DEMOGRAPHY OF YELLOW-BELLIED MARMOT POPULATIONS[1]

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Abstract. Marmot (*Marmota flaviventris*) populations are colonial or satellite. The number of adults of colonial populations is relatively stable; fluctuations occur primarily because of changes in numbers of young and yearlings. Population trends among five colonial populations are dissimilar. Satellite populations are unstable and reproduce at a lower rate than do colonial populations. Satellite marmots are shorter resident than colonial marmots. Both colonial and satellite females usually are longer resident than males. All adult colonial males and 41% of adult colonial females are recruited from other places; all satellite adults are recruited from other places. Losses of colonial marmots are attributed primarily to mortality during hibernation and emigration. Predation appears to be a minor source of mortality of colonial marmots, but may be of greater significance to satellite populations. Demographic relationships of individual colonies appear to be density-independent. Dispersal of colonial animals occurs primarily among yearlings, which have a higher expectation of reaching sexual maturity than young have. The major cause of dispersal is social pressure, but social stress is not simply density-dependent. The colonial social organization is more adaptive than the more nearly solitary (= satellite).

Key words: Colonial; demography; density-dependent; density-independent; dispersal; hibernation; mortality; population; predation; recruitment; residency; satellite; weather; yellow-bellied marmot.

INTRODUCTION

Few studies of mammalian populations provide long-term information on the demography of the population and the factors producing the observed demography. Most often the effect of only a single variable is considered, such as predation, food, social behavior, or genetics. Consequently, while a variety of species has been studied and some appreciation of their social biology gained (summary by Eisenberg 1966), a holistic view of the adaptive significance of mammal social organizations and its integration with the demography of mammalian populations has not been achieved. Social behavior causing dispersal of part of the population may be critical for population regulation of rodents (Carl 1971, Krebs et al. 1973). It is the intent of this paper to describe in detail certain yellow-bellied marmot (*Marmota flaviventris*) populations in south-central Colorado, to examine the factors influencing their demography, and to place these observations into the context of their social organization.

STUDY AREA AND METHODS

The populations are located near Gothic, Gunnison County, Colorado, elevation about 2900 m. Live-trapping, marking, and observation of these marmots began in 1962; the methods were detailed elsewhere (Armitage 1962, Shirer and Downhower

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1968, Armitage 1973, 1974). Marmots were classified by age and social status (Downhower and Armitage 1971). Young are animals in their first summer of life; yearlings are 1 yr old, i.e., in their second summer; adults are 2 yr old or older. Colonial marmots are polygynous groups consisting of one or more males and their harems. A peripheral animal is one that lives near a colony, probably has sensory contact with members of the colony, but may have no direct social contacts. The home range of the peripheral animal lies entirely outside the territory of the colonial male and the home ranges of the harem females. Transient marmots are those individuals of any age or sex that move through the study area but do not remain for more than a few days. An isolate is a male or female of any age that resides alone.

Localities occupied by isolates differed from those occupied by colonies mainly in size and topographic diversity (Svendsen 1973). Because more than one marmot may live at an isolate site, and because isolate sites are minihabitats with the most limited resource being burrows, the term satellite was applied to these localities (Svendsen 1973) and this term will be used in this paper.

Initially, study localities were chosen that appeared to correspond to places occupied by discrete marmot colonies. A marmot colony consists of one or more males and their harems (Armitage 1962, Downhower and Armitage 1971). Young and/or yearlings usually are present. Localities 1–5 and 7 harbored colonies. Satellites live in areas that usually have one or two marmots; young may be pres-

ent, but yearlings rarely are. Because satellite sites differ from colonial sites primarily in area and in number of burrows, there could be a gradient of sites from satellite sites harboring one animal to the colonial sites with their harems. Some sites could be intermediate. Locality 6 appears to be such a site; however, since its population structure and habitat characteristics were like satellite sites (Svendsen 1973), locality 6 was classified as a satellite site.

Intensive trapping was conducted at localities 1 through 7. Trapping ceased at locality 3 in 1965; data collected there are not included. Because a cabin was constructed on locality 2 in 1969, trapping ceased there also; however, the data collected there are included. Satellites were trapped and tagged, especially at those places annually sheltering one or two marmots or an adult female and her young. Intensively studied satellite sites were located near colonies. From 1962 through 1972, over 460 marmots were marked and released. The locations of the study localities were figured elsewhere (Shirer and Downhower 1968), and photographs showing general features of the localities were published previously (Armitage 1973, 1974).

All weather data used in this study are for Crested Butte, Colorado, 7 miles by road and about 250 m lower in elevation than our study area (U. S. Weather Bureau 1962–72).

Yellow-bellied marmots in the Gothic area usually emerge from hibernation in the first part of May. Females solicit the male (Armitage 1965), copulation ensues, and young are born in early June (assuming a gestation period of about 30 days). Most young emerge aboveground in the first half of July. Beginning in September the marmots hibernate for about 7–8 mo and do not emerge until the following spring.

RESULTS

Changes in number of individuals

The number of colonial animals trapped at localities 1, 2, 4, 5, and 7 and the total number of marmots trapped at locality 6 are summarized in Fig. 1. Peripheral and transient individuals trapped at the colonial sites are not included.

