SOCIOECOLOGY OF MARMOTS: FEMALE REPRODUCTIVE STRATEGIES[1]

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Abstract. The relationship between female reproductive success and both spring food and hibernacula resources was examined in a high-altitude population of yellow-bellied marmots (*Marmota flaviventris*). The number of offspring a female weaned was significantly associated with the estimated number she could potentially produce, based on food resources. The production of young by these females is probably food limited to varying degrees. Hibernacula may be a restricted resource; young reared in an area without a hibernaculum were not recaptured as yearlings. Delaying pregnancy until forage is available fails as a strategy because young have insufficient time to accumulate fat for hibernation. Adult females deposit fat at a single maximum rate regardless of reproductive history; few females gain weight prior to weaning their young. In areas with short growing seasons, measured as the period during which nonreproductive adults gain weight, females may occasionally or regularly fail to reproduce in consecutive years. The short period of time following weaning may not permit the accumulation of fat sufficient to provide energy for hibernation, postemergence activity, and reproduction. The growth rate (g/day) of young marmots is greater at high than at intermediate elevations. This increase in growth rate warrants further examination of the hypothesis that increased sociality among marmots living in areas with short growing seasons is a response to decreased growth rates of young animals.

Key words: Colorado; fat; food; growing season; growth rates; hibernacula; marmots; reproductive strategy.

INTRODUCTION

Yellow-bellied marmots (*Marmota flaviventris*) form colonies within favorable habitat, with one or more males each sharing its territory with one or more females (the harem) (Armitage 1962, 1965, 1973, 1974; Downhower and Armitage 1971; Svendsen 1974). Individual marmots may be broadly classified as aggressive, social, or avoider within an apparent continuum of behavioral profiles (Svendsen and Armitage 1973). Females may be social or solitary; individual reproductive success varies according to the social situation (Downhower and Armitage 1971, Svendsen 1974). All members of the genus *Marmota* hibernate; yellow-bellied marmots are active less than half of each year.

Two obvious habitat resources critical to reproductive success of yellow-bellied marmots are food and burrows. Although Downhower and Armitage (1971) postulated that limited food during gestation determined the reproductive success of females, marmots at 2,900 m in Colorado during gestation consumed only 1%–2% of the total available net primary production (Kilgore 1972). Armitage and Downhower (1974) suggested the number of available burrows did not affect the number of resident marmots within colonies, but could limit population size at the smaller satellite sites. They also noted large variations among years and among localities

in the percentages of young marmots recaptured as yearlings and attributed these differences in survival through hibernation to variation in winter conditions. Differences in survival could be affected by the quality of hibernacula and amount of fat accumulated for hibernation.

This study attempts to identify the environmental factors limiting the reproductive success of individual yellow-bellied marmots. The study was designed to examine three hypotheses concerning a high-altitude population, where environmental effects would be most pronounced; (1) that particular burrows, the hibernacula, are not a restricted resource; (2) that hibernacula do not vary in quality; and (3) that the reproduction by female yellow-bellied marmots is not food limited.

METHODS

Study area

The study area (Fig. 1) is located in North Pole Basin in the Elk Mountains of west-central Colorado (Gunnison County; United States Geological Survey Snowmass Mountain quadrangle). The basin, ≈ 3 km long, is at most 1 km wide, encircled, except at the north end, by a ridge ranging in elevation from 3,680 m to 4,100 m. The orientation of the basin affects the microclimates within those portions of the floor (3,380 m elevation) and lower sides making up the study area. Bedrock outcroppings with thinly developed soils bound the study area on the north and south, while stands of tall willow and krummholz
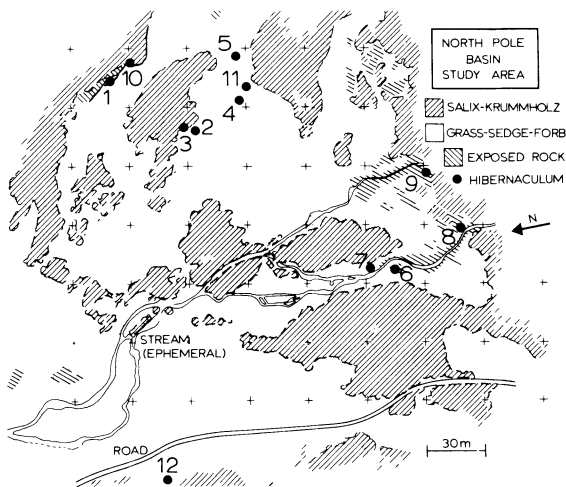
FIG. 1. North Pole Basin study area, showing locations of hibernacula. Hibernaculum 8 may be several hibernacula in close proximity, as several entrances were used independently throughout the summer. Hibernacula 1–7 were located by the presence of snow tunnels.

