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Effects of vegetative variation on weaning success, overwinter survival, and social group density in golden marmots (*Marmota caudata aurea*)

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(With 5 figures in the text)

We studied the effects of food resources on weaning success, overwinter survival, and social group density in golden marmots (*Marmota caudata aurea*), an Old World sciurid rodent. End-of-season standing crop, a measure of seasonal productivity, varied between marmot groups but seemed repeatable between years. We adjusted some of our measurements of potential food availability by marmot preferences because faecal analysis suggested that marmots foraged selectively. Some, but not all, measured fitness parameters were associated with variation in food availability. The probability of weaning young was associated with overall food availability the previous year, and there was a significant positive relationship between the early-season food resources and the proportion of years in which a group reproduced. Weaning date, a correlate of subsequent juvenile overwinter survival, was associated with overall food availability in the same year. Non-juvenile overwinter survival was weakly associated with food availability. Finally, marmot density was not associated with the availability of food resources. We suggest that obligate social behaviour may limit the degree to which demographic factors can track environmental variation.

Introduction

The distribution and abundance of food resources may influence social evolution via its effects on mating systems (Emlen & Oring, 1977; Wittenberger 1979). Specifically, for terrestrial mammals, food availability influences social structure by affecting reproductive success (Dobson & Kjelgaard, 1985*a, b*; Rayor, 1985; Boutin, 1990; Van Vuren & Armitage, 1991) and survival (Dobson & Kjelgaard, 1985*a, b*; Rayor, 1985). For obligate hibernators that attempt to breed and store resources for hibernation during often brief active seasons, food availability may be particularly important and may influence weaning success, overwinter survival, and density. In this paper, we examine the influence of food resources to a relatively social Old World sciurid rodent, the golden marmot (*Marmota caudata aurea*).

Marmots (14 species worldwide) are morphologically and physiologically similar yet live in a wide variety of habitat types throughout the northern hemisphere (Barash, 1989). In marmot habitats, published estimates of the aboveground primary productivity of plants range from 39 g/m^2 (Hansen, 1975) to about 800 g/m^2 (Frase & Armitage, 1989). Marmots have food preferences (Wood, 1973; Hansen, 1975; Andersen, Armitage & Hoffmann, 1976; Armitage, 1979; Holmes, 1979; Carey, 1985; Frase & Armitage, 1989; Swihart, 1991), and the herbivory of woodchuck (*M. monax*) and Olympic marmot (*M. olympus*) influences the productivity and structure of the vegetative community (Wood, 1973; Del Moral, 1984; Swihart, 1991). Yet marmot populations appear to be limited by factors other than overall availability of vegetation. Individual woodchucks reduce primary productivity only on a very small spatial scale (Swihart, 1991) and yellow-bellied marmots (*M. flaviventris*) consume less than 4% of above-ground energy (Kilgore & Armitage, 1978).

Holmes (1984) none the less suggested that overall primary productivity influenced the social structure of marmot populations and species but provided no specific mechanism linking primary productivity to survival, reproduction, or group size. Previous studies of yellow-bellied marmots have noted relationships between the length of the growing season and litter size (Van Vuren & Armitage, 1991), the frequency of reproduction (Van Vuren & Armitage, 1991), and overwinter survival of some age classes (Armitage & Downhower, 1974; Armitage, Downhower & Svendsen, 1976). Andersen *et al.* (1976) also found a direct relationship between the amount of food resources and the number of offspring weaned by yellow-bellied marmots living in a high-altitude population. In all of the above studies, marmots lived in areas with $\geq 100\,\text{g/m}^2$ of aboveground standing crop at the height of the growing season (summary in Holmes, 1984). If variation in food resources influences the social structure of marmot populations and species, then its effects should be even more pronounced in locations with low primary productivity.

