BEHAVIORAL AND ENVIRONMENTAL FACTORS IN THE
SPATIAL DISTRIBUTION AND POPULATION DYNAMICS
OF A YELLOW-BELLIED MARMOT POPULATION

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Abstract. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot (Marmota flaviventris) population were studied in 1971 and 1972 in Gunnison Co., Colorado. Yellow-bellied marmots are generally considered to be colonial; however, this is not their only option, depending upon the marmots' behavioral profile and the size and composition of the habitat. Of the adult-yearling group 75% lived as members of colonies, 16% lived at satellite sites, and 8% were transients. Satellite sites differed from colonies mainly in size and topographic diversity; they may be considered mini-habitats, with the most limited resource being burrow sites.

Marmots can be classified, by means of mirror-image stimulation (MIS), as aggressive, social, and avoider. Aggressive females tended to occupy small harems at large sites, or to live as solitary individuals regardless of the size of the site. Social females occurred primarily at large sites, in harems. Avoider females lived in peripheral burrows at colonies, or in satellite sites. All behavioral types reproduced successfully, but reproductive fitness was correlated with social structure. Aggressive females were most fit in small harems or at satellite sites, whereas social females were most fit in large social groups. Avoiders were least fit in all social situations. Data presently available fails to show that the behavioral profile of the female is reflected in the social tendencies of her young.

In general, social behavior is a major factor affecting the distribution and dynamics of populations of yellow-bellied marmots, but dispersion is also related to the distribution of suitable habitat.

Key words: Behavior; behavioral profiles; ecology; environmental factors; ethology; marmot; mirror-image stimulation; population dynamics; reproduction; resource allocation; spatial distribution; territories.

INTRODUCTION

The observation that domestic chickens recognize one another as individuals (Schjelderup-Ebbe 1922, 1935, Masure and Allee 1934) and that a "peck order" dominance relationship exists within the flock, marks the beginning of modern studies of vertebrate social behavior. Dominance hierarchies, territoriality, sex pairing, and leadership are basic processes in the organization of animal groups (Allee 1952). These social structures tend to control aggressive and competitive behaviors which are selected for in individuals but are disruptive to social life and the advantages the group offers to the individual for survival (Etkin 1964, Schneirla 1952); aggressiveness may isolate individuals and disperse the group (Ito 1970).

That aggression could serve to limit breeding populations through dominance and spacing behavior was suggested by several authors (Burt 1940, Lorenz 1952, Errington 1962, Christian and Davis 1964, Archer 1970). Lack (1954, 1966) argued that territorial behavior does not limit breeding populations, and Hinde (1956) could find no unequivocal field evidence to support limitation in numbers through territorial behavior in birds, although he thought the evidence strongly suggested this. Wynne-Edwards (1962) argued that the primary function of social behavior was to maintain the population beneath the carrying capacity of the environment, and numerous other authors have suggested the importance of behavioral interactions in regulation of small-mammal populations (Chitty 1952, Southwick 1955, Bronson 1964, Krebs 1970, Downhower and Armbrtage 1971, Meyers and Krebs 1971). Evidence for "increase" and "decrease" genotypes corresponding to different phases of population density in Microtus were presented by Gaines and Krebs (1971), and corresponding differences in behavior were also noted (Krebs 1970).

The types of behavior involved in the establishment of social systems or dominance are affected also by the spatial distribution of food resources (Moss 1969) and the physical structure of the environment (Jenkins 1961, Watson 1964, Terman 1963, Buechner 1961). These features have also

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been shown to have a marked effect on reproduction in some species of rodents (Calhoun 1963, Southwick 1955).

The yellow-bellied marmot, *Marmota flaviventris*, is a colonial mammal whose social behavior is an integral part of its biology (Armitage 1962). Marmots are diurnal and occupy a variety of environments ranging from low-elevation meadows to alpine situations (Hall and Kelson 1959, Pattie 1967). They are active for about 5 mo of each year, but are classical hibernators during the remainder (Kilgore 1972). Young are born in early summer (Nee 1969, Armitage 1962) and many disperse during their 2nd yr (Downhower 1968, Shirer and Downhower 1968). Marmots may live as residents of colonies, as transients, or as isolates (Downhower and Armitage 1971). The category “satellite” will be used in this study to include all isolates. Individual marmots are characterized by unique behavioral profiles that affect their relationship with other marmots (Svendsen and Armitage 1973).

The role of the noncolonial individual in the population biology of the marmot is not well understood. Many dispersing 2nd-yr animals eventually establish themselves in a colony. Others remain apart from social groups. It is not known whether these individuals are outcasts, either physically inferior or behaviorally subordinate, and represent a nonreproductive surplus not contributing to the gene pool, or whether they are as reproductively fit as those animals in large social units but are behaviorally suited to live in small groups or occupy sites whose physical limitations prevent inhabitation by large social groups.

The present study tested three hypotheses of the behavioral ecology of the yellow-bellied marmot: (1) there are no differences between habitats at colonies and those at satellite sites occupied by non-colonial individuals; (2) there are no behavioral differences between animals living in colonies and those found in satellite situations; and (3) there are no reproductive differences between residents of colonies and of satellite sites.