The most striking observation is that the population trends are not similar for any two localities. Localities 1 and 2 are near each other, but whereas the population of locality 2 increased to a peak of 21 residents in 1967, the population of locality 1 declined to a low in 1968. A second general observation is that the number of resident adults was fairly stable over the 11 yr, although there was some slight overall decline. The greatest range in the number of adults occurred at locality 1, where from 2 to 8
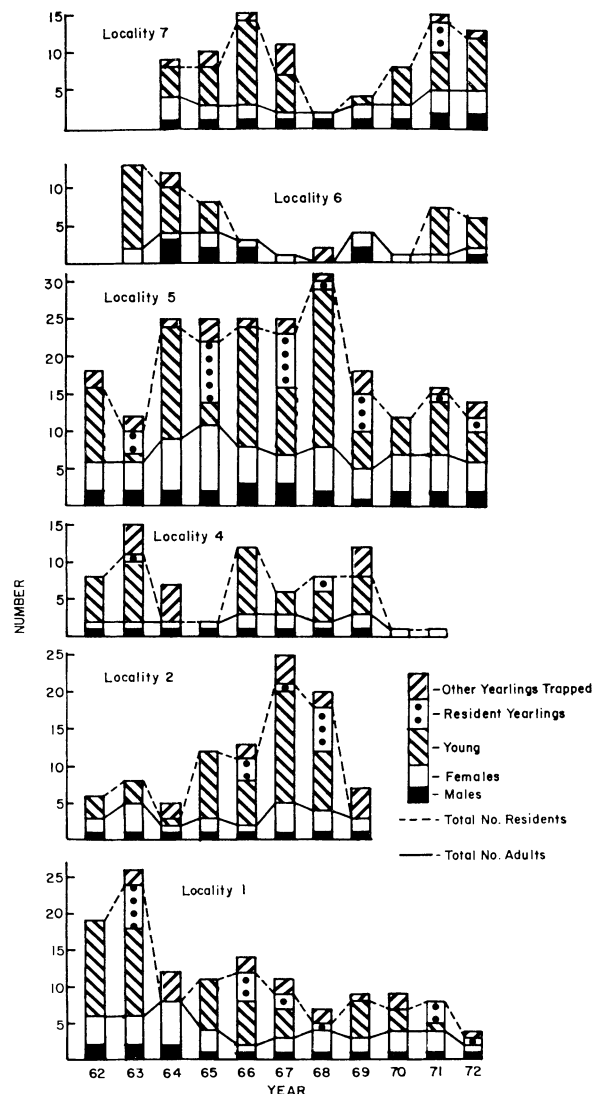

FIG. 1. Marmot population levels at six localities. Locality 6 is a satellite locality; all others are colonial. Other yearlings trapped refers to transients born elsewhere than in the locality where trapped and to those that emigrated from their natal locality before mid-August.

adults were present. At locality 5, which usually had two harems, the number of adults varied between 5 and 11. Most of the fluctuation in residents resulted from changes in numbers of young and yearlings. The exchange of animals among localities was rare.

Population structure has no obvious correlation with population size within a locality. At locality 2 two females in 1963 produced no young, whereas in 1965 another two females produced nine young. At locality 4 only one female was trapped each year from 1962 through 1965, yet young were produced only in 1962 and 1963. At locality 5, in 1965 nine

TABLE 1. Recapture data for colonial and satellite marmots. Transient adults trapped in colonies were considerd colonial. Chronological age of individuals first trapped as adults was approximated by assuming them to be 3 yr old (age category 3–4) when first captured unless their body weights were typical of 2-yr-old marmots, in which case they were classified as 2 yr old (age category 2–3).

Sex and estimated age at first capture	Number at first capture	Estimated age at each recapture						
		1–2	2–3	3–4	4–5	5–6	6–7	7–8
Colonial males								
Young	116	54	3			2	1	
Yearling	4							
2-yr-old	9			2	1	1		
3-yr-old	19				10	7	4	3
Colonial females								
Young	131	61	28	18	12	6	4	1
Yearling	6		2	2	1			
2-yr-old	11			5	4	2	2	2
3-yr-old	7				5	3	3	
Satellite males								
Young	24	1						
Yearling	5							1
2-yr-old	13			3	1			
3-yr-old	12				1	1		
Satellite females								
Young	26							
Yearling	6							
2-yr-old	11			1	1			
3-yr-old	16				4	3	1	

adult females produced three young; in 1968, six females produced 21 young.

The areas that we first defined as colonies have changed in social structure during the course of the study. In 1962–64 two adult males lived at locality 1. Since 1965 one male occupied the previously divided area, and in 1965–68 this male expanded his territory to include locality 2. Locality 4 supported a pair of resident adults the first 4 yr of our study. In 1966 a second adult female carried her litter to a burrow at locality 4. Subsequently, the resident female chased the new female repeatedly. Once she chased the new female and her young down the new female's burrow and then filled the entrance with rocks, sticks, and soil (Armitage and Downhower 1970). In 1967, the resident female was shot and in a matter of days the "new" female of 1966 moved into the vacated burrow system. She was the resident female of 1968 and was joined in 1969 by her daughter, who lived there through 1971 but never reproduced. Locality 5 had three harems in 1966 and 1967, one harem in 1969, and the typical two harems in 1970.

Locality 6 differs from the others in that it apparently is intensively used by wandering individuals or by individuals that have dispersed from localities 5 or 7; however, its population trends do not mirror those of either locality. Several adult males may occupy the site simultaneously and tolerate one another (usually all but one leave, but no aggressive encounters have been recorded). Reproduction is erratic, and apparently some females have moved into the locality with their young rather than giving birth there, or the females mated elsewhere and then moved into this locality. The almost total lack of yearlings is uncharacteristic of marmot colonies. For these reasons we consider locality 6 as inhabited by non-colonial marmots.

A total of 113 satellites of various ages was trapped in the course of this study. Of this number, 41 different individuals were marked at locality 6.

Length of residency

Of 116 young males trapped in colonies, 54 were recaptured as yearlings, but only 4 were recaptured as adults in the colonies of their birth (Table 1); of these one male became a resident in the colony of his birth. One male, born at locality 1 and trapped there as a yearling, was trapped as a 3-yr-old at locality 2. A third male, born at locality 4, was retrapped as a 2-yr-old transient at locality 7 and established a territory there as a 5-yr-old (Fig. 2: open bar, 5–6 age-class). Of the 30 adult males that entered our colonies (transients included) 28 were first captured as adults and were not previously captured in any part of the study area (Fig. 2). Only one of 24 satellite juvenile males was recaptured (at locality 6). One of the satellite adult males was recaptured as a resident of locality 5.