Golden marmots live in high alpine desert regions in the Karakoram, Hindu Kush, and Tien Shan mountains of Central Asia (Roberts, 1977), often in areas with $<100\,\text{g/m}^2$ of standing crop. The social behaviour of golden marmots was studied from 1988 to 1993 at Dhee Sar in Khunjerab National Park, Pakistan (36° 81′N, 74° 95′E, details in Blumstein & Arnold, In press). Marmots typically lived in 'monogamous' associations, but occasionally lived in groups with up to seven adults. All group members shared a common home range and burrow system. Groups were often contiguous; lacunae existed where vegetation was absent. At Dhee Sar, golden marmots had a 4–5 month active season (late April–late September), during which adults could potentially breed once. Reproduction was infrequent (only 17% of social group years—a social group studied for one year—weaned any young) and juvenile mortality was high (only 37% of juveniles survived to age 1) (Blumstein & Arnold, In press).

Other wild herbivores at Dhee Sar included Himalayan ibex (*Capra ibex sibirica*), Cape hare (*Lepus capensis tibetanus*), Royle's pika (*Ochotona roylei*), Royle's high mountain voles (*Alticola roylei*), Himalayan snowcock (*Tetraogallus himalayensis*), and snow pigeons (*Columba leuconata*). Dhee Sar was also grazed seasonally by domestic yak, sheep and goats (Blumstein, 1995). Domestic grazing reduced above-ground standing crop by an average of 32% (range 11.7–62.5%, $n=27$ paired exclosure results from three years of exclosure experiments—Blumstein, unpubl. data). We examined the effects of food abundance on three fitness parameters that could influence social structure: weaning success, overwinter survival, and density of older animals.

Materials and methods

General methods

The Dhee Sar study site is a relatively flat high alpine meadow (elevation 4,100–4,300 m a.s.l.) surrounded by steep lateral glacial moraines and punctuated with hilly terminal moraines. Our methods of trapping, individually marking, and observing marmot behaviour are described in detail elsewhere (Blumstein, 1994; Blumstein & Arnold, In press). Briefly, subjects were live-trapped and marked with eartags for permanent identification and with fur dye for identification from afar. We observed subjects from distant hides using binoculars and spotting scopes during their morning active period.

Variation in group composition was studied in detail from 1990 to 1993. All social groups were routinely observed in over 2,400 hours of direct observations during 465 days of field work; additional observations were made while regularly live-trapping marmots. A full census of each social group was attempted at least once each week, starting in the first week of May. An individual was considered to be a member of a group if it was observed within the group's estimated home range and it interacted affiliatively with at least one other resident. Because juvenile mortality was high (infanticide without cannibalism by unrelated males trying to join a social group accounted for at least 22% of first summer mortality, Blumstein, 1997), we excluded juveniles from analyses of social group size and focused instead on the number of marmots that survived at least one hibernation.

Early season (May and June) and late season (July and August) group home-range sizes were estimated in 1992 and 1993. We drew minimum convex polygons (Odum & Kuenzler, 1955) around the outermost locations where marmots were seen during daily observations to estimate home-range sizes for 16 social groups in 1992 and 19 social groups in 1993.

Food availability

We documented the variation among marmot social groups in the amount of vegetation within their home ranges by annually (1990–1993) sampling the standing crop around the end of the growing season (mid-August). The number of groups sampled varied: 6 in 1990, 11 in 1991, 18 in 1992, and 6 in 1993. Four groups were studied each of the 4 years, 6 for 3 years, 9 for 2 years, and 11 for a single year. Because there are over 120 plant species at Dhee Sar, some of which remain unidentified (Blumstein, 1995; Blumstein & Loomis, unpubl. data), we classified plants into 4 categories to simplify subsequent analyses: graminoids (7 identified species), legumes (6 identified species), shrubs (8 identified species), and other herbs (71 identified species). In mid-August we clip-harvested forty 0.2×0.2 m plots per marmot social group, each plot placed at 5 m intervals along four 50 m transects extended at right angles from the social group's main sleeping burrow. Where there was >1 main burrow, we chose a centrally-located burrow as the *main* burrow. Thus, the clipping array resembled an 'X' spread across a social group's home range. All aboveground vegetation was clipped in each plot. Samples were sun-dried on-site and later oven-dried (60–80 °C) to constant mass before weighing on an analytical balance.

