat reserves, in excess of those needed to survive hibernation, that are sufficient to initiate production of a litter. Thus, females breed on average 2 of every 3 years at localities where snow melts early, but only about every other year where snow persists.

The effects of late snow melt on frequency of reproduction and on litter size were similar; consequently, these two variables covaried (Fig. 2). Thus, females exposed to longer growing seasons responded both by breeding more often and by producing larger litters.

Young marmots that are born late in the season suffer relatively high mortality, apparently because they fail to accumulate sufficient fat to survive hibernation (Armitage and Downhower 1974; Armitage et al. 1976). Data on overwinter survival of young were not available for enough localities for analysis, but smaller sizes of young on 1 August at localities with delayed snow melt suggest that, in addition to lower fecundity, females at these localities may also bear the cost of higher overwinter mortality of their young. The lack of any positive relationship between time of snow melt and growth rates of young suggests that late-emerging young do not compensate with higher growth rates. Because only about one half of young survive until 1 year of age, presumably because of overwinter mortality (Armitage and Downhower 1974), natural selection has probably maximized growth rates regardless of time of snow melt. Young with inadequate fat reserves might delay hibernation, but benefits of such a tactic are questionable because the nutritive quality of postsenescence vegetation is low (Frase and Armitage 1989).

Our results suggest that time of snow melt, through its influence on growing-season length, is a major determinant of habitat quality for yellow-bellied marmots near RMBL. Females would gain a reproductive advantage by seeking out burrow sites that melt out early, but few, if any, do so. Such a search requires movement that entails the risk of predation (Van Vuren 1990), and better quality habitat may already be occupied by other marmots (Armitage 1988).

The negative curvilinear relationships between time of snow melt and both frequency of reproduction and litter size suggest effects may extend beyond habitat quality to habitat suitability. Snow may melt so late in some areas that the growing season is not long enough for a female to breed at all. Excessive persis-

tence of snow may explain why some sites that otherwise seem to provide adequate resources are not regularly inhabited by marmots.

Whether variation in life-history traits in ground squirrels represents genetic variation or phenotypic plasticity has been a topic of considerable interest (Bronson 1979; Dobson and Kjelgaard 1985; Barash 1989, pp. 315–316). Barash (1974) proposed that frequency of reproduction in yellow-bellied marmots was a heritable trait. Our results indicate otherwise. The eight localities studied were separated by distances that were well within those typically traveled by dispersers (Van Vuren 1990); 10 marmots moved between localities during the study. Thus, opportunities for genetic differentiation were limited. Rather, the adequacy of time of snow melt to explain most of the among-locality variation in frequency of reproduction and litter size suggests a phenotypically plastic response to environmental variation. This response is consistent with the suggestion that plasticity is the most advantageous response when the environment exhibits substantial spatial or temporal variation (Dobson and Murie 1987).

Acknowledgments

ANDERSEN, D. C., and JOHNS, D. W. 1977. Predation by badger on yellow-bellied marmot in Colorado. Southwest. Nat. 22: 283–284.

ANDERSEN, D. C., ARMITAGE, K. B., and HOFFMANN, R. S. 1976. Socioecology of marmots: female reproductive strategies. Ecology, 57: 552–560.

ARMITAGE, K. B. 1981. Sociality as a life-history tactic of ground squirrels. Oecologia (Berl.), 48: 36–49.

―――― 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. In Ecological aspects of social evolution: birds and mammals. Edited by D. I. Rubenstein and R. W. Wrangham. Princeton University Press, Princeton, NJ. pp. 303–331.

―――― 1988. Resources and social organization of ground-dwelling squirrels. In The ecology of social behavior. Edited by C. N. Slobodchikoff. Academic Press, Inc., San Diego, CA. pp. 131–155.

ARMITAGE, K. B., and DOWNHOWER, J. F. 1974. Demography of yellow-bellied marmot populations. Ecology, 55: 1233–1245.