Of 131 females first trapped as juveniles in colonies, 28 were recaptured as adults. Similarly 2 of 6 females first trapped as yearlings were recaptured as adults. In all, 28 of 48 colonial adult females were resident in their natal colonies. No young females
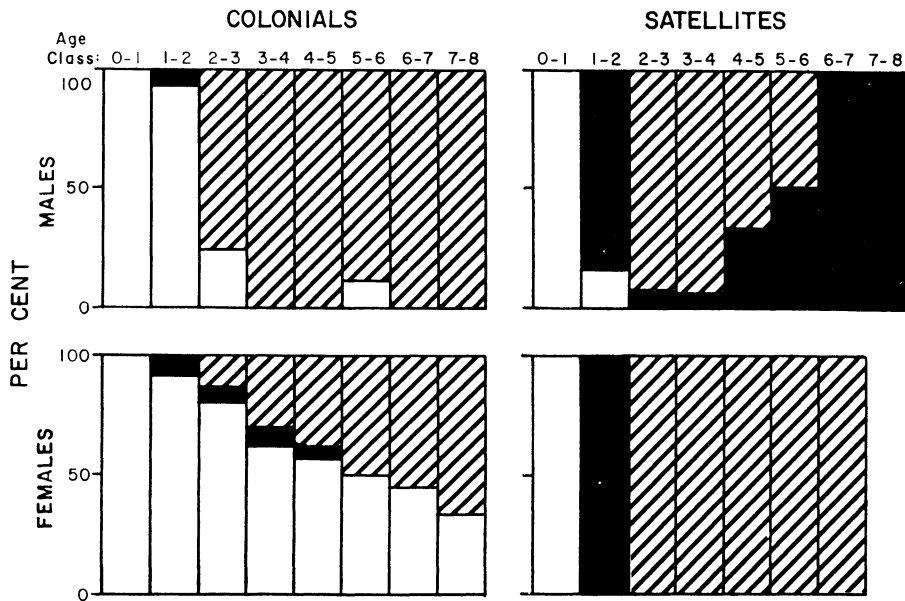
FIG. 2. Source of colonial and satellite marmots. Open bars = born in the locality of residence; solid bars = recruited (first trapped) as yearlings; cross-hatching = recruited (first trapped) as adults. Data summarized for all colonial and satellite localities. The percentages for each age class are derived from the estimated age distribution of Table 1.

born to non-colonial females were recaptured as yearlings, nor were any yearling females first trapped as satellites recaptured as adults (Fig. 2). Only 5 of 27 satellite adult females were recaptured in years subsequent to the year of first capture. One yearling transient at locality 5 was recaptured as a satellite the next year and one yearling resident at locality 1 was recaptured the subsequent 3 yr as a satellite. One colonial young was recaptured as an adult satellite. Two colonial adult females were subsequently recaptured as satellite females, but no adult satellite female was recaptured as a colonial female. Only one female rotated between satellite and colonial status from year to year, but she began as a colonial.

Animals first trapped as adults are of unknown age. However, marmots captured in June can be classified as 2 yr old or as 3 yr old or older by weight. Any animal with a body weight greater than that of a 2-yr-old was classified as a 3-yr-old. Because most adult colonial females were of known age, any errors in this method are likely minimal. More errors will result from applying this criterion to males, but no method is available for aging live marmots 3 yr old or older. Estimated age distributions were calculated for colonial and satellite males and females (Table 1). The numbers of males and females in the various age categories are remarkably similar, when one considers the potential error in estimating ages of animals 3 yr old or older.

The recapture data may be used to calculate the mean length of residency of colonial and satellite marmots (Table 2). Colonial males and females were, with one exception, longer resident than their satellite counterparts. Satellite yearlings males were longer resident than colonial yearling males. One satellite yearling lived for at least 8 yr, but no male

TABLE 2. Comparisons of mean length of residency between colonial and satellite yellow-bellied marmots

Age group and sex at first capture	N	Length of residency (years)	
		Mean	SE
Colonial			
Young males	116	1.017	0.057
Yearling males	4	0.500	0.0
Adult males	30	1.500	0.267
All males	150	1.121	0.069
Young females	131	1.445	0.139
Yearling females	6	1.333	0.542
Adult females	18	1.944	0.406
All females	155	1.498	0.129
Satellite			
Young males	24	0.542	0.042
Yearling males	5	1.900	1.400
Adult males	25	0.740	0.119
All males	54	0.745	0.138
Young females	26	0.500	0.0
Yearling females	6	0.500	0.0
Adult females	27	0.870	0.161
All females	59	0.669	0.077

TABLE 3. Comparisons of fecundity between colonial and satellite female yellow-bellied marmots. An adult female-year is one adult female in 1 yr

Females	Number of litters	Range	Number of young per litter $\bar{x}$	$\bar{x}$ SE	Number of young per adult female-year $\bar{x}$	$\bar{x}$ SE
Colonial	65	1–8	4.15	0.19	1.99	0.32
Satellites	13	1–8	4.46	0.39	1.14	0.50

first trapped as a colonial yearling was ever re-trapped as an adult. However, had this one long-lived satellite male not been discovered, the mean length of residency of the two groups of yearling males would have been identical.

Colonial males were, for all age groups, resident for shorter periods than colonial females. Satellite adult females were longer resident than satellite adult males. Satellite young males were longer resident than satellite young females. This difference occurred because one young male was recaptured as a yearling (Table 1); otherwise mean length of residency of satellite young males and females would be identical. The longer residency of satellite yearling males than of satellite yearling females was derived from the one yearling male recaptured 7 yr later; otherwise, there would be no difference between sexes among satellite yearlings. In short, the length of residency of marmots is enhanced in colonies as compared to satellites.

Sex ratios and litter sizes

Of 247 young born in colonies, 116 were males; 27 of the 50 young born to isolated females were males. Neither sex ratio differs significantly from 1:1 ($\chi^2 = 0.9$, $P = 0.3$). Pattie (1967) recorded a 1:1 ratio for young in the Beartooth Mountains of Wyoming. Armitage (1962) reported 1.16 males per female in his counts of young in Yellowstone.