We conducted an exclosure experiment to determine if end-of-season standing crop was a good estimate of overall primary productivity. In 1992, we established 4 randomly placed 1×1 m exclosures within the estimated home range of each of 5 marmot groups. Each exclosure contained two 0.35×0.70 m plots: one plot was clipped to a height of 0.01 m at approximately 3-week intervals, beginning in late May, and to the ground in mid-August. The paired plot was clipped only once (to the ground) in mid-August. We measured productivity as the sum of the masses from each clipping in the regularly clipped plots and correlated this measure with the end-of-season standing crop measurement from the paired plots in each exclosure. We also tested for evidence of compensatory growth by comparing the total biomass produced in regularly clipped exclosure with that in its unclipped paired exclosure.

To document vegetation phenologies, we noted the date of first appearance of different plant types in the exclosed plots described above. For each social group we calculated the median time of first appearance for each plant category. Phenology data were analysed with a Friedman non-parametric ANOVA blocked by social group.

Knowledge of marmot food habits was required to structure the remainder of the analysis. Because marmots were observed from stone hides (*c.* 100–600 m away), it was impossible to observe accurately what they were eating, so we used faecal analysis to study their diets (Sparks & Malecheck, 1968). Golden marmots defecated repeatedly in piles outside main burrow entrances, areas which we refer to as 'toilets'. We collected aggregated faeces at toilets from different marmot groups in late August 1992. Aggregated faeces permitted an overall description of food habits but made it impossible to associate faeces with individual marmots or to study seasonal variation in diets. We manually broke apart and mixed dried faeces from each of 16 social groups, selected well-mixed subsamples, and prepared these samples for microhistological analysis (Hansen *et al.*, 1974). Mounted slides and a reference collection of plants collected at Dhee Sar were sent for identification to the Composition Analysis Laboratory in Fort Collins, Colorado, U.S.A. The number of identifiable fragments from the 4 categories of plants was recorded in each of 60 microscope fields per social group (twenty 100× fields per slide, 3 slides per group).

We used the frequency of occurrence of identifiable plant fragments as an indicator of the proportion of each plant type in the overall diet. Because differential digestion of forbs was observed in a feeding trial of another marmot species, Frase & Armitage (1989) did not feel confident to report the exact proportions of different forb species eaten. However, in another feeding trial, Carey (1985) found no evidence of differential digestion between forbs and graminoids. Because we were unable to conduct feeding trials and/or directly observe food selection, the results from our faecal analysis remain unadjusted for potential differential digestion (e.g. Holechek, Vavra & Pieper, 1982).

To determine whether marmots had foraging preferences, we calculated D-scores for each food type (Jacobs, 1974: 416):

$$D=(r-p)/(r+p-2rp)$$

where r is the relative frequency with which a plant type (graminoid, legume, etc.) is eaten and p is the relative frequency with which a plant type appears in the environment (determined from 1992 clipping data). Standing crop estimates were then adjusted to reflect food availability according to marmot preferences. To do this we multiplied the end-of-season standing crop estimate of each plant type by the proportion of that plant type found in the faeces. We refer to the sum of these adjusted values as the 'total available food', and contrast this to overall biomass.

Specific questions

Weaning success

The influence of vegetation on weaning success was studied 3 ways. First, we used a logistic regression model to predict the probability of weaning juveniles as a function of available food in the previous year. We chose to examine available food in the previous year because it should influence a female's physical condition, and therefore her ability to reproduce in the following year. We used all available data in this analysis and some individuals and groups were represented more than once in the dataset (i.e. in multiple years). Here and elsewhere, following Hoogland (1995) we assumed independence of observations collected in different years. Second, because graminoids emerged earlier in the season than other plant categories and because preliminary analyses suggested that graminoids might provide an important lactational resource (Foggin, 1993), we also used a logistic regression model to examine the association between end-of-season graminoid biomass and weaning success in the same year. Third, we calculated a Spearman correlation coefficient between graminoid mass estimates in 1992 and the proportion of years that each marmot social group weaned young. We used data from 1992 because they formed the single most complete set. Variation in the rank order of graminoid biomass within social groups might vary among years (Friedman $\chi^2=6.0$, $P=0.11$, $n=4$ groups studied for 4 years); we acknowledge that this variation might confound the third analysis.