**Methods**

The field work was conducted during the summers of 1971 and 1972 on a population of marmots which occupies the East River Valley in the vicinity of the Rocky Mountain Biological Laboratory (RMBL), Gunnison Co., Colorado (Fig. 1). A detailed description of topography, geology, physiognomy and vegetational zones are given elsewhere (Langenheim 1955, 1956, Armitage and Downhower, pers. comm.).

The term “colony” is applied to a social group of marmots in a circumscribed habitat. The colony may consist of one or more harem; a harem is one or more adult females plus individuals of non-reproducing age associated with a territorial male (Armitage 1962, 1965, Downhower and Armitage 1971). Marmots that live in a colony throughout a season are classified as “residents.” The term “transients” is applied to wanderers of any age not remaining resident for a season, and “isolate” to animals living alone (Downhower and Armitage 1971). Because I found “isolate” too restrictive and difficult, I will use “satellite” instead; a satellite site is defined as one where animals live as isolated pairs at established homesites, as well as those where single marmots live. Satellite sites typically are inhabited by adult immigrants, and yearlings are found there infrequently. At colony sites a great percentage of the recruitment comes from within, and yearlings are common (Armitage, in press). The satellite category assumes that only minimal interaction with other marmots occurs, such as for mating. The social status of an individual marmot may change with time, so an animal living as a colony resident one year may be in one of the other categories the next.

Localities containing seven colonies and seven satellites were chosen for habitat comparisons. The criterion for colony selection was that a harem of more than one female inhabited the site for a majority of the years of previous study; this was neces-
sary because harems may be reduced to a single female under certain conditions. The satellite sites were those that had a history of occupancy by a single animal or by a pair of marmots, or were occupied intermittently. Principal locations are generally as described by Shirer and Downhower (1968), except that their locality 6 is considered to be a satellite site in this study and is given the letter (1). Localities of colonies are designated by numbers, satellite sites by letters. Locality 1 is a bluff overlooking the river in the alluvial grassland south of RMBL (Fig. 1); satellite sites a, b, c, d, and e are located nearby in similar habitat. Locality 4 and satellite g are situated in small meadows, on relatively flat terrain. The remaining sites are talus or rock outcrops on the lateral slopes of the valley, surrounded by meadow and bordered by spruce and aspen.

Animals were trapped at regular intervals throughout the summer; techniques of trapping, handling, and marking are described elsewhere (Armitage 1962, in press, Downhower and Armitage 1971). Each marmot was assigned to an age category—young, yearling, or adult—determined by live weights (Armitage, Downhower and Svendsen, unpubl. data) if the history of the animal was not known. In addition to numbered ear tags and Nyanzol fur dye to mark animals, we used different colored fluorescent streamers to identify marmots during field observations. Vinyl plastic flagging, 1/32-in wide (Forestry Suppliers, Inc., Jackson, Miss.) served as streamer material. A 13-in piece was folded and attached to a No. 1 hog ring with a falconer’s jess knot cemented with Epoxy. The streamer was attached to the loose skin at the back of the neck with the hog ring. The rings remained intact indefinitely and no skin reaction was noted.

Information on the composition of the vegetation at sites inhabited by marmots was obtained from data on the numbers, linear extent, and frequency of occurrence of individuals of different species intercepted by a series of 60-m line transects through the stand. Relative density, dominance or cover (as percent ground cover), total coverage, relative dominance, frequency, relative frequency, and importance value were calculated (Cox 1967).

Behavior data were collected by two different methods. General relationships among animals within a social group and between sites were ascertained through field observations. Individual behavioral differences were determined experimentally by means of mirror-image stimulation (MIS). The experimental procedure, data collection techniques, behavioral categories, and multivariate analysis of the data are the same as described by Svendsen and Armitage (1973).

Results

Habitat relationships

All resident marmots trapped during the summers of 1971 and 1972 occupied open areas relatively free of shrubs and trees (Fig. 1). Vegetation at sites in grassland habitat is characteristic of the Festuca thurberi community (Langenheim 1955), with several species of Festuca, Bromus, and Poa the dominant grasses. Some of the dominant forbs associated with this community include Viguiera multiflora, Senecio crassulus, Erigeron speciosus, Taraxacum officinale, Artemisia tridentata, Potentilla gracilis, P. fruticosa, Linum lewisii, Vicia americana and Lomatium simplex. On the driest exposures Rosa woodsii, Berberis repens and Eriogonum asperum are common.

The remaining occupied sites are found on slopes where showy perennial forbs are abundant. These include Epilobium angustifolium, Aquilegia caerulea, Thalictrum fendleri, Delphinium barbeyi, Mertensia ciliata, Phacelia heterophylla, Heracleum lanatum, and Veratrum californicum. Various species of Bromus and Poa are also well represented. In general, satellite sites are similar in species composition, density, and percent ground cover to sites occupied by colonies in the same area (Svendsen 1973). The understory vegetation of the forested areas is highly variable. Vegetation beneath aspen is lush, with 97% ground cover. The vegetation includes many grasses and herbs and is similar to that found in open meadow. In contrast, the species composition beneath the canopy of spruce is impoverished, consisting of a shrub layer and a few herbs; ground cover is less than 15%.

