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Author(s): Dennis W. Johns and Kenneth B. Armitage

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Behavioral Ecology of Alpine Yellow-Bellied Marmots

Dennis W. Johns and Kenneth B. Armitage

Rocky Mountain Biological Laboratory and
Division of Biological Sciences, University of Kansas, Lawrence, Kansas 66045, USA

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Summary. 1. An investigation of the behavior and ecology of several contiguous harems of yellow-bellied marmots (*Marmota flaviventris*) was conducted in an alpine area of North Pole Basin, Gunnison County, Colorado. At an elevation of 3,400 m, the study site differed from those of previous marmot studies in that no forest restricted interharem movement or social contact.

2. Meadow vegetation was patchily distributed and covered half the study area; clumps of willow comprised most of the remaining vegetation. Eighty-two marmot burrows within the study area (most of which were unoccupied) were randomly distributed. The 26 most frequently occupied burrows (hibernacula and summer residences) also had a random spatial distribution.

3. Two or more marmots commonly occupied the same hibernacula and summer residence burrows, resulting in a highly clumped spatial distribution of marmots.

4. Ecological densities of adult and yearling residents in North Pole Basin were usually higher than densities at East River Valley study sites in the same region (Table 9).

5. In contrast to annual reproduction commonly observed at lower elevations, no alpine female marmot was observed to produce young in consecutive years.

6. Burrowmates were generally much more closely related than nonburrowmate members of the same harem (Table 4).

7. The intensity of foraging activity varied throughout the active season, being low in May, June, and September and very high in July and August (Fig. 1). Forage ranges of individuals varied in size from 0.1 to 2.2 ha (Table 5), and were larger in the year of low food availability. The average degrees of forage range exclusivity for each level of social organization were: individuals, 10%; burrow groups, 41%; and harem groups, 88%.

8. Rates of social interactions changed throughout the active season; agonistic and sexual rates of interactions generally decreased and the amicable interaction rate generally rose between early June and late August (Fig. 6).

9. Among burrowmates, social interactions were predominantly amicable. But between nonburrowmate members of the same harem and between members of different harems, agonistic interactions predominated.

10. Yearling offspring that remained resident in their natal harem throughout the summer had predominantly amicable social interactions with their parents. Social interactions of these yearlings with nonparent adults were primarily agonistic ones in which the yearlings were subordinant.

11. Environmental parameters, population dynamics, resource utilization patterns, and social dynamics were evaluated in terms of their relationships to population density, intraspecific competition, parent-offspring relations, and male territoriality.

Introduction

The basic unit of yellow-bellied marmot social organization consists of a territorial male with a harem (Armitage, 1962, 1965, 1974, 1975; Downhower and Armitage, 1971). The term harem in this paper refers to a social unit that includes an adult male, adult females, and their offspring. Previous studies of the social behavior and population biology of yellow-bellied marmots (Armitage, 1973, 1977; Armitage and Downhower, 1974; Barash, 1973a; Svendsen, 1974) generally dealt with single-harem populations or (infrequently) multiharem populations in which encounters between members of separate harems were rarely observed. In these studies, forest expanses and substantial distances between harem home ranges usually acted as barriers to interharem contact. However, harems are contiguous in some marmot populations, especially in alpine habitats, where there is no forest to restrict movement or social contact between harems.

This paper describes the results of an observational study of several contiguous harems that comprised part of an alpine population of yellow-bellied marmots. The general purpose was to investigate the relationships of habitat resources to marmot population biology and social organization.

The principal structures of mammalian social systems are influenced and modified by the interactions of environmental variables and species characteristics (Crook et al., 1976). Two resources that are critical to the reproductive success and survival of yellow-bellied marmots are food and burrows (Andersen et al., 1976). Limited availability of either of these resources may result in some form of interference or exploitative competition (Miller, 1967). Marmots might exhibit one or more of the following as a result of interference competition: territoriality (Noble, 1939; Brown, 1964), maintenance of individual distance (Hediger, 1941), and dominance (see Wilson, 1975, for a thorough discussion). One objective of this study was to evaluate intraspecific competition in terms of the relationships of food and burrow resources to the dynamics and structure of marmot social organization.