Armitage (1962, 1965) found 3 males in 34 adults at Yellowstone, and Pattie (1967) recorded 6 males in 28 adults. These findings reflected the social structure of this species and suggested differential mortality of males. In the Gothic area we have

recorded 55 males in a total of 126 adults. This ratio of males to females is not significantly different from 1:1 ($\chi^2 = 2.03$, $P = 0.1$). Our findings differ from those previously reported because we trapped extensively for satellites whereas the other studies centered on colonies. Hence, only one of the three adult males trapped at Yellowstone was a wanderer (Armitage 1962). Nee (1969), who also trapped extensively, found an adult sex ratio of 1:1.

In our study area, mean litter size (=number of young appearing aboveground) of colonial females was 4.15 and of satellite females, 4.46 (Table 3). Thirty-one of the 65 colonial litters had 5 or more young. The average size of 19 litters in the Yellowstone area was 5.26 young/litter. Nee (1969) reported 5.23 young/litter for 3 litters. Litter sizes for *M. monax* are somewhat smaller. Grizzell (1955) reported an average litter size of 4.6 young for woodchucks in Maryland. Snyder and Christian (1960) found that adult females of *M. monax* in Pennsylvania produced, on an average, 3.97 young per litter. Litters produced by yearling females were smaller, averaging 3.13 young. The larger litter size of *M. flaviventris* is probably related to the longer prereproductive period in comparison with *M. monax*. We have no record of a yearling female producing a litter, and only 6 of 23 known 2-yr-old females had litters.

Reproduction does not cease with old age. One of four females known to be 6 yr old and one known 7-yr-old female had litters; two of three presumed 6-yr-old and one of two presumed 7-yr-old females had litters.

While litter sizes of satellite and colonial females

TABLE 4. Life table statistics for female colonial *Marmota flaviventris* based on a cohort of 1,000

Age class (years)	l_x	m_x	$l_x m_x$	d_x	q_x	e_x
0–1	1,000	0.000	0.000	531	.531	1.679
1–2	469	0.000	0.000	254	.542	2.013
2–3	215	0.727	0.157	54	.251	2.805
3–4	161	1.185	0.191	40	.248	2.575
4–5	121	1.588	0.192	30	.248	2.260
5–6	91	1.600	0.146	18	.198	1.841
6–7	73	1.000	0.073	24	.329	1.158
7–8	49	1.000	0.049			
			$\Sigma = 0.808$			

were comparable, colonial females produced 1.7 times as many young as did satellite adult females (Table 3). Hence colonial females realize a greater reproductive potential than do satellites (cf. Downhower and Armitage 1971).

From the foregoing data on survival and fecundity of colonial marmots, we constructed a life table using known-age animals only (Table 4). Summarized within the table are the number surviving (l_x), the number of young females/adult female (m_x), the number dying (d_x), the life expectancy for each age group (e_x), and the rate of mortality (q_x) (Deevey 1947). The life table ends at 7 yr because no females known to be 8 yr old have been captured. R_o is 0.808. This value is less than one for the following reasons: the mean number of resident females in recent years has been lower than the mean number of females in the early years (Fig. 1); a few litters in 1971 and 1972 had males only, probably a rare event, but it reduced the values of m_x; progeny of satellite females may make up all or part of the difference (Svendsen 1973), and some of the surviving 7-yr-old females could produce more young.

Effects of the environment

The properties of the environment significant to ecology are those that influence an animal's chance to survive and reproduce (Andrewartha and Birch 1954). In our study area losses of animals are related to mortality and dispersal. The following five component-categories of the environment (Maelzer 1965) affect reproduction and the losses of marmots.

Mechanical stressors.—One young was found dead from a presumed fall over a cliff. Eight adults, one yearling, and five young died as a result of accidents during trapping. These trap-deaths are the single largest cause of mortality known to us.

Predators, parasites and pathogens.—Although marmots harbor fleas and various internal parasites, we have no evidence that parasites or pathogens cause mortality. Sick animals are never found and all animals make weight gain.

We have recorded no losses of colonial marmots to predation. Badgers (*Taxidea taxa*), marten (*Martes americana*), and long-tailed weasels (*Mustela frenata*) have been observed and/or trapped at various localities, but known losses of marmots have not accompanied their presence. In fact, on several occasions we observed marmots chase weasels and marten. However, it seems likely that marten kill some of the young before they are 3 to 4 wk of age, i.e., before they emerge from their burrows to begin aboveground activity (Powell 1972). This presumed loss may account for 10 litters having only one or two young. Possibly entire litters may have been lost to predation, but we have no direct evidence

bearing on this problem. Coyotes (*Canis latrans*) were observed at localities 3, 4, and 5. At colony 3 a coyote walked through the colony in full view of half a dozen marmots. He was "whistled" at as he moved (acoustically mobbed?) through the locality. At locality 4 a coyote "moused" in the meadow between 0530 and 0600 MDT, in full view of the residents. No alarm calls were sounded, and the coyote captured five mice. A coyote chased a satellite marmot into a burrow one-half mile south of locality 1. Marmot skulls and fragments were collected from an active golden eagle aerie on the face of Gothic mountain. These skulls were primarily yearlings.

In 1967 and 1968, eight marked individuals were shot. This loss is the single largest loss due to predation known to us.

Resources.—The two major resources of marmots are food and burrows. Populations of herbivores probably are not limited by food (Hairston et al. 1960, Ehrlich and Birch 1967) and this apparently is true of marmot populations. At localities 1 and 4, marmots utilize only about 2%–3% of the energy available to them (Kilgore 1972). A similar situation apparently prevails at locality 5 (Svendsen 1973). Food resources of satellites do not differ from those of colonial animals (Svendsen 1973); thus satellites probably are not limited by food.