Rock outcrops and boulders are common to both open and forested areas, but those in the forest receive little use. Marmots use rocks to burrow beneath, for lookout, and for sunning. However not all talus slopes and rocks located in openings with herbaceous vegetation harbor marmots; those that do not are composed of flat (5–10 cm thick), sedimentary rocks averaging less than 40 cm in diameter. These rocks are too small to burrow beneath and too deep and tightly packed to enable marmots to get to the underlying soil, although rocks of similar size mixed into the soil seem to be used for burrow support. Some open meadow with an abundance of large boulders support no resident marmots. These rocks were cone-shaped with only their peaks exposed. The large subsurface rock volume probably prevented marmots from constructing burrows beneath such rocks. At sites where suitable rocks are numerous, marmots have excavated burrows beneath nearly every rock at one time or another during the colonies’ many years of occupancy. For example, the talus slope at colony 5 is estimated to have 78
burrows in various stages of use on an area measuring approximately 0.85 ha.

The open areas occupied by colonies become snow free earlier in the year than does the adjacent coniferous forest areas. Snow pack begins in October and lasts into May. The area around locality 1 was snow free on 10 May 1972, while up valley at 5 and 7, an average of 67 cm of snow remained on the open slopes and 97 cm in the forest. Snow melt averaged 7.57 and 8.93 cm per day at 5 and 7, and 2.7 cm per day under the spruce canopy. Snow-free patches of ground appeared on the open slopes almost 2 wk before ground showed beneath the spruce. Snowmelt in the aspen was approximately the same as in the open areas, but heavier accumulations of snow were noted.

All hibernation burrows located in the spring of 1972 were situated in places where snow cover persisted and emerging marmots had to burrow up through the snow. One hibernation site was in the path of a snowslide that deposited 1.9 m of snow over the burrow from which the marmot emerged. However, average snow depth was less than 1 m at most burrows at time of emergence.

Patches of bare ground appear early on the steep slopes receiving full exposure to the sun. Green sprouts of plants appear from beneath the snow and are several millimeters high when the snow cover is gone. The average height of Potentilla gracilis, a species used extensively for food by marmots, was 33 mm on 10 May at locality 1. The average height of all vegetation appearing along a receding snow bank at locality 7 was 27 mm. Several species of grasses, Potentilla acericus, Heracleum lanatum, Thalictrum fendleri, Delphinium barbeii, Mentertia nelsoni, Aquilegia coerulea, Claytonia lanceola, Ranunculus nutans and Erythronium grandiflorum were represented. All but the last are known to be used for food by marmots.

Marmots are inactive during the first few days after emergence from hibernation (Armitage 1965). They stay within a few meters of the burrow entrance and gradually increase the range of their daily travels. Patches of snow-free ground within the boundary of the colony are visited frequently during this time and provide an early food source. Animals at satellite sites were active as early as those in colonies and followed the same pattern of activity.

Marmot burrows are located on well-drained exposures, but low marshy areas, run-off streams, and other sources of water are found within the home range of the animals. Proximity to wet areas provides an additional source of lush vegetation. The soil at marmot sites is very coarse and porous; water from snowmelt and rain sinks into the ground and little surface runoff is evident.

### Table 1. Physical features and number of animals at seven localities containing colonies and seven satellite sites

<table>
<thead>
<tr>
<th></th>
<th>Colony sites (n = 7)</th>
<th>Satellite sites (n = 7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area of opening (ha)</td>
<td>58.0 ± 10.15</td>
<td>6.57 ± 3.55 ***</td>
</tr>
<tr>
<td>Mean distance to trees (m)</td>
<td>95.29 ± 15.56</td>
<td>42.57 ± 12.08 ***</td>
</tr>
<tr>
<td>Degree of slope</td>
<td>33.0 ± 12.15</td>
<td>18.43 ± 11.93 **</td>
</tr>
<tr>
<td>Mean vegetation height (cm)</td>
<td>45.14 ± 21.94</td>
<td>45.43 ± 17.72 ns</td>
</tr>
<tr>
<td>Ground cover (%)</td>
<td>81.86 ± 13.22</td>
<td>77.71 ± 12.16 ns</td>
</tr>
<tr>
<td>Mean resident population</td>
<td>3.16 ± 0.89</td>
<td>1.39 ± 0.50 ***</td>
</tr>
<tr>
<td>Mean resident female population</td>
<td>2.08 ± 0.74</td>
<td>1.03 ± 0.58 ***</td>
</tr>
<tr>
<td>Number of resident burrows</td>
<td>3.0 ± 0.82</td>
<td>1.14 ± 0.38 ***</td>
</tr>
<tr>
<td>Number of used burrows</td>
<td>14.0 ± 6.75</td>
<td>2.29 ± 1.11 ***</td>
</tr>
<tr>
<td>Angle of vision from lookout (°)</td>
<td>352.0 ± 21.48</td>
<td>355.0 ± 55.90 ns</td>
</tr>
<tr>
<td>Angle of vision from burrows (°)</td>
<td>147.0 ± 39.69</td>
<td>262.0 ± 78.11 ***</td>
</tr>
</tbody>
</table>

* t-test, * = 0.05, ** = 0.01, *** = 0.001. Because of the large differences in variances the data were also treated with the Mann-Whitney U-Test and levels of significance were found to be similar.

Satellite sites differed significantly from areas occupied by colonies in size of the opening containing the social group, number of used burrow sites, number of active resident burrows, and degree of the slope where the site is located (Table 1). The area of the opening containing animals is significantly correlated (P < 0.01) with the mean number of resident females (r = .856) and with the total number of resident adults (r = .833).