The use of burrows as nurseries, refugia from predators, and hibernacula (Svendsen, 1974) suggests that the distribution of marmots may be a function of suitable burrow sites. Food resources may also play an important role in

the distribution and population density of marmots. Although Kilgore and Armitage (1978) found that population density of marmots is probably not restricted by food abundance, food limitation may occur in the form of specific nutritional requirements or as a result of the pattern of food distribution. A second objective of this study is to evaluate the effects of the distribution of burrows, food, and cover vegetation on the population density and distribution of marmots in different localities.

Finally, the timing of dispersal and the maintenance of the male territory will be discussed in terms of individual selection, kin selection (Hamilton, 1964, 1972), and parental investment theory (Trivers, 1972, 1974).

Materials and Methods

1. Basic Marmot Biology. Yellow-bellied marmots (*Marmota flaviventris*, Sciuridae) are diurnal, semifossorial ground squirrels that occupy a range of middle elevation to alpine environments throughout the western mountains of the United States (Hall and Kelson, 1959). Marmots are generalist herbivores during the four to five months of activity each year and are classical hibernators during the remainder (Kilgore and Armitage, 1978). Adult females often reproduce annually (Downhower and Armitage, 1971). Copulation occurs during the two weeks following emergence from hibernation (Armitage, 1965; Nee, 1969). In the Rocky Mountains, young are usually born in June following approximately four weeks of gestation, then spend three to four weeks in the burrow prior to weaning (Armitage, 1962). Many offspring disperse during their second summer (Armitage and Downhower, 1974). Yearlings have not been observed to breed; two-year-olds usually do not breed; most litters are produced by females that are three to seven years old (Armitage and Downhower, 1974). Individuals may live in colonies as members of social groups, as isolates, or as transients (Downhower and Armitage, 1971). The basic mating system of yellow-bellied marmots is one of polygyny (Downhower and Armitage, 1971) in which the harem male maintains a territory throughout the active season (Armitage, 1974).

2. Study Area. Field work was conducted during the summers of 1973 through 1976 on a 270 × 270 m study site located on the floor and lower slopes of North Pole Basin (NPB) of west-central Colorado. At an elevation of 3,400 m in the Elk Mountains of Gunnison County, the site is about 500 m higher than the East River Valley study areas (see Svendsen, 1974, for description), located 8–12 km to the southeast. The glacially scoured basin is a 3.2 × 1.6 km hanging valley that opens to the northeast. The slopes and floor of the basin support essentially a single expanse of open meadow dominated by upland grasses, sedges, and forbs. Willow thickets (*Salix*) are common in the wet meadows along the ephemeral stream and frequently cover the rock outcrops of the central basin. Gooseberry (*Ribes*) and Englemann spruce (*Picea engelmannii*) are also scattered over the outcrops. Although these clumps of woody vegetation are a common feature of the central basin, they are not extensive enough to appreciably restrict marmot movements. Consequently, the open and accessible nature of the entire basin provides a marked physical contrast to the enclosed and isolated subalpine meadows that characterize marmot habitat of the East River Valley. Vegetational abundance, diversity, and productivity in the NPB study site were reported elsewhere (Andersen, 1975).

The study site was divided into a grid by markers set 30 m apart. The low, somewhat level, central portion of the study site (through which the basin's major stream flowed) remained saturated with meltwater for several weeks each spring. The grid encompassed the hibernacula and summer burrows of 25–35 adult and yearling marmots each year. These marmots were members of four to five harems that comprised a small segment of an apparently continuous population that extended throughout and possibly beyond the basin. Photographs of the study area were taken every seven to ten days in each season to record changes in ground exposure during the period of snowmelt. Vegetative growth began in early May, as soon as receding snow opened small patches of ground, and continued into September.