ARMITAGE, K. B., DOWNHOWER, J. F., and SVENDSEN, G. E. 1976. Seasonal changes in weights of marmots. Am. Midl. Nat. 96: 36–51.

BARASH, D. P. 1974. The evolution of marmot societies: a general theory. Science (Washington, D.C.), 185: 415–420.

―――― 1989. Marmots: social behavior and ecology. Stanford University Press, Stanford, CA.

BILLINGS, W. D., and BLISS, L. C. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology, 40: 388–397.

BRONSON, M. T. 1979. Altitudinal variation in the life history of the golden-mantled ground squirrel (Spermophilus lateralis). Ecology, 60: 272–279.

―――― 1980. Altitudinal variation in emergence time of golden-mantled ground squirrels (Spermophilus lateralis). J. Mammal. 61: 124–126.

DOBSON, F. S., and KJELGAARD, J. D. 1985. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63: 2105–2109.

DOBSON, F. S., and MURIE, J. O. 1987. Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. Am. Nat. 129: 382–397.

DOWNHOWER, J. F., and ARMITAGE, K. B. 1971. The yellow-bellied marmot and the evolution of polygamy. Am. Nat. 105: 355–370.

FAGERSTONE, K. A. 1988. The annual cycle of Wyoming ground squirrels in Colorado. J. Mammal. 69: 678–687.

FRASE, B. A., and ARMITAGE, K. B. 1989. Yellow-bellied marmots are generalist herbivores. Ethol. Ecol. Evol. 1: 353–366.

JOHNS, D. W., and ARMITAGE, K. B. 1979. Behavioral ecology of alpine yellow-bellied marmots. Behav. Ecol. Sociobiol. 5: 133–157.

KENAGY, G. J., and BARNES, B. M. 1988. Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. J. Mammal. 69: 274–292.

KIELL, D. J., and MILLAR, J. S. 1980. Reproduction and nutrient reserves of arctic ground squirrels. Can. J. Zool. 58: 416–421.

KILGORE, D. L., JR., and ARMITAGE, K. B. 1978. Energetics of yellow-bellied marmot populations. Ecology 59: 78–88.

KNOPF, F. L., and RALPH, D. F. 1977. Annual periodicity of Uinta ground squirrels. Southwest. Nat. 22: 213–224.

MICHENER, G. R. 1979. The circannual cycle of Richardson's ground squirrels in southern Alberta. J. Mammal. 60: 760–768.

MORTON, M. L., and SHERMAN, P. W. 1978. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. Can. J. Zool. 56: 2578–2590.

MURIE, J. O., and HARRIS, M. A. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (Spermophilus columbianus). J. Mammal. 63: 431–439.

MURIE, J. O., BOAG, D. A., and KIVETT, V. K. 1980. Litter size in Columbian ground squirrels (Spermophilus columbianus). J. Mammal. 61: 237–244.

PFEIFER, S. R. 1982. Variability in reproductive output and success of Spermophilus elegans ground squirrels. J. Mammal. 63: 284–289.

PHILLIPS, J. A. 1981. Growth and its relationship to the initial annual cycle of the golden-mantled ground squirrel, Spermophilus lateralis. Can. J. Zool. 59: 865–871.

―――― 1984. Environmental influences on reproduction in the golden-mantled ground squirrel. In The biology of ground-dwelling squirrels. Edited by J. O. Murie and G. R. Michener. University of Nebraska Press, Lincoln, NE. pp. 108–124.

SHAW, W. T. 1925. The seasonal differences of north and south slopes in controlling the activities of the Columbian ground squirrel. Ecology, 6: 157–162.

SVENDSEN, G. E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology, 55: 760–771.

THOMPSON, S. E., JR. 1979. Socioecology of the yellow-bellied marmot (Marmota flaviventris) in central Oregon. Ph.D. dissertation, University of California, Berkeley, CA.

VAN VUREN, D. 1990. Dispersal of yellow-bellied marmots. Ph.D. dissertation, University of Kansas, Lawrence, KS.