Overwinter survival

Small sample sizes (due to high juvenile mortality) prevented us from studying directly the effect of overall biomass or available food on juvenile overwinter survival. However, previous results suggest that weaning date (estimated from the date of juvenile emergence) influences the probability of juvenile overwinter survival (Armitage *et al.*, 1976; Blumstein & Arnold, In press). Thus, for all group-years with litter and forage data, we examined the relationship of forage and survival indirectly by regressing a group's available food against the group's weaning date.

The influence of vegetation on non-juvenile overwinter survival was also studied with logistic regression models. We examined the probability of overwinter survival for all non-juvenile marmots as a function of available food in the summer before hibernation. In both analyses, we used all available data and some individuals or groups were present more than once in the dataset (see above regarding independence of observations).

Density

The influence of food on marmot density was studied in 3 ways. Because some marmots moved between groups both within and between years (Blumstein & Arnold, In press), we examined the relationship between food resources and density in a single year (1992). First, we calculated the correlation coefficient between available food in a group's home range and the modal number of non-juvenile marmots in the social group. Second, we calculated the correlation coefficient between the density of non-juvenile marmots and the available food in a group's home range (from the 1992 modal number of marmots and home-range estimates). Third, we fitted linear models to study home-range size as a function of available food and the modal number of marmots in each social group.

Statistical analyses

Parametric and non-parametric descriptive statistics were calculated with StatView 4.01 (Abacus Concepts, 1992) and logistic regressions with SPSS for Windows, Release 5 (Norusis, 1992). Statistical significance was set at $P < 0.05$. We used one-tailed probabilities when testing *a priori* directional hypotheses and used parametric tests whenever possible. We scrutinized residuals from linear models and transformed data when necessary to meet assumptions of normality.

Results

Food availability

End-of-season standing crop was a good estimate of vegetative productivity ($r_s = 0.90$, one-sided $P = 0.04$, $n = 5$ group means from the paired exclosure experiment). In the four groups studied for four years, overall standing crop varied annually from a mean of 21.9 g/m^2 to 51.1 g/m^2 (Fig. 1). There was no evidence of compensatory growth when plants were artificially clipped: end-of-season standing crop was not significantly different from the total amount of vegetation clipped throughout the season in the paired plots (Wilcoxon $P = 0.54$).

Within a year, there was significant among-group variation in overall end-of-season standing crop ($F_{17,702} = 1.67$, $P = 0.04$; $n = 18$ groups, 1992 data). Between years, there was a positive association between total standing crop in 1991 and total standing crop in 1992 ($r_s = 0.6$, one-sided $P = 0.05$, $n = 9$ groups studied in both years). Vegetation within the home ranges of four groups was clipped during four consecutive years. For these groups, there was a moderately significant group effect in total end-of-season standing crop after statistically controlling for between-year variation over the four years of study (Friedman $\chi^2 = 6.9$, $P = 0.08$, $n = 4$ groups studied for four years). Thus the relative magnitude of each social group's end-of-season standing crop appeared consistent between years: some groups tended to have more primary productivity than other groups.

Within a year, there was also evidence of differential plant availability over time. Graminoids appeared before legumes and shrubs in the permanent exclosures (Mann–Whitney U-test conducted on the median week of appearance of each plant type in five groups; $P = 0.03$ for graminoid × legume, $P = 0.03$ for graminoid × shrub, $P = 0.44$ for graminoid × other herbs).

Finally, marmots had general forage preferences: they preferred legumes over all other plant categories (Table I). We used the average relative frequency of food items in the marmots' diet to adjust overall productivity estimates to reflect actual food availability more closely.