3. *Trapping and Observations.* Field work usually began in mid-May and continued through mid-August. However, in 1974 work was extended through the first week in October, and in 1976 work began in late April to allow identification of marmots as they emerged from their hibernacula. Subsequent movements to and between summer burrows were also recorded. Marmots were trapped, tagged, color marked, sexed, and classified as young, yearlings, and adults (Armitage, 1962, 1973, 1974). In 1976 trapping was also conducted in an 18-ha area peripheral to the 8-ha study area. Because trapping sessions were only seven to ten days long in various portions of the peripheral area, the numbers of marmots captured in this area were considered to represent a minimum estimate of population size. By combining the numbers of yearlings and adults trapped in the study area with the numbers trapped in the peripheral area (8 ha + 18 ha = 26 ha), population density of the central basin as a whole was estimated. In 1974 the daily trapping routine was interrupted twice a week in order to conduct full-day observations of marmot activities and social interactions. In other years, observations were confined to periods of high marmot activity, generally 0600–1000 and 1300–1800 MST. For each 20-min census period, the identification, grid location, activity, and social encounters of each marmot seen above ground were recorded on coded forms and in field books.

4. *Measures of Dispersion.* The pattern of marmot distribution among burrows within the study area was determined by calculating the coefficient of dispersion (i.e., variance/mean ratio, Sokal and Rohlf, 1969) for the frequency distribution of marmots among all available burrows. A random distribution is indicated by a coefficient of dispersion (CD) of approximately 1.0; a uniform distribution by a CD of less than 1.0; and clumped distribution by a CD of greater than 1.0.

The spatial distributions of burrows and marmots within the study area were determined by the nearest neighbor technique described by Clark and Evans (1954). In this technique the observed mean distance to the nearest burrows (or marmots) was compared to the mean distance expected if they were randomly distributed. The ratio (R) of the observed mean distance to the expected mean distance serves as an index of departure from randomness: in a random distribution, $R = 1$; under conditions of maximum clumping, $R = 0$; in a maximally uniform distribution, $R = 2.15$. The significance of departure of the observed mean distance from the expected mean distance was tested by calculation of the standard variate (c) of the normal curve.

The criterion for significance for all analyses in this paper is the 0.05 level of probability. Significance levels (P) are listed after each test value. The form for reporting statistical results is: test statistic, significance level, and mean \pm the standard error of the mean.

5. *Forage Range Measures.* Forage range refers to a subregion of the home range in which foraging activities commonly occur. A prerequisite to forage range calculation is that locations of foraging behavior must be partitioned from the locations of other behaviors. Direct field observations allowed this partitioning, since foraging locations were recorded separately for each member of the population as part of the censusing routine. Estimates of forage range size, shape, and orientation were derived from a statistical analysis using the home range program of Koepl et al. (1975). A percentage confidence ellipse (CE), based on the bivariate normal probability distribution, calculated for each individual's scatter of location points, represented the forage range graphically. For example, a 99% CE, when superimposed on a grid map of the study area, enclosed an area in which a marmot was expected to be found 99% of its foraging time.

The 99, 95, and 90% CE's encompassed most of the data points, but did so by describing an area well beyond the region of concentrated foraging activity. Concentrated foraging activity was generally confined to an area bounded by the 75% CE. Consequently, the 75% CE was used in all forage range measures.

Overlap was determined by superimposing CE's on a grid map of the study area and measuring the areas of sympatry with a compensating polar planimeter. The area of sympatry was divided by the area of the 75% CE of a given forage range. The resulting proportion served as an index of the amount that a given forage range was overlapped by other forage ranges. Areas of multiple overlap were treated as single areas. This technique was not considered to bias the results, since the objective of measuring overlap was to determine the degree to which individuals or groups maintained forage range exclusivity.

Kruskal-Wallis nonparametric one-way analysis of variance (Sokal and Rohlf, 1969) tested

for differences in forage range size between various marmot groups. Significance was determined by comparing a test statistic (K-W) to a Chi-square value with $(n-1)$ degrees of freedom, where n equals the number of groups compared.

6. Kinship Determinations. The degree of relatedness or coefficient of relationship (r) measures the fraction of genes identical by descent between two individuals. We assumed that the young emerging from the burrow of a postpartous female were siblings and that the harem male fathered all young born in his territory, unless his presence during the breeding season was not verified.

Pairs of siblings and parent-offspring pairs were assigned r values of $1/2$. Other pairs of individuals of known relationship were assigned appropriate r values. Immigrants were assumed to be distantly related to established residents. Three values ($1/16$, $1/32$, $1/64$) were used separately to calculate an approximate average r for immigrant-resident pairs. The r values were used to calculate the average degree of relatedness of burrowmates and of nonburrowmates within harems.