There are always burrows in excess at localities harboring colonies. Some burrows are not used every year; other burrows may house several adults. On the other hand, sites harboring satellites have significantly fewer burrows (Svendsen 1973), and the lack of burrows may limit the population there. We have not been able to evaluate the quality of burrows and cannot eliminate burrow quality as a possible factor limiting marmot populations. However, the pattern of use of burrows seems more related to social behavior than to presumed differences in burrow quality (Armitage 1962, 1965, 1973). It is therefore unlikely that burrow quality affects the numbers of colonial marmots.

Weather.—Seven young died probably from exposure during summer storms. No losses of yearlings or adults to exposure are known to us.

Mortality during hibernation is unknown quantitatively, but likely is significant. Virtually all losses of adults occurred between our departure in late August or September and our return in late May or early June. This does not prove hibernation mortality, but is consistent with such a hypothesis. Several times marmots, in cleaning out burrows, expelled skulls of adults that probably died in the burrows during hibernation. One adult male, a resident at locality 1 for 5 yr, lost about 1 kg of body weight just prior to hibernation and did not reappear the next year.

TABLE 5. Kendall rank correlation coefficients (γ) and partial rank correlation coefficients (underlined) of weather factors with percentage survival and reproduction ranked from high values to low values. Number of days of snow cover was ranked from low to high; last accumulated snow was ranked from early dates to late dates. First snowfall and first accumulated snow were ranked from late dates to early dates. N = 10. Although there is no test of significance for the partial correlation coefficients, those values of probable significance ($P \leqslant 0.05$) are marked with an asterisk

Weather factors	Young		Female yearlings		Adults		Females with litters	
Number of days of snow cover	0.157	−0.273	−0.067	−0.166	0.182	0.086	0.161	0.727*
Last accumulated snow	0.511*	0.545*	0.111	0.234	0.360	0.343	0.068	−0.046
First snowfall	0.067	0.272	0.202	0.267	0.227	0.266	0.391	0.595*
First accumulated snow	0.023	0.226	−0.068	−0.071	0.0	0.071	0.302	0.438

Weather factors	Mean number of young per female		Total number of litters		Mean number of litters per female	
Number of days of snow cover	0.382	0.348	0.318	0.081	0.318	0.277
Last accumulated snow	0.289	0.021	0.405	0.384	0.315	0.116
First snowfall	0.494*	0.479*	0.136	0.107	0.068	0.025
First accumulated snow	0.205	0.111	0.046	−0.022	0.092	0.067

The number of young recaptured as yearlings varies considerably from year to year. Only 7% of the marked young in 1969 were recaptured as yearlings in 1970; 77% of the young of 1970 were recaptured as yearlings in 1971. The average for all years (1963–74) was 49%. In 1969, all the young of locality 1 were observed until they hibernated. There was no evidence of dispersal or predation; however, only one of five was recaptured as a yearling in 1970. In 1970, again at locality 1, the three young were observed until they hibernated and all were recaptured as yearlings in 1971. At locality 4, in 1969, four young were observed until hibernation; none were recaptured in 1970. The 5-yr-old female and resident male also failed to return. There is also considerable variation among localities in some years in the number of young recaptured as yearlings. In 1967, 75% of the young of the previous year at localities 1 and 2 were recaptured, but only 37% were recaptured at localities 4, 5, and 7.

Possibly the loss of young is due to early dispersal by yearlings shortly after emergence from hibernation. However, in 1969 and 1972, we began our work early when marmots were emerging from hibernation, and the percentage of young of the previous year recaptured as yearlings was 53 and 55 respectively, not much different from the overall average of 49%. Undoubtedly we do miss some yearlings because of early dispersal, but early dispersal seems inadequate to account for the observed difference in disappearance rates. Additionally, extensive observations in May 1972 revealed that marmots do not disperse across the snow, but that their movements are gradually extended as the snow melts. Even male yearlings remained in their home localities and were active in close proximity to adult males

until snow melt permitted dispersion within the locality and eventual dispersal from it.

Mortality during hibernation is suggested by two additional lines of evidence. Fifty-eight percent of the young that first appeared aboveground prior to July 15 were recaptured as yearlings; only 19% of the young appearing aboveground after July 15 were recaptured as yearlings. Young appearing after mid-July weigh about 1.16 kg by mid-September whereas young appearing before mid-July weigh 1.4 to 1.8 kg. Young that hibernate in poor condition (= less weight) have less chance to survive a hibernation of 7–8 mo.

Survival doubtlessly is related to winter conditions. The more severe the winter, the greater is the probability of mortality. Severity of winter for hibernation may depend on its length or on the timing of its onset and termination. Onset and termination of winter were estimated from dates of first snowfall and first accumulated snow and of last accumulated snow. Length of winter was estimated from the number of days of snow cover.

Kendall rank correlation and partial rank correlation cofficients (Siegel 1956:213) were computed between the weather data and percentage survival of young, female yearlings, and adults (Table 5). Data from all colonies were lumped. Analysis of data from localities with populations large enough for analysis revealed no significant differences from those reported in Table 5. Generally, γ was low, but an γ of 0.315 or larger ($P \leqslant 0.15$) is considered of possible biological significance for the following reasons. The probability of obtaining such a high γ is low unless there was an overriding weather effect. The weather conditions in our study area are probably related in some pattern to the weather data from Crested Butte, but we do not know the nature of

TABLE 6. Spearman rank correlation coefficients (r_s) for demographic factors. All factors were ranked from high values to low values. Female yearlings were considered resident if they remained in a colony until the time observations ceased (usually August 15). $n = 11$, except $n = 10$ for factors that include yearlings. * indicates $P \leqslant 0.05$

Number and status of females	Number of young per female	Number of litters per female	Number of female yearlings	Percentage of female yearlings becoming resident
Number of female residents	−0.181	−0.193	−0.248	−0.467
Number of female recruits	−0.370	−0.258	−0.109	−0.530
Percentage of female yearlings becoming resident	0.230	0.612*	−0.100	

this pattern. Weather conditions are not the same at all our study areas. Snow cover may be absent at localities 1 and 2 in May when 60 cm or more may blanket localities 5, 6, and 7. Also, any general relationship between weather and survival would have to override the effects of unusual events (Ehrlich et al. 1972) that might not be reflected in the available weather data.