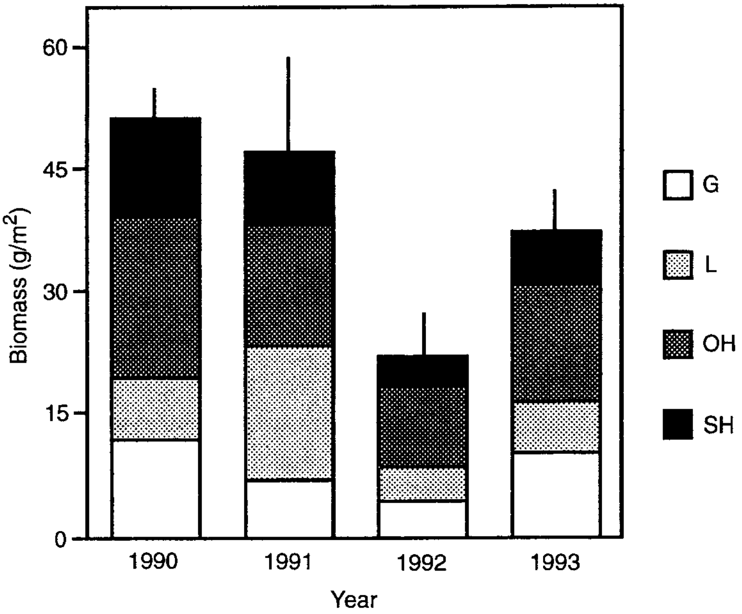

FIG. 1. End-of-season standing crop (+1 S.E.) and its components: G = Graminoids; L = Legume; OH = Other Herbs; SH = Shrub. Figure illustrates annual variation in the four marmot social groups studied for four years.

Food and weaning success

The probability of a group weaning young was significantly explained by the log of available food in the previous year (Fig. 2; logistic regression model $P = 0.03$, $n = 33$ group-years). Predicted values aid in interpreting this result. A group with one standard deviation more than the average available food would be 5% more likely to wean young, while a group with one standard deviation less than average would be 8% less likely to wean young.

In contrast, the probability of a group weaning young in the same year was not significantly explained by the availability of 'early season' food resources (Fig. 3). Neither the end-of-season graminoid biomass, the end-of-season other herb biomass, nor the sum of the end-of-season graminoid and other herb biomasses significantly influenced the probability that a group weaned young that year

TABLE I

Overall relative frequencies of vegetation present in diets and in the environment in 1992. Jacobs' (1974) preference coefficient is a measure of food selection based on availability and intake

Vegetation type	Diet	Environment	Preference[1]
Graminoid	0.02	0.14	−0.8
Legume	0.71	0.28	0.7
Other Herb	0.15	0.36	−0.5
Shrub	0.13	0.22	−0.3

[1] Jacobs' D-statistic ranges from −1 to +1. Positive values indicate preference.

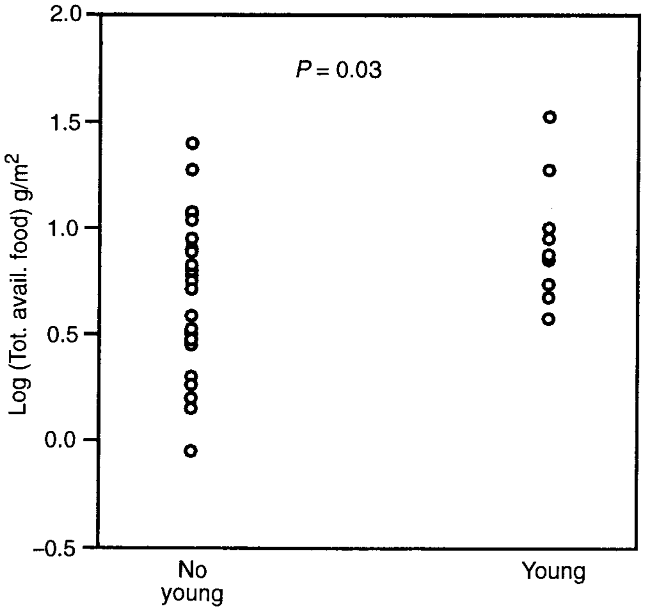

FIG. 2. The probability of weaning young as a function of available food in the previous year ($n = 33$ group years).