7. Social Behavior. Social dynamics among yellow-bellied marmots are characterized by amicable, sexual, and agonistic interactions (Armitage, 1973, 1974, 1975, 1977). In this study the amicable category included greeting (Armitage, 1962) and mutual groomings (Armitage, 1973). Sexual behavior included genital sniffing, grasping, grappling, and mounting (Armitage, 1962). Agonistic interactions involved chases, flights (Armitage, 1962, 1973), fights, and avoidance behavior. Avoidance behavior refers to occasions when an individual alters its path or position to avoid contact with another marmot.

In the analysis of social behavior, interactions involving young of the year were not included. By classifying individuals according to four age-sex groups – female yearling, male yearling, female adult, and male adult – ten unique sex-age pairs of interactions were possible. In this paper no consideration is given to which member of the paired encounter initiated the interaction. With the exception of Fig. 7, victors of agonistic encounters are not indicated.

Observations were also partitioned according to the degree of association that existed between interacting marmots. Marmots occupying the same burrow formed closely associated burrow groups whose interactions are designated as intraburrow. Harem members that lived in separate burrows were less closely associated; their encounters were termed interburrow. Finally, interharem interactants had the lowest degree of association because they occupied separate burrows located in territories of different males.

Results

I. Environmental Parameters

Snow cover, vegetation, and burrows were identified as potentially important in evaluating the influence of resources on marmot density, dispersion, and social organization.

1. Snow Cover. By mid-May, when snow blanketed all but the steepest rock faces of the basin, marmots had dug emergence tunnels through the snow at sites of most hibernacula. The pattern of subsequent snowmelt was essentially the same in all years, but its timing varied from year to year (Fig. 1). In 1975 snowmelt began and ended relatively late, while in 1974 and 1976 the dissipation of snow was two to three weeks ahead of the 1975 pattern, and forage was available correspondingly earlier in the season.

2. Vegetation Distribution. The meadow vegetation that was somewhat evenly spread over the slopes of NPB was more patchily distributed in the study

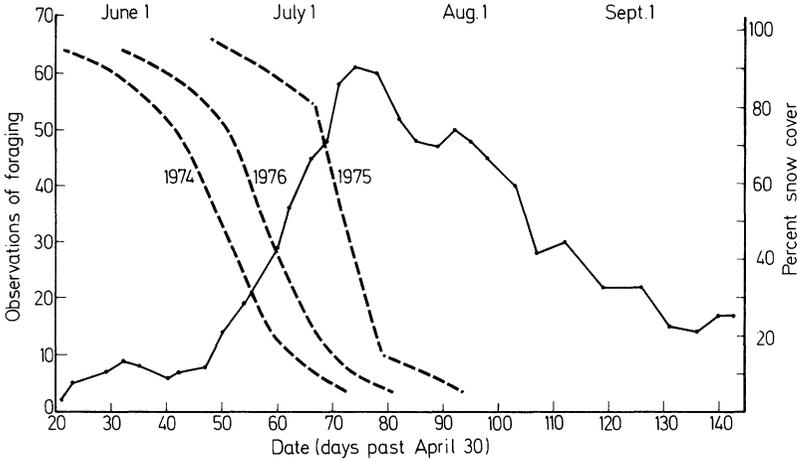


Fig. 1. Snowmelt pattern (*dashed line*), measured as percent snow cover in the study area during each active season, and seasonal distribution of foraging activity in 1974 (*solid line*). Frequencies are based on counts made during 32 days of observation (dawn to dusk) of foraging behavior of three adult males and thirteen adult females. Because counts were made at 20-min intervals, each marmot could potentially score three foraging behaviors per hour of observation. A three-point running average was used to produce the values on the graph

site because of numerous willow thickets (Fig. 2). Patches of open meadow covered 50% of the study area, shrubs and willow thickets occupied another 43% of the area, while rock surfaces and the stream bed accounted for the remaining 7%.