form the boundaries on the east and west. The resulting square of ≈ 7 ha contained the hibernacula, summer burrows, and most of the home ranges of about 20 adult marmots.

The vegetation within the study area characterized a weakly developed "upland herb" community (Langenheim 1962) with typical alpine species in drier sites and local concentrations of snowflush and streamside species at wetter sites. Portions of the winter snowpack remained in the study area until the last week of July in 1974, and even later in 1973. An ephemeral stream (Fig. 1) disappeared into bedrock at the southern boundary of the study area by mid-August (1974), but reappeared as a continuously flowing spring 100 m downstream of the northern boundary. A listing of the plant species found in the study area is given in Andersen (1975).

Observations and trapping

Yellow-bellied marmots resident in the study area were trapped intensively from the third week of May through the first week of October 1974, in the manner described by Armitage (1974). Approximately every third day during the study period trapping was discontinued and continuous day-long observations were made to record location and activity of individual marmots at regular intervals. Data on the survival of young as yearlings were obtained from the 1974 May-to-August study period.

Weights and growing season

Marmots were weighed and released within a few minutes of each capture, allowing some individuals to be trapped repeatedly during a single day. In such cases, only the first weighing was included in the analyses. Fall 1973 weights were estimated from regression lines based on weights obtained earlier in that year. Minimum weights recorded during the 1974 active season were used as estimates of lean body weight. The difference between the minimum and highest weight was used as an estimate of the amount of body fat. Comparative data for East River Valley (16 km south, 2,900 m elevation) marmots were taken from weights collected between 1967 and 1973 (Armitage et al. 1976). Analysis of data included the use of biomedical programs (Dixon 1968) for regression analysis. Where appropriate, statistical tests are included in the text as the statistic (t or F), the degrees of freedom (df), and the probability level (P), in the form (t or F, [df], P). Statistical significance was assumed as the 95% probability level throughout the analyses.

The length of the growing season in North Pole Basin was estimated from temperature data collected on a continuously recording hygrothermograph, from snowpack information collected as a series of photographs taken at approximately regular intervals, and from daily personal observation of local weather conditions.

Food resources

Preferred forage plants were determined by visually monitoring the free-ranging adults with the aid of a field telescope (40–80×). Plants in which acceptance could not be verified were considered acceptable as forage in energy calculations. Food plant preferences reported in the literature (e.g., Pattie 1967, Downhower 1968) were not extended to this study because some of the reported food plants were not used by marmots in North Pole Basin. These differences may reflect food plant availability during foraging as well as intraspecific differences in palatability known to exist in some plants (Freeland and Janzen 1974).

The study area was divided into seven vegetation zones on the basis of cluster analysis performed on lists of species from 77 quadrats (each 1 m^2) located randomly within the foraging areas (Sokal and Sneath 1963:185). Standing crop within each vegetation zone was estimated by clipping individual plant species within a 0.125-m^2 quadrat located inside each of the larger quadrats (Wiegert 1962). Preferred species were oven-dried (60°C) to constant weight and their biomass determined (Andersen 1975). Quantitative sampling began 18 June, 90% occurred after 23 June, and sampling was considered adequate by 12 July. The latter date was used to designate the end of the time period for which food resources were potentially limiting. After this period, food resources were in excess.

Energy values of whole shoots, leaves, or flowers

were determined in a Parr 1411® semi-microcalorim-
eter and corrected for ash content determined by
baking samples at 500°C for 4 h (Paine 1971). A
single energy value was assigned to each plant species
utilized or assumed acceptable to the marmots prior
to 12 July (Andersen 1975). Both seasonal and
spatial differences in the energy content of single
species have been noted (Golley 1961, Bliss 1962,
Hadley and Bliss 1964, Rochow 1969). The final
energy value was in most cases (and in all cases
involving common species) the average of several
(2–18) values obtained from samples taken ran-
domly within the study area. The effect of intra-
specific variation of plants on the energy available
within foraging areas is considered minimal.