The onset of winter had little relationship to survival except for females that produced young (Table 5). Higher survival of these females was associated with a later onset of winter. Females with litters begin weight gain much later than do nonreproducing animals, and some females may not store sufficient fat to survive hibernation in years of early winter. The lack of any other relationship between the onset of winter and survival is not surprising because hibernation in ground squirrels occurs as a stage in a circannual rhythm (Davis 1967, Pengelley 1968, Armitage and Shulenberger 1972). The survival of young and adults was better the earlier winter terminated (last accumulated snow). Length of winter (number of days of snow cover) had little relationship to survival except for females that had litters.

A Spearman rank correlation analysis (Siegel 1956:202) indicates that weather affected the number of transients trapped at our localities. There were more transients when there was an early snowfall ($r_s = 0.682$, $P < 0.05$) or an early accumulation of snow ($r_s = 0.676$, $P < 0.05$) the previous autumn. Possibly the early onset of winter induces movement as animals seek hibernacula. These animals may continue wandering the following summer, as our studies in early spring have shown that burrows used as hibernacula are frequently not used as summer burrows (the converse is also true). Because early snowfall is more severe at high elevations, many of the transients may be marmots forced down from higher elevations.

Weather also affected reproduction (Table 5). More young per female and more litters were produced when winters were short, began late, and terminated early. Although patterns of statistical sig-

nificance differ, the general trends are consistent with those we reported earlier (Downhower and Armitage 1971). Because food is available as the snow melts in the spring (Svendsen 1973), this relationship between weather and reproduction probably is expressed through the general physiological condition of adult females emerging from hibernation. However, we cannot exclude an indirect action of weather on food, which in turn affects the condition of adult females, or a combination of weather effects on food and on hibernation condition.

Members of the same species.—As described earlier in this paper (e.g., Table 3) and elsewhere (Downhower and Armitage 1971), the social system of marmots enhances reproduction. Furthermore, because monogamous females are more fit than polygamous females, we predicted that conflict among adult females and/or between female adults and female yearlings would cause mortality, dispersal, or reduced reproduction. Presumably, social mechanisms affecting survival and/or reproduction are density-dependent (Christian and Davis 1964). If density-dependent mechanisms operate, they should be expressed demographically.

Relationships among several sets of demographic data were tested by Spearman's rank correlation (Table 6). Data from all colonies were combined to obtain mean values for each year. These analyses also were performed on data from localities 1 and 5, the two localities whose populations were large enough and fluctuated sufficiently to permit such analyses. Trends were no different than those reported here for combined data. Although the number of litters per female and the number of young per female were negatively related to the number of female residents, all r_s were statistically insignificant. Higher values of r_s were obtained when reproduction was related to the number of adult female recruits, but all r_s again were statistically insignificant. These results were consistent with reproductive patterns at the individual localities as determined by inspection of Fig. 1 and as revealed by analysis of data from localities 1 and 5.

When the data from all colonies were lumped, recruitment of new adult females into the colonies was inversely related to the number of returning (=an animal who was present in the preceding year) females ($r_s = -0.76$, P 0.01). Although the number of new females was inversely related to the number of returning females at individual localities, the correlation was not statistically significant (locality 1, $r_s = -0.375$; locality 5, $r_s = -0.481$; $P = 0.1$). About 40% of the recruits were born outside the colony in which they became resident. These females are transient and probably wander long distances (Shirer and Downhower 1968, Armitage 1974). Thus our entire study area is effectively a single population for these wanderers that move into a subpopulation (= colony) whenever and wherever they can. Because some localities, e.g., 4 and 7, normally have only one or two females, they are too small to test for density effects on recruitment. However, they were populated by females born elsewhere and these effects of recruitment are expressed in the r_s obtained for all colonies.

Recruitment of female yearlings was lower when the number of female residents was high or when the number of adult female recruits was high (Table 6). However, r_s was not statistically significant. The recruitment of female yearlings was positively correlated with the number of litters per female. This result is contrary to that postulated in our model of polygamous mating in marmots (Downhower and Armitage 1971). However, the contradiction may be more apparent than real. The number of litters per female tends to be high when the number of resident females is low and when the recruitment of female adults is low. Recruitment of female yearlings is high when the number of resident females is low. Thus, apparently a female yearling has a better chance of becoming a resident when the number of female adults is low, even though those females are pregnant. Because the size of the home range of an adult female is independent of the density of adult females, a small number of resident females usually occupies only a portion of the available area of a locality. Thus female yearlings may remain and develop home ranges that overlap only in part with the home ranges of the adult females (Armitage 1973). It must be remembered that we are considering overall trends in our study area and the details of events in the various localities are much more complex.

Virtually all male yearlings disperse, primarily in order to avoid the territorial adult male. However, the movements of male yearlings may be encouraged by agonistic behavior on the part of not only the adult male, but also adult females (Armitage 1974).

Half of the female yearlings dispersed during their second summer of life. This dispersal is related to agonistic behavior. Half or more of the agonistic behavior may be directed by adults to yearlings even though yearlings are less than one-fourth of the population (Armitage 1962, 1973).

We recorded several instances of dispersal by adult females. One female moved from locality 2 to locality 1 and expelled four females (Armitage 1973). Three females that appeared at locality 5 in 1965 dispersed later in the summer. Another that appeared in 1968 remained only a few days and went to locality 6, where she was still resident in 1972. Three females introduced into locality 7 in 1969 were excluded by the two female adult residents. At localities 5 and 7, either the resident females were agonistic toward the new females or the new females avoided the residents. The ultimate pattern of avoidance is dispersal.

In summary, mortality during hibernation is variable, but probably of major importance. We recorded no obvious losses of adults or yearlings to predation, but some of the small litters probably result from predation on young before they appear aboveground. The brunt of the predatory loss must be borne by satellites and dispersers. For satellite marmots, no young were recorded as reaching maturity and all satellite adults were recruited from other places (Fig. 2). Virtually all adult colonial males and 41% (averaged over all age groups) of all adult colonial females were recruited from outside their localities of residence. The major population loss to the colonies was dispersal, primarily by yearlings, but also by a few adults. Dispersal of yearlings from marmot colonies and extensive recruitment of adults from outside the colonies is so striking that it must be viewed as an adaptive feature of the population biology of this species.