### Populations

Marmots occupying the study area in 1971 and 1972 had a clumped distribution (CD = 0.5) patterned closely to the mosaic formed by forested and open meadow habitat (Fig. 1). Within suitable habitat, social structures ranging from single individuals to large colonies were found. Marmots of different temperaments characterized the population (discussed later) and no one behavioral type was exclusive to any one environmental or social situation.

An effort was made to trap and identify every animal inhabiting the study area at least once during each summer. During the summer of 1971 59 adult and yearling marmots were trapped or identified, and 52 marmots in 1972. The average adult-yearling population density in the total acreage encompassed by the study area for the two summers was .042/ha. The population increased to 95 and 85 respectively during the late summer when the young appeared aboveground, and average density increased to
.069/ha. Since marmots occupy open and treeless habitats and 68% of the study area (Fig. 1) contains trees and shrubbery vegetation or other unsuitable habitat, the ecological density (number per unit of habitat space, Odum 1971) is 1 adult or yearling per 10 ha of inhabitable space, rising in late summer to approximately 2 marmots per 10 ha.

The adult sex ratio for the 2 yr of the study was 1 δ:1.56Ω, the yearling ratio was 1 δ:1.8Ω, and the combined ratio was 1 δ:1.6Ω. The ratio of adults to yearling to young during the study period was roughly 3:2:3. The spring population in 1972 was 54% of the previous fall population. About 50% of the adult females living in colonies in 1971 were recaptured in 1972, whereas only 2 of 12 satellite females were recaptured.

Seventy-five percent of the adult-yearling group live in colonies. Fourteen adult females were colonial both years. Satellites composed 16% of the 1971-1972 population, and 8% were transients. Ten of the 95 marmots studied in 1971, and 4 of the 85 in 1972 were placed in an "uncertain" category because not enough was known about their habits (Table 2). Of these, the 10 uncertain yearlings were probably transients, and of the 4 adults, 2 lived as a pair and most likely were satellites, while the other 2 appeared to live by themselves. Eighty-eight percent of the yearlings were colonial and none lived as satellites, but yearlings made up about 45% of the transients. All of the adult transients were males.

The satellite group was composed of 8 females and 4 males in 1971, and 3 females and 1 male in 1972. Two of the nine sites were occupied during both years, and only 1 satellite female occupied a site for consecutive years.

### Reproduction

Five of 14 (36%) of the adult colonial females had litters appear above ground in 1971, and 8 of 14 (57%) in 1972 (Table 3). By comparison, 6 of 8 (75%) of the satellite females had litters in 1971 and 2 of 3 (67%) in 1972. The mean litter size appearing aboveground was 2.77 for females living in colonies and 3.63 for satellite females. This compares to aboveground litter size of 4.17 and 4.75 for colonies and satellites respectively 1962-70 (Armitage, pers. comm.). The sex ratio of the young above ground in colonies was very close to 1:1 and a satellite sites 45 δ:55 Ω. The sample size was too small to test significance.

Survival of young during their 1st yr differs considerably between those born to colonies and those born to satellites. Of 20 young born to satellites during 1971, none were recaptured in 1972; in contrast, 7 of 13 born in colonies were accounted for in 1972.

The earliest that young appeared aboveground during this study was 20 June at locality 1. Most litters appeared above ground during the first half of July. Litters were recorded as late as the 1st wk in August. There was no difference in the date of appearance of young above ground between colony and satellite sites. The variance in the date of the appearance of young among females was as great as among sites. Weight gain of 20 young born to colonies averaged 191 ± 137 g per week, and 5 young at satellite sites averaged 152 ± 40 g per week, not a significant difference (U = 98, P > 0.1).

### Field behavior

Information pertaining to the social behavior of animals living at satellite sites is difficult to collect from field observations because interactions with...
other animals are rare. Some nonsocial behavioral differences were observed. As marmots feed they intermittently look up or sit up and scan the surroundings (Alert). Armitage (1962) found that an adult female spent more time in Alert when feeding near the edge of the locality than when feeding near the center. Observations on three colonial adult females and four adult females at satellite sites during the morning active feeding periods over 2 wk in early July (Table 4) showed that the satellite females spent a significantly greater proportion of their feeding time in Alert than did colonial females.

An observer of marmots soon discovers that certain individuals are more conspicuous than others. Some animals seem to seek out exposed sites with a commanding view of the landscape, where they too become visible. These animals are very vocal when disturbed and, rather than dashing to the safety of their burrow, seek a rock or exposed area and sound their alarm. The less conspicuous animals move and feed in heavier vegetation, and when disturbed they rush silently to the burrow. The more conspicuous reappear from the burrow sooner after a disturbance than do the other type. Both types are found in colony and satellite sites but the more secretive type appears to be less so when associated with a colony.

Females 381 and 761 at satellite sites both produced litters above ground in 1971. A male associated with the latter moved off and was relocated when it invaded a nearby cabin. Young of 761 appeared aboveground on 4 July at site d, and of 381 on 19 July at e. On 17 July, 761 left its litter and was not observed in the study area thereafter. Female 381 left its litter on 29 July but was observed about 300 m from the burrow the next day. It returned to the litter on 10 August and was retracted the next day. During the next week it was gone from the burrow site except for one afternoon.