Foraging areas expanded from near zero during
and immediately following emergence to the size
estimated to be available to the individual females
by 12 July. The accompanying increase in available
energy was provided for by weighting portions of
each foraging area, defined by a series of five con-
tours outlining progressive snowmelt, according to
the proportion of days, between emergence and 12
July, that those areas were snow-free. Overlapping
foraging areas were treated by dividing the area of
overlap equally among all users.

Energy required for production of young

The quantity of energy each adult female in the
study area would have required to produce one
young was calculated using equations developed by
Kilgore (1972). For example, Kilgore found that
digestive efficiencies of adult females vary with
season (time of year) and body size; thus female
143 had an average digestive efficiency of 62%,
and female 192, 55%. We assumed that birth weight
of yellow-bellied marmots was equal to the 27 g
reported for *M. monax* (Snyder et al. 1961) and
that linear growth of young occurred during each
of the 30-day periods presumed necessary for gesta-
tion and lactation. Young probably were observed
the first day they emerged from their natal burrow,
and all were weighed within a few days of first
sighting. Hence, these weights are an estimate of
size at weaning. Because the mean weight of male
young (464 g, $n = 20$) was not significantly different
($t = 1.25$, df $= 31$, $p < 0.90$) from that of female
young (419 g, $n = 13$), a pooled estimate of the
mean weight of young marmots (446 g) was used.
Thus we estimated that during gestation young grew
at a rate of $(27/30) = 0.9$ g/day, and during lac-
tation $(446-27)/30 = 14.0$ g/day.

The date of conception for each female, and thus
the degree of development ($=$ cost) of her offspring
by 12 July, was estimated by subtracting 60 days
from the date her young were first observed. For
females whose mammae and weight data suggested

that litters were started but lost, conception dates
were extrapolated from those estimated for other
members of the same harem.

A litter size of six was selected as the maximum
which could be attained by all adult females in the
study area. While this number is not critical to the
analysis, six represents a high but common value
reported for litter sizes (Nee 1969, Downhower and
Armitage 1971) and as such serves as a realistic
reference point. A female was considered to be
food limited if the energy within her foraging area
was insufficient to allow her to carry a litter of six
young to 12 July. For example, if a female pro-
duced three young, she was considered food limited
if the energy available to her was insufficient for
production of an additional three young. We stress
here that finding individual females to be food
limited does not imply that the population was food
limited, nor does such a finding imply anything con-
cerning the carrying capacity of the environment.

RESULTS

Hibernacula

Up to 20 adult females may have hibernated
within the study area during the winter of 1973–74.
Seven hibernacula (Fig. 1) were identified by the
presence of snow tunnels. Five additional burrows
located in rock outcroppings where marmots were
active during the emergence period were considered
hibernacula. The sole use of a hibernaculum by an
adult female was established in one case, and
suspected in several others; however, most females
shared the hibernaculum with another adult female.
In two cases, three females may have shared the
same hibernaculum. Agonistic encounters between
females and between males were observed during the
study, but no unambiguous overt defense of hiber-
nacula *per se* was established. All territorial males
shared their hibernacula, both in 1973–74 and 1974–
75, with one or more adult females. For each of
the three males having all or most of their territory
within the study area, the most commonly used
summer burrow was also the hibernaculum both
winters. The hibernaculum was thus the focal point
of each male's territory for most of the summer.
All hibernacula found within the study area were
within a male's territory throughout the summer.
Three resident females did not use their hibernac-
ulum as their principal summer burrow.