DISCUSSION

Yellow-bellied marmots in the Gothic area are exposed to a short growing season, a large portion of which is past when young first appear aboveground; gestation and maturation to weaning represent a large part of the growing season, especially in view of the extensive period of hibernation ahead of the young. Not only is the growing season short, it is variable, as evidenced by year-to-year differences in the onset, length, and termination of winter.

The dispersal of yearlings from marmot colonies is related to levels of agonistic behavior (Downhower 1968). Aggressiveness of an adult female, if she is pregnant and produces a litter, peaks at about the time of parturition (Armitage 1965), but may remain high at the time young emerge aboveground (Armitage 1962, Downhower 1968). Yearlings apparently respond to these sources of aggression, and for the most part yearlings that disperse do so prior to the emergence of young. Furthermore, colonial

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TABLE 7.   Fecundity of adult females at localities 1 and 5 as related to replacement of resident males. Turnover means that the resident male was different than the male of the previous year. Return means the resident male was the same male of the previous year

Locality	Number of young		Number of females		Number of young per female	
	Range	Mean	Range	Mean	Range	Mean
Turnover						
Locality 1	0–7	2.75	3–6	3.75	0–2.33	0.92
Locality 5	3–15	7.2	4–9	6.25	0.33–2.14	1.08
Mean		4.97		5.00		1.00
Return						
Locality 1	0–12	5.4	1–4	2.0	0–6	2.7
Locality 5	1–21	9.6	3–6	4.6	1.25–3.5	2.52
Mean		7.5		3.3		2.61

yearlings might be expected to survive to sexual ma-
turity (Table 4), unless they dispersed as young, as
satellites do. Dispersal, then, occurs when the dis-
persers (yearlings) are most "fit." Dispersal as an
adult female would be disadvantageous not because
longevity would be reduced, but because the prob-
ability of such a female rearing young would be re-
duced (Table 3 and 4). The delay of dispersal to the
yearling age is possible because older animals are
socially tolerant of the young.

Although food appears not to limit marmot pop-
ulations, it could be critical in the early part of the
growing season. If food limited reproduction, either
by fewer females' becoming pregnant or by fewer
females' being able to carry a litter to term, in those
years of reduced production of young there should
be an increased recruitment of yearlings. Such re-
cruitment would occur because of reduced aggres-
sion by nonpregnant females. This model implies
that the number of residents is carefully tuned to
resources. When young are produced, yearlings are
expendable because resources will be utilized by the
young. When young are not produced, resources are
more fully used by recruiting yearlings. These re-
cruits would thereby have an increased probability
of living to maturity and reproducing (Tables 2 and
4).

In this model the number of yearlings should be
inversely related to the number of young. For lo-
calities 1 and 5, the number of young was plotted
against the total number of yearlings, against the
number of resident yearlings, and against the num-
ber of resident female adults and yearlings. These
relationships were tested by Olmstead and Tukey's
corner test for association (Sokal and Rohlf 1969:
538). Although the number of young tended to be
inversely related to the total number of yearlings and
to the number of resident yearlings at locality 5,
neither relationship was significant ($P > 0.1$). At
locality 1, few if any relationships were evident and
all were insignificant ($P > 0.1$). These results are
consistent with rank correlation analysis of yearling

recruitment (Table 6) in which yearling recruitment
seemed more nearly related to the number of adult
females than to the number of young per female.
Thus the model of yearling recruitment based on re-
source utilization is not supported.

The postulated relationship between the number
of young and the number of yearlings is influenced
by the behavior of the male. In those years in which
a new male replaced the male of the previous year
(= male turnover), the production of young was
reduced (Table 7). The extreme case occurred at
locality 1 in 1964, when two new males appeared
and no young emerged. Breeding failed at locality
4 in 1964, when there was a turnover in males. Many
satellite females are not associated with males. One
such female produced young her 3rd yr (4 yr old)
after a male joined her in midsummer of the previ-
ous year.

The timing of male turnover is obviously of critical
importance. We usually do not know exactly when
such turnover occurs, but at locality 5 in 1970 the
second male appeared in mid-July. At locality 1, a
new male appeared in mid-September of 1970 and
was resident the next spring, but he had little if any
contact with the resident females until spring. The
presence of a strange male in a harem is a period
of social stress (Armitage 1974) and this stress may
reduce reproduction because either fewer females be-
come inseminated or some females resorb or abort
their embryos (Parkes and Bruce 1961). The mean
length of residency of territorial males with a harem
(which excludes transients) is 2.4 yr. Thus the so-
cial system characterized by longer tenure of resi-
dent males relative to other colonial males increases
social stability and production of young.

The plot of number of young against the numbers
of resident female adults and yearlings was scat-
tered, because of a shift toward a positive relation-
ship from the negative relationship evident in the
other plots. Therefore, the number of young was
plotted against the number of resident female adults
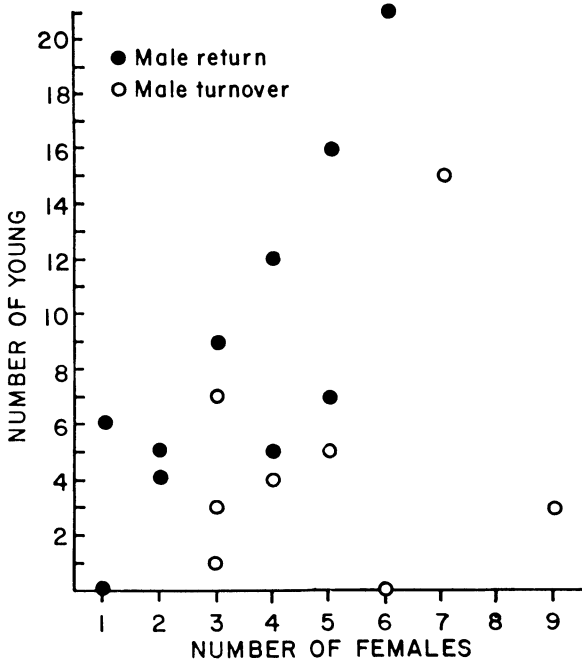and the relationship tested by Olmstead and Tukey's