Both females left their litters when the young were about 2 wk aboveground, weighed about 1.2 kg each, and were quite self-sufficient. This phenomenon was not observed with any colonial females. In colonies the young may wander off when they are able to fend for themselves, but the female remains in the colony with the remaining young. At the same time that the two satellite females left their litters, satellite female 870 was not observed at its burrow. Although trapping of young continued at the site, I could not confirm that the female had left. It was retracted at the site the following spring and produced another litter, and was not observed to leave in 1972.

The young at site e evidently left or fell victims to predators before hibernation. The following spring there was evidence that animals had collected grass and worked on the burrow the previous fall but there was no activity at the burrow during the spring. I excavated the burrow system but found no corpse or skeletal material.

**Mirror-image stimulation (MIS)**

A total of 59 adult and yearling marmots representing over 90% of the individuals living in the study area during 1971–72, were exposed to MIS. Eigenvalues above 1.0 were extracted from the 59 × 59 correlation matrix. Factors were reextracted until the communality estimates stabilized and the factor matrix was rotated to simple structure by Kaisers’ Normal Varimax Method (Rummel 1970).

Six factors were extracted from the behavioral data, accounting for 93% of the original variance, 85% of which is explained by the first three factors. Factor I, “approach,” is represented by marmots who spend most of their time in the front half of the arena, sitting or lying near the mirror, oriented toward or parallel to their image. Animals in this group include both aggressive and social animals. Factor II is designated “avoidance” because animals in this group sit or lie at the back of the arena, oriented toward or parallel to their image, and do not approach the mirror or do so hesitantly. Factor

### Table 4. The amount of feeding time (in minutes) spent in alert by female residents of colonies and satellite sites

<table>
<thead>
<tr>
<th>Resident females</th>
<th></th>
<th>Satellite females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total time feeding</td>
<td>Time in alert</td>
<td>Time in alert/10</td>
</tr>
<tr>
<td>755</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>14</td>
<td>8</td>
<td>5.71</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>3.75</td>
</tr>
<tr>
<td>21</td>
<td>7</td>
<td>3.33</td>
</tr>
<tr>
<td>683</td>
<td>8</td>
<td>3.75</td>
</tr>
<tr>
<td>1076</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>9</td>
<td>3</td>
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\[\bar{x} = 2.44\]

\[\bar{x} = 3.80 \text{ ***}\]

\(*) (\tau = P < 0.001).\)
III, called “socialibility,” is an axis containing marmots that engage in overtures of nonaggressiveness such as nose contact, pawing, and muzzling of the image, and in arena activity. A three-dimensional plot of the animals in the space of orthogonal factors I, II, and III gives a biologically interpretable visual representation of the data (Fig. 2).

Ten adults from satellite sites are included in the analysis and are designated by numbered blackened circles; all other animals are designated by open circles. Males 1079 and 1048, and females 9 and 1023 are found in the “avoidance” group. Among the animals arranged along the sociability continuum are five satellite females and one male. Male 603 and female 1029 are located towards the social end of the continuum, whereas females 1063, 111, 870, and 381 are at the nonsocial extreme. The latter four exhibited aggressive behavior toward the image during MIS and directed their attention to the image during the entire 15-min exposure period.

Behavioral profiles of 16 adult colonial females are included in the analysis. In the avoider group are two siblings living at the edge of colony 5, one of which was the only avoider female known to have reproduced. The remaining 14 are in the sociability continuum, equally distributed between sociable and aggressive extremes. None of the colonial males is at the sociable end of the continuum or in the avoider group. The ratio of sociable to aggressive to avoider females is about 3:3:1 in colonies and 1:4:1 at satellite sites.

Twenty-seven young marmots from nine litters were exposed to MIS after they had been above ground for about 1 mo and were quite self-reliant. Six of these animals were also exposed to MIS as yearlings, and year-to-year comparisons were made. Young were classified into the aggressive, sociable, and avoider categories derived from the factor analysis, using step-wise discriminant analysis with the option for classification of new cases. This multivariate technique allowed the classification of new animals on the basis of known groups, and was necessary because certain aspects of juvenile behavior are probably not comparable to behavior of more mature yearlings and adults, although certain sequences or combinations of behaviors may be similar.

The analysis includes 17 females and 10 males (Table 5). Five young (3♀, 2♂) were classified as aggressive, 15 (9♀, 6♂) as sociable, and 7 (5♀, 2♂) as avoider. The sex ratio in each category does not differ significantly from that of the total sample ($\chi^2 = 0.29, P > 0.5$) and the distribution of individuals in each category does not differ significantly from 1:1:1 ($\chi^2 = 6.22, P > 0.1$).

Ten of the young from litters of 3 satellite females (litters 1, 2, and 3, Table 5) were exposed to MIS. One young was classified as aggressive, 6 as sociable, and 3 avoider. Two of the 3 adult females were very aggressive, and of their young (litters 1 and 2) 1 was aggressive, 2 sociable, and 3 avoider. The behavioral profile of the 3rd female was unknown; all 4 young were sociable. Eleven young (litters 4, 5, and 9) were from localities 2 and 5 where colonies resided; of these 3 were aggressive, 6 sociable, and 2 avoider. The profiles of the mothers of three of these litters were known. At locality 5, the male offspring of an avoider female was also an avoider, whereas the 2 male offspring of a very sociable female were 1 aggressive and 1 sociable. The profiles of 8 young at locality 2, 4 from each of 2 litters, were 2 aggressive, 5 sociable, and 1 avoider. Four of these young were littermates of a sociable female and were classified as 1 aggressive, 1 sociable, and 2 avoider.