If hibernacula differ in factors affecting the rates
at which marmots within them expend energy while
hibernating, then variation in the amounts of fat
used by hibernating marmots should be greater be-
tween, rather than within, hibernacula. A compari-
son of the hibernating costs of adult females asso-
ciated with different hibernacula was inconclusive
(Table 1). Data were available for only two animals

TABLE 1. Estimates of the amounts of fat stored and utilized by North Pole Basin ♀♀ from one active season into the next (through the winter 1973–74)

		Season					
		Fall	Winter		Spring		
Female No.	Lean weight (kg)	Total fat stored prior to hibernation (kg)	Fat used in hibernation		Fat utilized in reproduction and maintenance		No. of young produced
			kg	% total	kg	% lean wt.	
173	2.4	2.4	1.7	71%	0.7	29%	0
175	2.4	2.4	2.0	83%	0.4	17%	NR
143[a]	2.7	1.8	1.7	94%	0.1	4%	5(4–6)
192[a]	3.3	1.5	1.5	100%	0.0		5(4–6)
184[b]	1.8	0.9	0.9	100%	0.0		3
183[b]	1.8	0.7	0.5	71%	0.2	11%	0
257[b]	2.1	0.9	0.8	89%	0.1	5%	NR

[a] Hibernated together.
[b] 2-yr-olds.
NR = nonreproductive.

known to have hibernated together. Both expended relatively low amounts of fat and eventually produced large litters, which might be interpreted as due to a high quality hibernaculum. However, confounding factors may also explain the large litter sizes (see below). Variation between age classes is likely due to factors related to maturity or size.

Food resources

The energy available from preferred vegetation within each adult female's effective foraging area varied from 5,732 kJ to 157,193 kJ (1,370 to 37,570 kcal) (Table 2). Yellow-bellied marmots do not breed as yearlings and only 25% of the 2-yr-old females produce litters (Armitage and Downhower

TABLE 2. Real and potential reproductive success of adult ♀♀ in North Pole Basin. Energy available is a measure of net primary production, through 12 July, of preferred vegetation within each ♀'s foraging area, modified for snowmelt patterns and overlapping home ranges. The percentage of each foraging area not shared with other ♀♀ is 100 minus the sum of the values in the table. To convert kilocalories to kilojoules (kJ), multiply by 4.184

| | | | A | No. | B | C | Potential | Foraging area | | |
| | | | No. weaned young | yearlings | Cost per young carried to | Energy still | reproductive success to | True | Percent shared with other females | |
Female No.	Age	Date young weaned	emerging	recaptured	12 July (kcal)	available (kcal)	12 July A+(C/B)	size (m²)	w/1	w/≥2
185[a]	>3	20 Jul	6	3	5,144	7,359	>6	1,742	15	3
248[a]	>3	27 Jul	6	6	3,947	5,472	>6	2,305	10	85
187[a]	>3	5 Aug	1	1	1,789	1,371	1	680	42	45
139[a]	>3	11 Aug	3	0	415	6,519	≫6	1,103	80	0
173[a,b]	>3		0		3,328[c]	8,919	2	3,627	32	46
175	>3		NR		2,341[c]	5,130	2	1,492	52	0
141	>3	16 Jul	3	3	5,735	6,718	4	980	37	0
143[d]	>3	17 Jul	5(4–6)	0	5,532	6,190	6	2,586	79	16
192[d]	>3	17 Jul	5(4–6)	0	6,487	32,342	≫6	6,768	42	12
431	≥3		NR		NC	37,571†	----	3,707	21	0
184	2	6 Aug	3	1	1,149	14,010	≫6	2,316	17	3
183[b]	2		0		2,773[c]	2,836‡	1–2‡	1,459‡	9	90
257	2		NR		NC	9,430‡	----	3,784‡	28	33