3. Burrow Distribution. Within the study area, 82 marmot burrows were identified (Fig. 2). The burrows were distributed randomly ($R=0.95$, $c=0.76$, $P>0.05$). Sixteen of the burrows served as hibernacula during at least one overwinter period. Summer residences included these hibernacula plus four other burrows. Six additional burrows were used for one to three weeks during the active season, while the rest of the burrows were occupied for only three or four days or not at all. The 26 most frequently occupied burrows (=home burrows) were also randomly distributed ($R=0.89$, $c=1.08$, $P>0.05$). Of the 26 home burrows, 21 were located among substantial rock structures of meadow areas and within 5 m of shrubs or willow thickets. All 26 were located on terrain that sloped 15–35°.

At several locations within the study area, two or more burrow entrances were clustered, and entrances were connected underground. Others were probably connected because they were used interchangeably by the same marmots. Such locations were considered to have a single burrow with multiple entrances. Of the 20 residences, 15 had multiple entrances, while most of the unoccupied burrows had but single entrances. Because the entrances of most burrows passed through rock fissures or rocky soils, the size of most burrow openings could not be enlarged. The distances between the occupied burrows of a harem group varied from 6.6 to 114.6 m with a mean of 62.3 m (± 5.6 m).

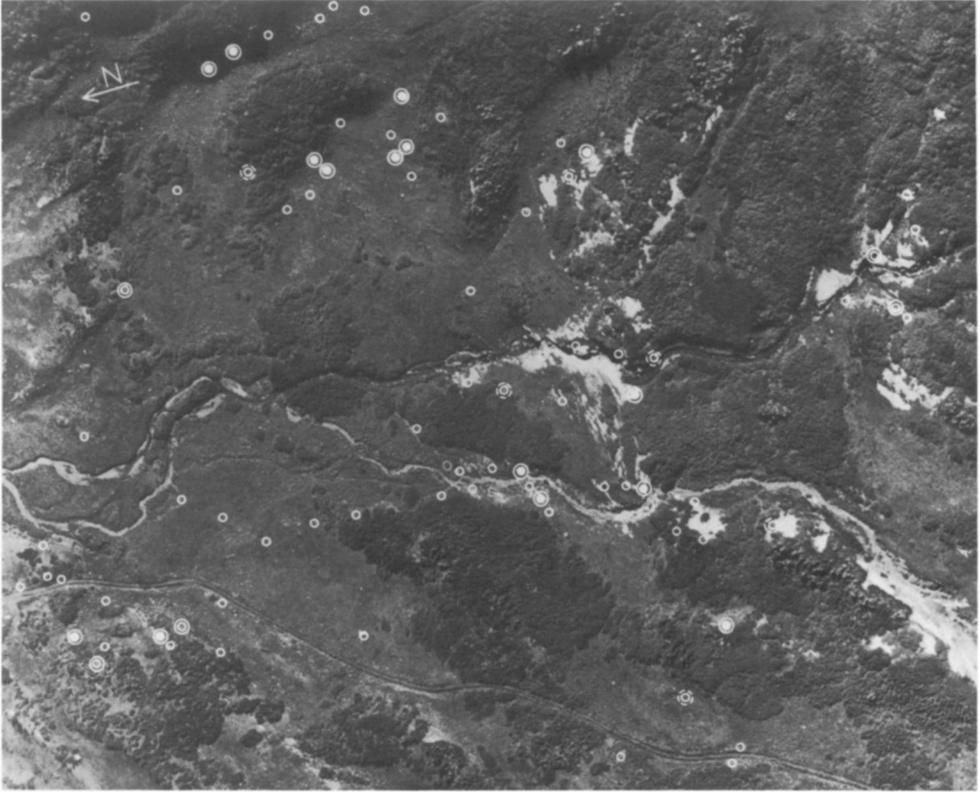


Fig. 2. North Pole Basin study site. An ephemeral stream flows through the site until August in most years. Clumps of vegetation are predominantly willow thickets. Locations of marmot burrows are indicated by circles: \circ = unoccupied burrow; \otimes = short-term summer residence (less than four weeks); \oplus = full summer residence; \bullet = used as a hibernaculum and summer residence. Aerial photograph (by Alanson Hegeman of Crested Butte, Colorado) was taken at approximately a 70° angle

No systematic assessment of burrow distribution was made outside the study area. However, most of the burrows found throughout the basin were located in or near open meadows.