Table 5. Behavioral categorization of 27 young marmots grouped into categories of aggressive, sociable, and avoider.

<table>
<thead>
<tr>
<th>Litter</th>
<th>Aggressive male</th>
<th>Aggressive female</th>
<th>Sociable male</th>
<th>Sociable female</th>
<th>Avoider male</th>
<th>Avoider female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
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</tr>
<tr>
<td>4</td>
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<td>1</td>
<td>2</td>
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<tr>
<td>6</td>
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<table>
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<th>Litter</th>
<th>Aggressive male</th>
<th>Aggressive female</th>
<th>Sociable male</th>
<th>Sociable female</th>
<th>Avoider male</th>
<th>Avoider female</th>
</tr>
</thead>
<tbody>
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<td>2</td>
<td>3</td>
<td>6</td>
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<td>2</td>
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Table 6. Reproductive characteristics of aggressive, social and avoider type female marmots

<table>
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<th></th>
<th>Aggressive</th>
<th>Sociable</th>
<th>Avoider</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total potential breeding females</td>
<td>14</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Total litters</td>
<td>11</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>Litters/female</td>
<td>0.78</td>
<td>0.46</td>
<td>0.15</td>
</tr>
<tr>
<td>Total young</td>
<td>37</td>
<td>26</td>
<td>3</td>
</tr>
<tr>
<td>Young/litter</td>
<td>3.36</td>
<td>4.33</td>
<td>1.50</td>
</tr>
<tr>
<td>Young/female</td>
<td>2.64</td>
<td>2.00</td>
<td>0.23</td>
</tr>
<tr>
<td>Contribution to every 100 young</td>
<td>56</td>
<td>39</td>
<td>5</td>
</tr>
</tbody>
</table>

The behavioral profiles of 8 young female marmots who were collected from four different sites, housed together, and subsequently introduced as a group into an area from which all other marmots were removed were 2 aggressive, 3 sociable, and 3 avoiders. One aggressive and 1 sociable were lost between the fall of 1971 and spring 1972. The remaining 6 animals were reexposed to MIS as yearlings, and only one was in a different category than it had been classified as a young. This animal tested aggressive as a young but avoider as a yearling, although not strongly so.

Discussion

Yellow-bellied marmots are generally considered to be colonial. However other options are available, depending upon the marmots' behavioral profile, and the size and composition of habitat available to it. Armitage (1962) suggested that not all marmots had the requisite behavioral characteristics to persist in a colony. Downhower (1968) found behavioral differences an important consideration in the dispersal of yearlings. The more aggressive female yearlings either remained at their birth site in the colony or dispersed, whereas subordinates tended to move to the periphery of the colony if sites were available.

In the present study, certain behavioral types tended to be found in certain conditions. Aggressive females usually occupied small harems at large sites, or lived as solitary individuals regardless of the size of the area. Social females occurred primarily at large sites with other marmots, and avoider (subordinate) females occupied peripheral burrows at large sites or lived at satellite sites. Resident, territorial males were aggressive, whereas avoider males were transient. All behavioral types of females reproduced, but reproductive success, measured by the number of offspring produced above ground, was correlated with the female's position in the social structure (Table 6). Peripheral and satellite animals cannot be considered social outcasts and reproductively inactive since females at satellite sites averaged more young per female than did those in colonies (Table 3). On the other hand, loss of subadults during the 1st yr is greatest at satellite sites, though it is not known whether this loss is due to emigration or mortality.

Adult males typically establish a territory at suitable sites (Armitage, in press), and one or more adult females plus subadults and young occupy burrows within this area. The resident male excludes all other adult and yearling males. Excess adult males live as transients or peripherals and occupy sites as soon as they are vacated by the resident male. Satellite males appear to be territorial, even if no female is present. For example, 603, which behaved quite sociably during MIS, was observed chasing and harassing a yearling-sized marmot that had wandered into its domain. The smaller animal was gone the following day.

The colonial adult females subdivide the territory, and the degree of exclusive use of the area by any female depends upon the behavioral profile of the individual (Svensden and Armitage 1973). Since polygamous males exhibit maximum fitness, it has been suggested that they should "solicit" females to join their harem (Downhower and Armitage 1971). On the other hand, since monogamous females have higher fitness than those in harems, they should react aggressively to one another. Partitioning of a male-defended territory by resident females approximates this situation.

Armitage (1965) showed that, in the Yellowstone colony during reproductive behavior, females congregated at the male burrow and subsequently dispersed throughout the site. In this study males were not observed to solicit females to their harem. Males react sociably to a new female, and during the get-acquainted period there is a great deal of social interaction (Armitage, in press), possibly establishing the social bonds for a polygamous existence. However, the new female must be accepted into the already-established harem in order to stay. In other polygamous mammals, harems are most obvious during mating. In elk (Altman 1952) and pinnipeds (Bartholewem 1952, Bartholewem and Hoel 1953) the harem masters herd and collect females or actively compete for those in estrus (Strohsker 1967, Peterson and Bartholewem 1967). None of this behavior was evident during the mating period of yellow-bellied marmots. Females did not congregate around the male burrow in early spring; rather, the male traveled from female to female. At locality 5 the female sites were close to the burrow from which the male emerged, and its trips were regular and of short duration. At 7 the females were widely distributed throughout a large territory, and the male stayed with each female for a day or more.