[a] Indicates females whose complete foraging areas were inside the study area for which estimates of both (B) and (C) have minimal error.
[b] Started but lost litters.
[c] Values of (B) were calculated using conception time of burrow mates.
[d] Shared the same burrow, and together produced 10 young; 4–6 represents the most likely litter size for each. NR = nonreproductive; evidence of having started litters. NC = conception time could not be calculated.
† This estimate of available energy is accurate; however, female 431 was not observed inside the study area prior to 23 June.
‡ Indicates minimum estimate due to probably foraging outside the study area; actual values may be 50%–100% higher.
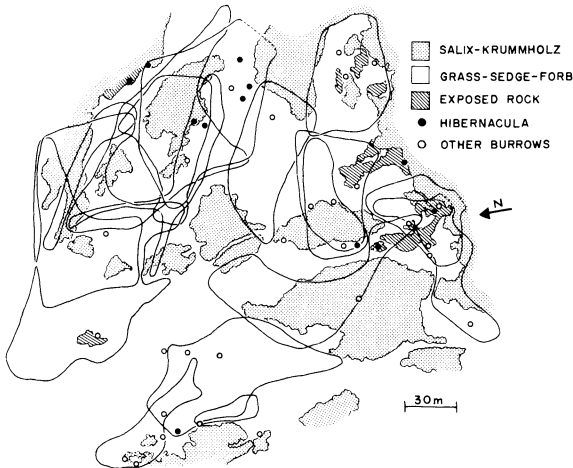
FIG. 2. Foraging areas of adult ♀♀ through 12 July. Open circles are auxiliary and home burrows used during the 1974 active season.
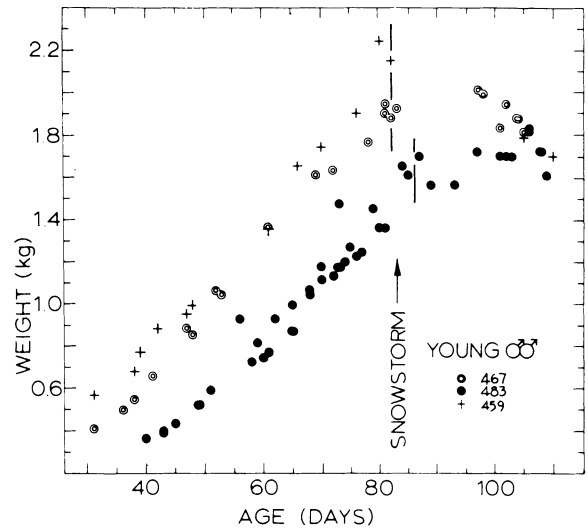

FIG. 3. Scatter diagrams of weight data for three young from North Pole Basin. Age is based on first sighting at age 30 days (= age at weaning). Linearity of growth prior to the snowstorm (12 September) was typical of all young and adult ♀♀ during period of growth. Mothers of 467, 483, and 459, were 185, 248, and 192 or 143, respectively.

1974). Woodchucks (*Marmota monax*) breeding as yearlings produce smaller litters than older females (Snyder and Christian 1960). Because the litters of the 2-yr-old females may reflect age-specific effects, or factors related to primiparity, these animals were not considered in the following analyses.

There is a significant relationship between the number of young emerging above ground and the potential number of young a female could have produced on the basis of available energy for the first six females of Table 2 (Olmstead and Tukey's corner test for association; $0.05 > p > 0.02$; Sokal and Rohlf 1960:539). The same trend is reflected among the remaining females, although significance cannot be determined. We conclude that the females are food limited to varying degrees. This conclusion assumes that these females are unaware of limiting factors that may affect their potential reproductive success and do not adjust their foraging areas accordingly. The validity of the qualifying assumption is supported by the apparent initiation but subsequent loss of litters by at least two females. The loss of litters is inferred from the physical development of the mammae in preparation for lactation, and weight drops either prior to or near the time harem mates underwent parturition, followed by an almost immediate attainment of the maximum rate of weight gain. Also, most females could increase the energy available to them only through encroachment into neighboring foraging areas. The expanding home ranges of the females left few portions of the study area unexploited by 12 July (Fig. 2). Areas not used were typically those flooded by runoff during the period of intense snowmelt following the last spring snowstorm (5–8 June), or which contained dense concentrations of *Geum rossii*, a plant relatively common but never observed to be utilized.

Growth rates of young

Young in the North Pole Basin study area showed linear growth prior to the 12 September snowstorm which generally terminated growth (Fig. 3). Only weights obtained before 12 September were included in the analysis of growth rates. For East River Valley young, only weights obtained prior to 15 September were utilized (Armitage et al. 1976).

No significant differences in the rate of weight gain (g/day) were found among 18 of the 20 male young (Table 3) born in the study area ($F = 1.49$ [17, 179] $P \cong 0.90$). One male gained weight significantly faster ($F = 1.73$ [18, 189] $P > 0.95$), and another, significantly slower. The latter was found dead with no apparent external injuries in mid-August (about 90 days old), suggesting disease, congenital defect, or internal injury, any one of which could result in the low weight gain observed. No significant differences were found in the rate of weight gain among nine of the ten female young emerging within the study area ($F = 1.46$ [8, 73] $P < 0.90$). One female (Table 3) grew exceptionally fast ($F = 3.46$ [9, 84] $P > 0.99$), at a rate comparable to most young males.