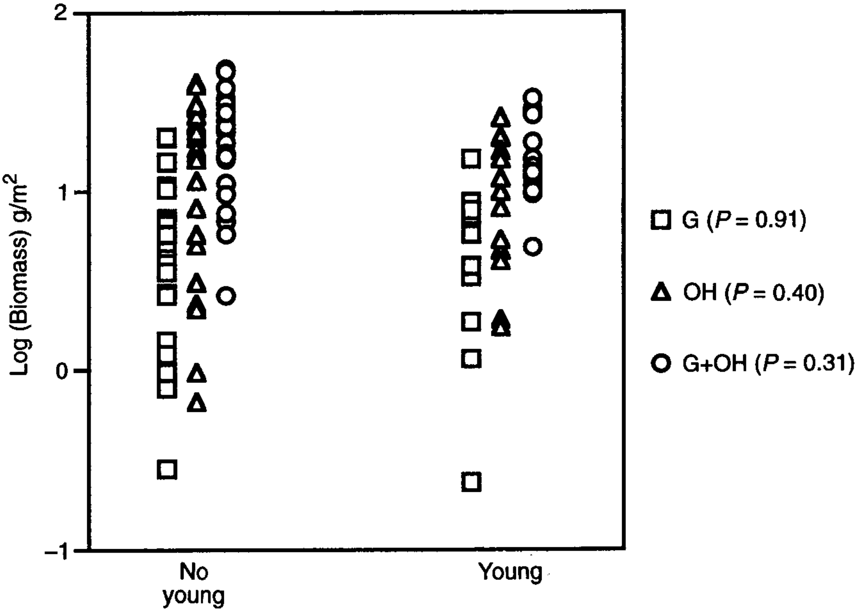

FIG. 3. The probability of weaning young as a function of early season food resources (graminoids and other herbs) estimated as end-of-season standing crop ($n = 39$ group years). Other experiments demonstrated that the end-of-season biomasses plotted here are correlated with early season productivity. For explanation of abbreviations see Fig. 1.

TABLE II

Spearman rank order correlation coefficients of the 1992 end-of-season standing crop and the proportion of years in which a group reproduced. In all cases, sample sizes were 17 marmot social groups

Vegetation type	r_s	One-tailed *P*-values
Graminoid	0.38	0.07
Other Herb	0.20	0.21
Legume	0.22	0.19
Shrub	−0.16	0.27
Graminoid + Other Herb	0.45	0.04
Available Graminoid + Other Herb	0.28	0.13

(logistic regressions conducted on log biomass measurements, model $P = 0.91$ for graminoids, model $P = 0.40$ for other herbs, model $P = 0.31$ for the sum of graminoids and other herbs). However, there was evidence of a positive relationship between early-season food resources and the proportion of years in which a social group weaned young. The 1992 combined end-of-season standing crop of graminoids and other herbs was significantly associated with the long-term proportion of years that a group weaned young (Table II, $P = 0.04$). We found that only standing crop biomasses, and not adjusted forage biomasses, are associated with multi-year weaning success. This result might be due to seasonal changes in food preferences (e.g. Del Moral, 1984; Carey, 1985; Frase & Armitage, 1989).

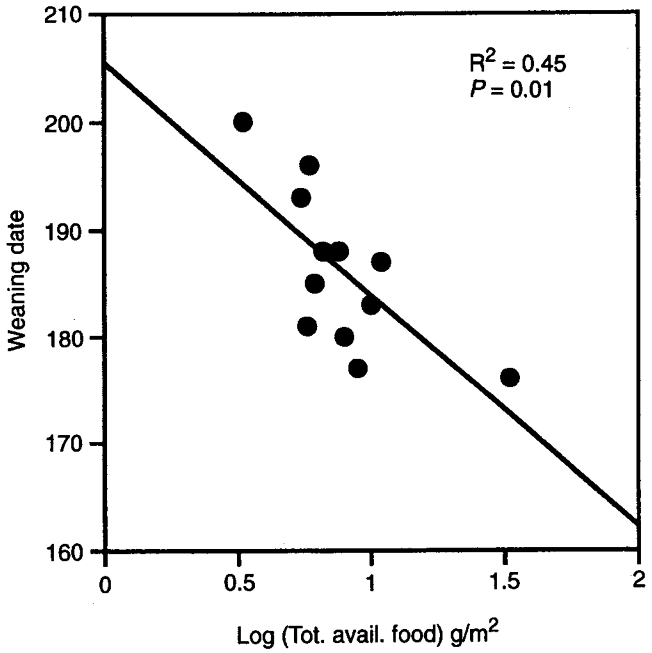

FIG. 4. Weaning date (days since 1 January) as a function of the log of that year's available food. One extreme outlier was removed from this analysis.