II. Population Parameters

1. Changes in Density. Population censuses were derived from counts of marmots of each age–sex class residing in the study area during the first two weeks of June, July, and August of each year (Fig. 3). Much of the annual fluctuation in population size resulted from changes in numbers of young and yearlings, while the mean number of adults remained fairly stable from year to year. Both yearlings and adults generally declined in numbers from early spring to August. This decline was most dramatic among male yearlings, whose numbers

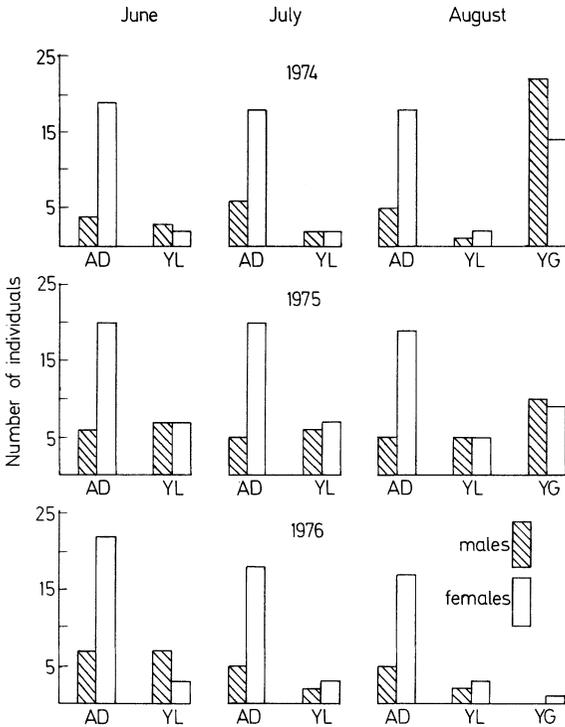


Fig. 3. Numbers of adults (*AD*), yearlings (*YL*), and young (*YG*) of each sex, as censused during three periods (June 1–15, July 1–15, and August 1–15) each active season, 1974–1976. Those adults and yearlings present in August were resident all summer

decreased an average of 53% during the active season. By comparison, numbers of yearling females declined an average of only 17%, while numbers of male and female adults declined an average of 12 and 11%, respectively. Young were weaned in late July and early August each year. In the year of highest litter production (1974 = nine litters), two-thirds of the young were weaned within the first week (July 16–23) of the month-long period of emergence.

Population density, ranging from 3.5 to 8.5 marmots per hectare (Table 1), was usually highest in August after the emergence of young of the year, except in 1976 when only one young was weaned.

Population density was also estimated in 1976 for a 26-ha area that included the study site (8 ha). Fifty-nine adults and 16 yearlings were trapped in the area, yielding a minimum density estimate of 2.9 residents per hectare. Because the 26-ha area covers at least one-third of the central basin, the resident density estimated for it is probably a good estimate for the central basin as a whole.

2. Sex Ratios. Males and females were not equally represented among all age groups (Fig. 3). August sex ratios for each age class were averaged for the three-year period and compared to a ratio of 1:1 (Table 1). Neither young nor yearlings had sex ratios that significantly differed from a 1:1 ratio. However,

Table 1. Sizes of study site, population densities, and sex ratios of marmots in the North Pole Basin study area, 1973–1976

	1973	1974	1975	1976	Mean
Size of study site (in hectares)	6.9	7.3	8.1	8.1	
August population density (individuals/hectare)					
Adults, yearlings, and young	4.5	8.5	6.5	3.5	5.8
Adults and yearlings only	3.8	3.6	4.2	3.3	3.7
Adults only	2.5	3.2	3.0	2.7	2.8
August sex ratio (male:female)					
Young	1.5:1	1.6:1	1.1:1	0.0:1	1.3:1 NS
Yearlings	1.3:1	0.5:1	1.0:1	0.7:1	0.9:1 NS
Adults	0.3:1	0.3:1	0.3:1	0.3:1	0.3:1 ^a

NS = not significantly different from a 1:1 ratio, $P > 0.05$

^a = significantly different from a 1:1 ratio, $P < 0.001$

adult females significantly outnumbered adult males by a factor of greater than three.