Groups of ten male and ten female young from the East River Valley population had significant differences among individual patterns of weight gain (♂♂: $F = 5.54$ [9, 27] $P > 0.99$; ♀♀: $F = 3.21$ [9, 25] $P > 0.975$). However, removal of only one female with a significantly low growth rate and two males with significantly higher growth rates (Table

TABLE 3. Rates of weight gain (95% confidence interval) for young yellow-bellied marmots from high (3,380 m) and intermediate elevation (2,900 m) sites. Common rates are obtained as the weighted average of the slopes of those animals showing no significant within-group differences in weight gain rate (Snedecor 1956:398). n = number of marmots, N = total number of weighings

		Common			Individual	
Site	Sex	g/day	n	N	g/day	N
North Pole Basin	♂ ♂	29.3 ± 0.9	18	195	32.9 ± 2.7	12
					19.3 ± 5.5	10
	♀ ♀	23.8 ± 1.3	9	91	30.8 ± 3.6	13
East River Valley	♂ ♂	16.8 ± 2.1	8	37	27.4 ± 2.4	6
					26.4 ± 13.4	4
	♀ ♀	19.4 ± 1.7	9	40	13.0 ± 1.3	5

3) resulted in the remaining within-group differences becoming insignificant at the 0.90 level (♂ ♂ : F = 1.43 [7,21]; ♀ ♀ : F = 1.80 [8, 22]). Examination of the records for these individuals indicated nothing to justify their exclusion from the analysis a priori.

The rate of weight gain, based on the common regression estimates, is significantly greater at the higher elevation (♂ ♂ : F = 117.8 [1, 222] $P > 0.99$; ♀ ♀ : F = 62.6 [1,96] $P > 0.99$). The two fast-growing males from East River Valley grew as fast as the grouped males of North Pole Basin (F = 1.50 [19, 185] $P \cong 0.90$), however, all ten males from East River Valley have a common regression estimate (20.4 ± 1.8) significantly below that of the North Pole Basin group of 18 males (F = 84.5 [1, 258] $P > 0.99$).

Adult female growth rates

No female in the North Pole Basin study area gained weight significantly during lactation; only one gained weight during gestation which would be expected simply as a result of the increasing weight of the developing young. Thus, in order for females producing litters to accumulate summer fat stores comparable to those accumulated by nonreproductive females, they would have to either accumulate fat for a longer period of time, or at a faster rate. The onset of hibernation varied among the females within the study area and timing of hibernation was not correlated with reproductive history. In addition, the first major fall snowstorm (12 September) probably terminated weight gain for all adult females regardless of their fat accumulation or fall activity patterns. Only three adult females, including two who had litters, could be examined for weight changes subsequent to the storm; all lost weight. Two females, one of which produced a litter, lost weight at highly significant rates ($P > 0.99$). Seven adult females had adequate numbers of weighings prior to the fall storm to allow comparison of rates of weight gain (= fat deposition). The rates of

weight gain for six of the seven females were not significantly different (Table 4), although they had various reproductive histories. The growth rates of three additional females were equal to or higher than these six, but confidence limits could not be established. One female marmot had a growth rate significantly lower than the rest.

DISCUSSION

If hibernacula are a limited resource, all adult females should either include a hibernaculum in areas within which they have exclusive use (non-social animals) or they should freely associate with females who would share an accessible hibernaculum (social animals). Females within our study area fit both patterns. Because breeding occurs shortly after emergence (Armitage 1965, Nee 1969) and travel during this period is extremely limited (Armitage 1965, Armitage and Downhower 1974), the number of females hibernating within a male's territory is proportional to his potential reproductive success. Thus male yellow-bellied marmots should include all possible hibernacula within their territories. This

TABLE 4. Rates of weight gain (95% confidence interval) for adult ♀ ♀ having various reproductive histories, examined during the period of maximum fat deposition. Weight data and mammary development suggest ♀ ♀ 173 and 183 terminated pregnancy at or before the onset of lactation. The first six ♀ ♀ have rates not significantly different from one another (F = 1.96 [5,43] $p < 0.90$); the common rate (see Table 3) for that group is 28.3 ± 2.0 g/day. NR = nonreproductive

Female number	Litter size	Period examined	Rate of weight gain (g/day)	No. of weighings
185	6	post-lactation	33.4 ± 9.0	10
173	0	post-termination	29.9 ± 6.2	9
175	NR	entire	28.7 ± 2.7	9
184	3	post-lactation	21.0 ± 8.5	12
183	0	post-termination	32.7 ± 26.5	5
257	NR	entire	27.5 ± 1.7	10
248	5	post-lactation	9.5 ± 15.7	10

pattern was evident in North Pole Basin. These lines of evidence are consistent with the hypothesis that hibernacula are a restricted resource and may limit the reproductive success of individual females.