Physical conditions at the sites and the limited activity typical of recently emerged marmots prevents
interchange between sites in spring. Females at satellite sites did not seek resident males from colonies to mate with, and colonial males were not observed pursuing females from satellite sites. Reproductive females located at satellite sites evidently mated with males at those sites.

If monogamous females are more fit than polygamous they should react aggressively to other adult females, but as seen in field observations (Armitage 1962, 1965) and experimentally through MIS (Svendsen and Armitage 1973), the degree of aggression between females depends upon the balance between aggressive and social behavior of the individuals. Aggressiveness is probably enhanced by pregnancy and by the possession of a home burrow site but it is not known whether the tendency for aggressiveness or sociability is genetic or learned or both. The subject of learned and inherited components of behavior is treated extensively by McBride (1971) and Lehrman (1970); their results are inconclusive but generally favor genetic control. My evidence from the offspring of known females does not decide the question, but there was no tendency for the young to be the same behavioral temperament as the mother; on the contrary, a majority were of a distinctly different type from the mother. There is some evidence to support the hypothesis that early experience influences behavioral type (Scott 1958). The young from two satellite litters which had no opportunity to interact with other marmots outside of their litter mates were all of the social and avoider types. The only aggressive young were from sites where several adults and yearlings also lived and had opportunity to interact with the young. The sample size is small and further information is needed to draw any conclusions to this nature-nurture problem.

Very aggressive adult females are more likely to live alone or in a harem of two than are social animals. Nine out of 10 of the most aggressive females live in harems of two or less, and 8 live alone. Of the 8 most social adult females, 5 live in harems larger than two. Regardless of the size of the male territory, a very aggressive female can reduce the harem to itself. The more restricted the physical area suitable for occupancy, the easier this reduction would be. Most adult females at satellite sites are aggressive and two of those that produced a litter aboveground are of this type.

The aggressive yearling female has two options: establish a place in the social group where it was born, or disperse to a new area. The subordinate animal tends to move to the periphery. As expected, the choice sites in a colony or the most suitable satellite sites were occupied by the more aggressive animals, and the marginal sites by the subordinates.

Female 9 is an example of an avoider (subordinate) and the sites it inhabited are known. This animal was born to a resident of locality 1 in 1966, lived at the extreme edge of the colony as a yearling, and as a 2-yr-old and 3-yr-old at peripheral sites it had little association with colony residents. In 1970 it was captured back at colony 1 and as a 5-yr-old at satellite site (a) in 1971. It was the only adult female present at locality 1 in early spring of 1972. During the 5 yr when it was potentially reproductive, it never produced a litter above ground.

Reproductive success of the various behavioral types is shown in Table 6. For the purpose of separating aggressive and sociable animals, the behavioral continuum was arbitrarily divided into halves (Fig. 2), those animals scoring low on Factor II and high on Factor I being aggressive, those scoring high on Factor II and low on Factor I being sociable. The avoider group is clearly demarcated. The aggressive group produced almost twice as many litters per female as the social group. For every 100 young produced, 56 were from aggressive females and 39 from sociable females. Avoider females contributed the least, 5 per 100 young. If one assumes that a small harem has a predominance of aggressive females, the finding of Downhower and Armitage (1971) that females in small harems produced more young per female than did females in large ones is consistent. In this study, satellite females produced more young per female and had more litters than did colonial females, but the data from 1962 shows a much lower reproductive rate for satellites (Downhower and Armitage 1971).
Reproductive success of aggressive and social females varied with harem size (Fig. 3). In monogamous situations, aggressive females produced more young above ground, whereas sociable animals produced more young in polygamous situations. How this occurs is unknown. Bibikow (1968) reports that reabsorption of embryos is common in all marmots and is a factor in population regulation. Reabsorption of embryos was documented in *Marmota monax* by Snyder and Christian (1960), and Nee (1969) found differences between number of corpora luteum and placental scars in *M. flaviventris*, suggesting resorption or abortion. Differential effects of social pressure on different behavioral types would account for the variation in number of young produced by different animals under different social pressures. Inhibition of mating and interference during early postnatal care and development are also possibilities.

Yellow-bellied marmots do not reproduce until they are 2 yr old, usually 3 (Armitage 1965). Young remain where they are born until, as yearlings, they may disperse. Yearling survival after dispersal is independent of harem size (Downhower and Armitage 1971). Survival of its offspring to the yearling age class is therefore an important factor in measuring the fitness of a female. The recapture success of young from satellite sites which survived to be yearlings was reported to be about 7% (Downhower and Armitage 1971); none were recaptured in this study. In comparison, Downhower and Armitage (1971) found that 50% of young born in colonies were recaptured as yearlings, and my recapture percentage was 60%.