3. Reproduction. If each adult female had produced a litter each year that she was resident, 65 litters would have been produced from 1973 through 1976. Instead, only 15 litters (totaling 61 young) were weaned (Armitage et al., 1976) during the four-year period, an average of 0.23 litters per adult female per year. A mean of 4.07 (± 0.45) young was produced per litter, or 0.94 (± 0.24) young per adult female were produced per year.

Most females were three to six years old when they produced litters; only one of four pregnant two-year-old females weaned a litter. No NPB female produced litters in consecutive years during six years (1973–1978) of investigation. From 1973 through 1976, fourteen adult females who were judged pregnant did not wean litters, including five females that had weaned young in the previous year.

4. Reproduction at Burrows. Burrows were censused each June, July, and August from 1974 through 1976, creating a total of nine month-long periods. Nine of the home burrows harbored adult females during seven or more of the month-long periods. The mean number of young produced per adult female occupant of these nine burrows was 0.42. Another six burrows were occupied by adult females during four to six month-long periods. The occupants of these six burrows yielded 0.26 young per adult female occupant. Five other burrows, occupied only during one to three periods, produced no young; nor did the few animals that occupied the remaining burrows within the study area. No burrows in which young of the year were weaned harbored yearling residents that season.

Table 2. Sources of population turnover in the North Pole Basin study area, 1973–1976

Source of turnover	Young		Yearlings		Adults	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Natality	35	26				
Immigration				1	6	3
Confirmed emigration			6		3	3
Confirmed mortality	3	1	1			
Disappearance ^a	0.12 ^b	0.12	6.4	3.3	1.6	1.3

^a Since the causes of most population losses were undetermined, they were categorized as disappearances

^b Disappearances during the active season (first value), overwinter disappearances (second value). In 1974 and 1975 the overwinter period began after final observations in mid-August (several weeks prior to hibernation)

5. Population Increases. Natalty and immigration accounted for population increases (Table 2). Although some outsiders became permanent residents, birth in the study area followed by continuous residency accounted for 91% of the recruitment in the population. Virtually all of the full-reason resident yearlings were born in the study area. The only yearling known to successfully immigrate disappeared within three weeks of its arrival. Territorial males were either present as adults when the study began or they were immigrants. Although four males born in the study area maintained residency until they were two years old, none became territorial or sired young while residing in the study area. Of the recruitment of adult females, 75% consisted of females that were born in and continued to live in the study area.

6. Population Losses. Mortality and emigration were sources of population losses (Table 2). It was often difficult to distinguish between emigration and mortality, because many marmots simply disappeared. Emigration was confirmed only when a missing marmot was later found living outside the study area. No losses were sustained late in the active season of 1974, when observations continued until October, by which time all but a few marmots had hibernated (Andersen, personal communication). However, the following spring only 15 of the 32 young that presumably overwintered in the study area emerged from hibernation, and an adult male also failed to emerge. This pattern of overwinter disappearance is consistent with the conclusion of Armitage and Downhower (1974) that overwinter mortality is a significant source of population losses.

During the active season, population losses were more likely due to emigration, since emigration accounted for 71% of all confirmed population losses between early spring and mid-August (Table 2). Although sources of mortality were rarely confirmed, predation was potentially significant during the active season. A badger (*Taxidea taxus*) preyed on a yearling marmot residing near the study area (Andersen and Johns, 1977). Golden eagles (*Aquila chrysaetos*) routinely soared over the basin. Coyotes (*Canis latrans*) frequently and red

Table 3. Frequencies of observed shifts in residency. Values are percentages of the total number of marmots observed to translocate from 1974 through 1976. Residents were yearlings and adults living in the study area; transients spent less than a week in the study area

Residency status	Translocations (% of total ^a)		
	May 16–June 15	June 16–July 15	July 16–August 15
Residents	31	50	19
Transients	19	54	27

^a 80 residential shifts (dispersal not included) and 113 transient movements were observed within the study area in three years

fox (*Vulpes fulva*) occasionally passed through the basin. Although alarm, alert, and retreat behaviors were observed frequently (usually several each day), the degrees to which the NPB marmots were subjected to the various modes of predator attack were not established. Another source of mortality, aggressive cannibalism, was observed on one occasion (Armitage et al., 1979).