The most pronounced effects of any variation in the quality of hibernacula might be among young marmots hibernating for the first time. The survival of young is significantly correlated with the termination of their first winter (Armitage and Downhower 1974). Such differential mortality among hibernating young may derive from inadequate fat stores caused by differential access to food resources during the previous active season. Access varies because young generally forage only in areas either utilized by or accessible to their mothers. The general uniformity of the growth rates of North Pole Basin young (Table 3) suggests that such differential access does not contribute to overwinter survivorship of young. Thus, it seems important that the female's reproductive strategy should include access by her young to a hibernaculum.

Few females produced the maximum number of young calculated as possible on the basis of their plant-food energy resources (Table 2). These calculations neglect conditions existing immediately after emergence. Females for whom the numbers of weighings were adequate lost weight from the time of emergence through 8 June, the last day of a 4-day spring snowstorm. Additionally, we observed female marmots active in areas that did not provide forage for a considerable period after emergence and no animal was seen to attempt the lengthy and presumably dangerous trips necessary to obtain forage available in those areas where snowmelt had preceded the resident's emergence or arrival. These observations and the general inability to gain weight prior to parturition suggest that parous females utilize body fat remaining after hibernation as a source of energy during the initial stages of reproduction, as woodchucks do (Snyder et al. 1961).

If females are limited not only by forage but also by spring fat reserves, a positive correlation should exist between the number of young produced above ground and a female's probable fat stores remaining upon emergence. The trend is negative (Table 1), suggesting that spring fat stores are detrimental to reproductive success. This paradox is resolved by considering individual reproductive strategies. If fat reserves are inadequate for reproduction, two options are open to a reproductive female. She can either move to an area in which forage becomes available early, or she can delay pregnancy until food becomes available within nearby areas. Both strategies minimize the dependence on spring fat reserves for reproduction and both were utilized by the females producing litters.

Females 143 and 192 were two of the three females resident on the study area who did not utilize their hibernaculum as a summer residence burrow. Although these two hibernated together, they independently abandoned the hibernaculum soon after emergence in late May. By 4 June, they had rejoined and were utilizing an area 100 m from the hibernaculum, the first area within the study site not already harboring marmots to become snow-free. The young of females 184 and 139 were the last to appear within the study area (Table 2). Thus their gestation occurred as forage became readily accessible within their foraging areas.

Although females 143 and 192 had high litter sizes, their reproductive success was not commensurate. None of the young of these females was recaptured as a yearling in 1975 (Table 2). Their strategy gambled short-term success, measured in numbers of young produced, against long-term reproductive success measured as the number of yearlings produced (Downhower and Armitage 1971). Females 143 and 192 subsequently appeared to have difficulty in re-establishing access to their previous hibernaculum; the location of their hibernacula the second winter is uncertain. Their young did not follow them into the area containing the previous year's hibernaculum, possibly because of the agonistic behavior shown towards them by other adult females utilizing the area. These young wandered unusually widely in late September presumably searching for a hibernaculum. Several of them probably hibernated in a burrow not identified as a hibernaculum. We attribute the loss of these young to their inability to obtain a suitable hibernaculum.

Females 184 and 139 and their young had little time following weaning to accumulate fat for hibernation. Over-winter mortality of small young ranges from 75% to 90% (Armitage et al. 1976). Although both females survived, only one of five young that hibernated (one young was cannibalized by an adult female) survived. Thus the strategy of delaying pregnancy until forage increases has severe limitations.

Large spring fat stores alone do not guarantee large litters. Female 173 had the largest fat reserves, but failed to wean a litter (Table 1). Food may have been insufficient (Table 2) following depletion of her fat reserves to adequately maintain the litter she probably started.