Vegetation and overwinter survival

Weaning date is inversely related to overwinter survival (Blumstein & Arnold, In press). About 45% of the variation in weaning date is explained by the log of that year's available food (Fig. 4, Adjusted $R^2 = 0.45$, $P = 0.01$). One extreme outlier (a group that weaned young early but which also had very little preferred foods owing to heavy domestic grazing and trampling) was excluded from this analysis.

There was also a weak tendency for non-juveniles living in areas with more food to have a higher probability of surviving the winter (Fig. 5, model $P = 0.09$, $n = 127$ non-juvenile marmot-years). Predicted values again aid in interpreting this result. Individuals living in an area with one standard deviation more than the average amount of available food are predicted to have a 95% chance of surviving the winter, while individuals living in an area with one standard deviation less than the average amount of available food only have an 88% chance of overwinter survival.

Food and marmot density

Food resources appeared not to be associated with group size and/or marmot density in any of the three ways we analysed the relationship. There was no association between the total available food and the long-term median number of non-juveniles in a home range ($r_s = 0.02$, one-tailed $P = 0.47$, $n = 17$ groups). Marmot density (n marmots/group home-range size) in 1992 was not associated with 1992's available food ($r_s = -0.30$, one-tailed $P = 0.13$, $n = 16$ groups). Finally, variation in the log of the maximum 1992 home-range size was explained by neither the log of 1992's available food, nor the modal number of non-juveniles in 1992 ($F_{2,13} = 0.90$, $P = 0.43$).

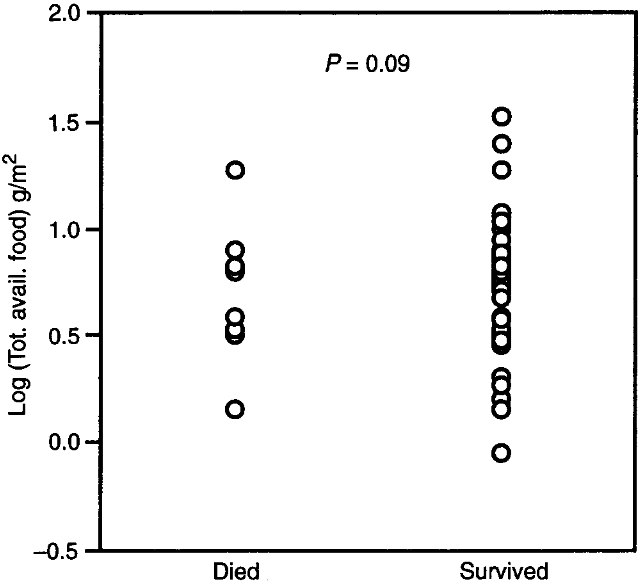

FIG. 5. The probability of surviving hibernation as a function of available food ($n = 127$ overwintering non-juveniles). There was a non-significant tendency for individuals living in areas with more food to survive hibernation (see text for details).

Discussion

Marmots, like most other ground-dwelling squirrels, exhibit an annual cycle of hibernation, reproduction, growth, and fat deposition. The timing of events is largely based on an endogenous circannual rhythm, but there should be some flexibility to allow for adjustments to small-scale temporal and spatial variations in environmental conditions such as duration of snow cover and/or food availability (Kenagy, 1986; Dobson & Murie, 1987; Van Vuren & Armitage, 1991). Golden marmots hibernate socially and may breed prior to their emergence from their hibernacula (Blumstein & Arnold, In press). While it is unlikely that vegetative factors trigger reproduction (e.g. Negus, Berger & Forslund, 1977), it is conceivable that, if social group home ranges vary in overall food availability, individuals or groups may track environmental variation by modifying group size, varying reproductive rates, etc.

Golden marmots are highly and perhaps obligately social. Adults live in social groups with 2–7 adults and younger offspring (Blumstein & Arnold, In press). Only a single female breeds per social group and breeding is infrequent. Juveniles delay leaving their natal home range for at least three years and group size increases primarily through offspring recruitment. Delayed dispersal may limit the ability of golden marmots to track natural variation in food resources immediately: only older animals disperse and thereby reduce group size.