Young may disperse out of the valley during the 1st yr or may die during hibernation or through predation. One marmot moved over 4 km in a year. Inexperienced yearlings dispersing long distances could suffer more losses to predators in contrast to marmots remaining in natal sites or dispersing short distances, as is more likely in colonies (Armitage and Svendsen, *unpubl. data*). If satellite sites are limited by the number of good hibernacula, overwinter mortality could also account for the loss.

It is difficult to assess the quality of various sites occupied by marmots, especially the subterranean aspects. Orians (1961) and Verner (1964) found that among Redwinged and Yellow-headed Blackbirds and Long-billed Marsh Wrens, polygamous males occupied sites with a greater abundance of food than did monogamous males. This correlation with food supply does not hold true for marmots. There are more differences in species composition and density of vegetation between grassland and herbaceous slopes than between colonies and satellite sites at either area (Svendsen 1973). Studying marmots in the same area, Kilgore (1972) estimated that marmots use only 1%–2% of the net primary production at localities 1 and 4, both grassland sites, and even if feeding was restricted to one-tenth of the area available they would still consume only 10%–20% of the available net production. He calculated the standing crop to be 248 g/m² in area 1 and 458 g/m² in area 4. By contrast, a sample of vegetation taken in July at five 1 m² plots at the herbaceous slope site 5 yielded a standing crop of 1273 g/m², indicating its values are indeed conservative.

Downhower (1968) could not find evidence that the availability of food in a colony had any effect on the numbers of individuals in the colony. However, if food is limiting, it would be most limited in the spring or fall. The availability of vegetation in spring is dictated by the depth of snow and rate of snow melt. Snow depth at marmot sites is variable because of uneven topography, snowslides, and wind action, and some areas are free of snow much earlier than others. Patches of bare ground were evident on 10 May 1972, yet an average of 67 cm of snow remained on the slopes. The 1971–72 winter had slightly less than normal accumulation of snow. If twice the snow depth (140 cm) and an average snowmelt of 8 cm per day are considered, I estimate that the appearance of bare patches of ground would be delayed no later than 1 wk. A greater snowfall would also produce more snowslides, which expose the ground in their path.

The dry season occurs during midsummer. Several species of plants tolerant of dry situations and known to be used for food by marmots occur at the marmot sites. These include *Potentilla gracilis*, *Taraxacum officinale*, *Thalictrum fendleri*, *Aquilegia coerulea*, and *Heracleum lanatum*. Dried grass heads provide another food source during this time. Succulent vegetation is also available at the moist areas close to colony and satellite sites.

Downhower and Armitage (1971) concluded that reproductive success of females was affected by the availability of food during gestation. When growing season was early, more young per female were produced, but mean harem size was smaller, apparently because of increased aggression among adult females. My behavioral data supports the hypothesis that behavioral composition of the group is a factor determining the degree and amount of aggressive interactions. Whether differences in growing season will also modify the intensity of aggression among individuals of specified behavioral composition has not been determined.

The conspicuous differences between colony and satellite sites are in topographic diversity. Colony sites tend to be larger and to have more occupied home burrow sites, more used burrows, more varia-
tion in the landscape, and greater area for partitioning between the residents for feeding and other needs. Satellite sites may be considered minihabitats, with the most limited resource being burrow sites (Table 1). Yellow-bellied marmots spend over 80% of their lives in burrows, and almost 60% in hibernation. Burrow site selection must therefore be critical. Kilgore (1972) reported burrow temperatures to deviate little from 10°C between June and October. During the 1972–73 winter at RMBL, where the snow pack was undisturbed, the ground never froze (George Sibley, Caretaker, RMBL, Crested Butte, Colorado, pers. comm.). Thus, it is quite likely that the yellow-bellied marmot spends most of its fossorial existence at around 10°C.

This is about the same mean temperature at which they are active above ground during the summer. Marmots are characterized by a bimodal daily activity pattern during the summer (Armitage 1962, Bronson 1964), with greatest activity from 0700 to 1100 and 1500 to 1900 hr. The mean temperatures recorded at RMBL during these periods from June to August was 9.02°C and 14.14°C. Goodrich and Lyman (1971) found deep hibernation in yellow-bellied marmots at $T_a$ 6°C and $T_h$ 11°C. Below $T_a$ 5°C $T_h$ fell and heart and respiratory rates increased. Marmots have steady, evenly spaced respirations once they reach a hibernating body temperature of about 11°C.

Data on locations of hibernation burrows from the study area and from a population of marmots located at North Pole Basin (3,500 m) about 8 km northwest of RMBL show that hibernation burrows are situated where snow accumulation is greatest and not where the snow melts earliest. In 1972 the greatest overwinter mortality occurred at elevations of the study area where snow accumulation was least and snow melt earliest. About 80% of the animals occupying sites 1, a, b, c, d, and e in 1971 did not return the following year; whereas at localities 5 and 7 the loss was about 10%. If burrows vary in the degree of protection they provide during hibernation, and if there are more adult and yearling females than “best” hibernation burrows, then either females must share burrows (Armitage 1962) or some must occupy sites where chances of survival are less.

Years with less than normal depths of snowpack would result in overwinter mortality in the poorly insulated burrows, and consequently spring populations would be low. Winters with heavy snowfall are usually milder and provide better insulation to the hibernators; the result would be a greater survival of animals, especially at burrows of lesser quality, and higher spring populations. The number of animals living in marginal sites would then be greatly affected. Tests of these predictions await gathering of additional data.

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