Female woodchucks (M. monax) use fat during the spring breeding season (Snyder et al. 1961), but data on the success of individual females are lacking. The loss of weight by our marmots following emergence from hibernation testifies to the importance of fat reserves. The quantity of fat in spring is a function of the total amount stored the previous fall and the amount utilized during hibernation. The optimal strategy for the individual female would

thus be to maximize the quantity of fat stored by fall and to minimize the use of fat during hibernation (select the best hibernaculum).

Because growth rate usually is maximized regardless of reproductive history (Table 4), the rate of weight gain cannot be the principal factor determining the size of fall fat deposits. The critical factor is the total length of time during which weight gain is possible. Those animals with the longest period of weight gain prior to hibernation will have the largest absolute amounts of fat. Females conceiving early in the spring will, in this respect, have an advantage because of the greater length of time available for fat deposition after weaning. However, early conception and/or early emergence from hibernation increase utilization of fat in maintenance and reproduction. Thus there is a strict limitation on the strategy of early emergence and early conception. Most females probably emerge and reproduce as early as possible (Armitage 1965, Nee 1969) and most depend on the post-weaning period to obtain adequate nutrition for hibernation and reproduction. At high elevations, the post-weaning growth period may not be sufficient to allow both survival through hibernation and reproduction. None of the 28 tagged females who were resident two or more years in our North Pole Basin study area has bred in successive years. By contrast, many females in the East River Valley breed annually.

Barash (1973a, 1974b) suggested that the gradient of sociality observed among species of Marmota is the result of a necessity to inhibit early dispersal and to closely regulate population size in severe environments. Predictions generated by his hypothesis were supported by studies examining social behavior of hoary marmots (M. caligata) and of yellow-bellied marmots (Barash 1973b, 1974a). A critical feature of the evolutionary scheme proposed by Barash is that young animals have retarded growth rates resulting from the decrease in growing season associated with harsh climates.

One factor which confounds the analysis of Barash's hypothesis is the determination of the length of the growing season. We used four criteria for estimating the 1974 growing season in North Pole Basin. The most significant estimate would seem to be the period during which positive weight gain occurred. In our study area that period of 96 days from 8 June to 12 September coincided with our second criterion, the period free of major snowstorms. Neither of our other two criteria, the longest frost-free period (60 days) and period free of snowpack (100 days from 25 June to 3 October) accurately reflected the marmot growing season. Barash (1973a:236) estimated the vegetative growing season experienced by Olympic marmots at 35–75 days, but his growth curves show marmots gaining weight

for up to 120 days, 24 days more than in North Pole Basin.

In contrast to Barash's suggestion that young animals have retarded growth rates at the higher elevations, our young had higher growth rates than both yellow-bellied marmots at lower elevations (120 days growing season) (Table 3) and young male Olympic marmots (3 g/day) with a longer growing season (Barash 1973a: Table 1). These differences imply that different selection pressures are adjusting the reproductive strategies of these two species. Thus an evolutionary model of marmot sociality based on universal selection pressures focused on retarded growth rates is invalid.

More attention should be given to the role of hibernacula availability as a factor in the evolution of marmot societies. The distribution, abundance, and quality of hibernacula may vary both locally and regionally along a gradient from the habitats typically occupied by the eastern woodchuck, with relatively flat topography and deep soils, to those featuring moderate topography and greater variation in soil depth inhabited by yellow-bellied marmots in the lower portions of the western mountains, and ending in the extremely localized habitat in which the high montane species may be found. For example, 19% of all burrow systems of the eastern woodchuck located in 40 ha of conterminous ("good") habitat in Ontario were hibernacula, at a density of 0.77 hibernacula/ha (de Vos and Gillespie 1960). In our study area, the density of hibernacula was 1.7/ha, comprising 30%–50% of all burrow systems. Thus, the extent and density of hibernacula within favorable habitat may determine the degree of sociality exhibited by a species.

In summary, we suggest that the optional reproductive strategy of a female yellow-bellied marmot includes the utilization of spring fat reserves which are accumulated in the previous growing season, the acquisition of a hibernaculum, and occupancy of a home range where forage appears early in the season. The degree of success of this strategy in any given year is affected by variation in the end of the previous growing season and the start of the current one and probably also by the quality of the hibernaculum.

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