FIG. 3. Production of young as a function of the number of adult females at localities 1 and 5. Male return = those years in which the resident male was resident the previous year; male turnover = those years in which the resident male was resident for the first time.
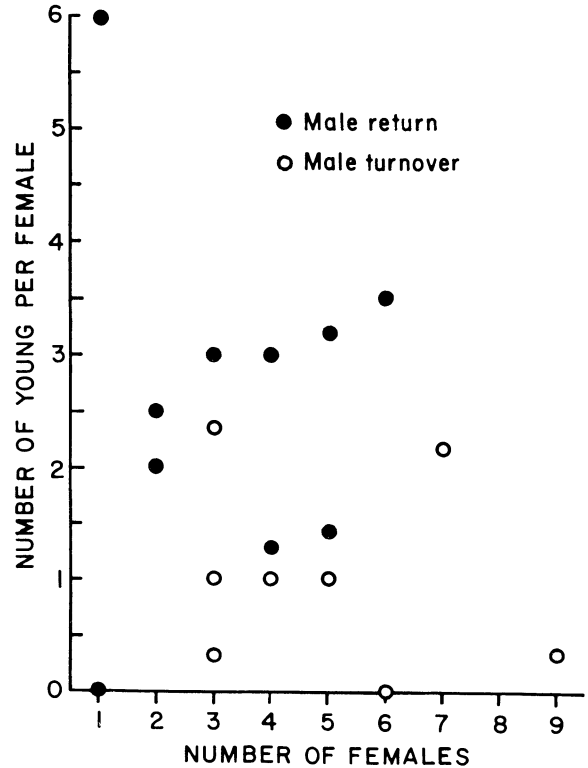

FIG. 4. The number of young per adult female as a function of the number of adult females at localities 1 and 5.

corner test for association (Fig. 3). The relationship was positive and significant ($P = 0.02$) for those years in which the resident male was present the year before, but there was no relationship for those years in which there was a turnover in the resident males.

Those years marked by male turnover also had a higher mean number of females (Table 7). Possibly the "male effect" was in reality an effect of female density. Any effect of female density should result in fewer young per female at high densities. Such an effect is not evident (Fig. 4). Thus the social system seems to maximize reproduction of the female population when the male, either by reducing conflict among females or by reducing conflict between strange males and the females, or both, provides elements of social stability.

Obviously there are upper limits to the population. The limits apparently are not determined proximally by resources (food quantity and burrow sites) or by predation. Although winter mortality may be significant, during most years at most localities there are more animals than will remain as residents.

The proximal factor most likely to control the relatively stable colonial populations is agonistic behavior, as suggested earlier from behavioral studies (Armitage 1962, 1973). Aggressiveness is directed primarily toward yearlings (Armitage 1962, 1973, Downhower 1968), but also toward adults, and some

adults may emigrate. Except as described previously, the fate of emigrants is unknown. Agonistic behavior, as in other ground squirrels (Bronson 1964, Yeaton 1972), is not finely tuned to numbers of residents (Armitage 1962, 1973, 1974), as evidenced by the lack of a clear relationship between the number of yearlings emigrating and the number of young added to the colony or the number of adults present (Fig. 1). The relationship is much more complex and is related to the behavioral characteristics of the resident animals, which show a wide range of sociability and aggressiveness (Svendsen and Armitage 1973).

Population control by emigration of surplus individuals occurs widely in rodents (Archer 1970, Krebs et al. 1973). Loss of numbers by emigration also occurs in the ground squirrels Citellus townsendii (Alcorn 1940), C. tridecemlineatus (Rongstad 1965, McCarley 1966), C. richardsonii (Yeaton 1972), C. parryi (Mayer 1953), C. beecheyi (Evans and Holdenreid 1943, Fitch 1948), C. armatus (Balph and Stokes 1963), and C. undulatus (Carl 1971); in the woodchuck M. monax (deVos and Gillespie 1960, Anthony 1962, Bronson 1964), and in the prairie dogs Cynomys leucurus and Cynomys ludovicianus (Tileston and Lechleitner 1966). Males,

especially juveniles, have a greater tendency to disperse than do females (Evans and Holdenreid 1943, Fitch 1948, Bronson 1964, McCarley 1966, Yeaton 1972). This pattern occurs in the yellow-bellied marmot except that dispersal occurs primarily in the 2nd yr of life.

Arctic ground squirrels form refugee populations (Carl 1971) similar to our satellite populations in that they are established by immigration, are highly unstable, and occur in habitats significantly different from those occupied by colonial populations. Carl found no evidence that reproduction occurred in the refugee population, whereas satellite marmots do reproduce, although at a rate much lower than that of the colonial animals (Table 3).

In summary we view the social structure of yellow-bellied marmots as being adaptive to a rigorous environment with a relatively short growing season. The social tolerance of young into their second summer of life clearly is related to the short growing season and enables most of the maturation to occur in an environment where food is relatively abundant, where shelter (i.e., burrows) is abundant, and where predation is at least minimal.

The adaptive advantages of the social organization are several. Colonial females on the average produce more young than do satellite females. Young of colonial females are longer lived than those of satellite females, and dispersal of nonreproductive individuals occurs later in life when expectation of further life is higher. In colonies dispersal involves yearlings primarily, whereas non-colonial marmots disperse when they are young. A yearling is more apt to reach sexual maturity than a juvenile, and so dispersing marmots from colonies are more "fit" than their satellite counterparts. Finally, the increased fecundity and longevity evidenced among colonial females and their offspring is related to the continued presence of the adult male who prevents disruption of the colony by wandering males.

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