There was no relationship between early season food resources (graminoid abundance) and weaning success in a given year; however, over multiple years there was a positive association between social group weaning success and graminoid abundance. Given infrequent reproduction (for instance, no females bred in 1989) and apparently only a single breeding female per group, the short-term result might have been expected. Because virtually no females breed in successive years (Blumstein & Arnold, In press), there is a time lag between breeding episodes during which females presumably regain adequate condition. In the long run, though, groups with more early season food resources wean young more frequently.

Groups with more available food also weaned young earlier and thus had more of their young survive their first hibernation. However, for a juvenile to survive its first year, it must avoid unrelated and potentially infanticidal males from different social groups, and it should hibernate only with relatives. Thus, social factors may weaken the link between food resources and overwinter survival.

Non-juvenile overwinter survival was slightly influenced by food availability. The non-significance of this association probably resulted from somewhat constrained non-juvenile intergroup movement. There appeared to be some costs associated with changing social groups: while older animals did change social groups, sometimes repeatedly, transients and immigrants were often subjected to intense aggression from residents. If intergroup movement had no costs, the relationship between food availability and non-juvenile overwinter survival might be stronger.

Variation in marmot social group density, however, was not explained by our measures of food availability. Animal density often increases in response to food addition (Boutin, 1990), and spacing systems such as territoriality may ‘break down’ when food distribution or abundance becomes economically undefendable (Lott, 1991). Yet delayed dispersal and obligate sociality may ‘buffer’ a species’ response to short-term environmental fluctuations. Because dispersal reduces group size, golden marmots (and other species that delay dispersal) may be less likely to track environmental variation precisely by moving from areas with less food to areas with more food.

For golden marmots, the ultimate benefit from grouping may be more related to the social thermoregulation of young during hibernation than to maximizing forage intake *per se.* Arnold (1993) documented a greater survival of juveniles that hibernate with older relatives in alpine marmots

(*M. marmota* L.), and there are suggestions that a similar phenomenon exists in golden marmots (Blumstein & Arnold, unpubl. data). Thus, non-dispersing older golden marmots might tolerate some variation in food abundance in order to increase their indirect fitness by helping thermoregulate younger siblings. Nevertheless, food availability in the summer preceding hibernation still tended to influence non-juvenile overwinter survival.

Observing considerable variation in golden marmot group size and social structure over a relatively small spatial scale provided the initial impetus for this study. Is natural variation in food resources responsible for variation in marmot social group characteristics? Clearly, for golden marmots, food is important for both survival and reproduction. However, for obligately social species, the effects of food resources on parameters such as weaning success, overwinter survival, and social group density may be muted. Our results suggest that factors other than overall forage availability may be most important in determining social group size and hence 'social organization.' Many juveniles die in their first year, but if a juvenile survives it tends to remain in its natal group for at least two more years. Thus, recruitment plays an important role in determining social group size. Offspring recruitment is influenced in turn by group stability and by the number and type of older group members. These in turn may be associated, perhaps weakly, with food availability. However, group size and other parameters appear not to be strongly related to the distribution and abundance of food resources. Rather, in the long run, they are indirectly related to food resources through differential survival and reproduction.

At least some social variation can be accounted for by non-resource-based explanations and may be the result of unique (i.e. chance) events. A chance encounter with an infanticidal male or a predator can wipe out an entire litter. Conversely, once a breeding pair first recruits offspring, the survival of subsequent offspring should increase (the social environment becomes more amenable to reproduction). However, if larger social groups have unrelated individuals in the hibernaculum, juvenile overwinter survival may decrease (Blumstein & Arnold, In press). Since dispersal is delayed, environmental conditions can potentially deteriorate markedly before animals leave the social group. Thus social factors may mute the ability of golden marmots to track variation in environmental conditions; a condition perhaps most adequately described as 'social inertia'. In conclusion, some, but not all, measured demographic and fitness parameters of golden marmots were associated with natural variation in food availability. Weaning young in one year was associated with food availability in the previous year, as would be expected if females could maintain body condition over hibernation. Abundant early-season food resources also increased the likelihood of weaning young in the long term (though not in the same year), and greater forage availability was associated with earlier weaning dates. However, natural variation in food resources was not associated with marmot density, and there was only a weak relationship between food availability and non-juvenile overwinter survival. Social behaviour may thus limit the degree to which individual and group 'demographic factors' track environmental variation.

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