7. Shift in Residency. With the exception of high losses of male yearlings, harem membership showed relatively little change during the active season. Adult males typically remained associated with the harem group and maintained their territories throughout the active season. However, adults and yearlings commonly moved between hibernacula and summer residence burrows. An average of 61% of all residents changed burrows within the study area at least once in a given year. Half of the burrow changes occurred between mid-June and mid-July (Table 3). Of 113 transients detected in three years, 54% traveled through the study site between mid-June and mid-July.

8. Survival Rates. Survival rates were calculated as the proportion of individuals in an age–sex class that remained in the study area from one year to the next. Marmots (including young) that were resident in August of one year and were trapped in the study area the following spring were considered part of the surviving population. Rates of survival were about equal for male and female young (51 and 48%, respectively). Male yearlings had 24% survivorship, which was much less than the 64% survivorship of female yearlings. Male adults also had a much lower rate of survival than their female counterparts, 53 and 90%, respectively.

9. Kinship. Regardless of which approximation of average immigrant–resident relatedness was used, the results were roughly the same (Table 4). Burrowmates had an average r of 0.34–0.36, while nonburrowmates had an average r of 0.09–0.13. Therefore, burrowmates generally were three to four times more closely related than nonburrowmates.

Table 4. Average coefficients of relationship (r) of: (A) burrowmates and (B) nonburrowmate harem members. Estimates are based on 73 pairs of burrowmates and 64 pairs of nonburrowmates from three years of burrow occupancy data. Three separate estimates are made for each category, using different values to represent the average r between immigrants and established residents

Average r between immigrants and residents (approximated values)	A Burrowmates	B Nonburrowmates	A:B
1/16	0.36	0.13	2.8:1
1/32	0.35	0.10	3.5:1
1/64	0.34	0.09	3.8:1

III. Resource Utilization Patterns

1. Use of Burrows. Burrows served as refugia from predators and as retreats in times of inclement weather. On days of extremely cold temperatures, marmots delayed their morning emergence and remained above ground for only short periods. In midsummer, marmots generally remained below ground during the heat of the day. Marmots were also observed to return to their burrows for the duration of snowstorms and rainstorms.

Visual assessment of the distribution of marmots throughout the basin was made when spring snowpack enhanced the visibility of marmots and their burrow entrances. It was evident that the central basin, which included the study area, had a greater concentration of marmots than the slopes of the basin. Within the study area marmots were clumped in spatial distribution in all years (1974: $R=0.10$, $c=8.22$, $P<0.001$; 1975: $R=0.15$, $c=9.21$, $P<0.001$; 1976: $R=0.29$, $c=5.78$, $P<0.001$).

Although as many as 12 adults and yearlings shared a home burrow, home burrows were most frequently occupied by one to five marmots. Clearly, marmots aggregated at only a few of the burrows available to them. The frequency distribution of marmots among 82 burrows in the study area was clumped in each of three periods during the active season ($CD=4.31$, 2.40, 5.00 in June, July, and August, respectively). Marmots also hibernated together in groups of two to eleven individuals; no NPB marmot was known to hibernate alone. Thus hibernating marmots had a clumped distribution among burrows ($CD=5.81$ and 3.00 during spring emergence in 1975 and 1976, respectively).

2. Foraging Patterns. For the first four weeks following hibernation, foraging activity was low; but beginning in mid-June, foraging increased as snow cover continued to decrease, and peaked in mid-July (Fig. 1). The peak of foraging roughly coincided with the disappearance of snow from the study area. This peak also occurred just before young of the year began to emerge. After mid-July, foraging gradually declined through mid-September, when marmots began hibernating. Marmots tended to forage individually and often gave chase upon encountering nonburrowmates while foraging. Most individuals, especially adult females, appeared to maintain an individual distance toward nonburrowmates.

Spatial patterns of foraging activity were also investigated. Forage range size, as represented by a 75% confidence ellipse (CE) around the scatter of forage ranges, varied from 0.1 to 2.2 ha (Table 5). The size of yearling forage ranges (determined in 1975 only) was not significantly different from that of adults ($K - W = 0.60$, $P < 0.05$). Adult males had significantly larger forage ranges than adult females ($K - W = 4.44$, 4.63 and 4.05, $P < 0.05$ in 1974, 1975, and 1976, respectively). For this reason adult females were used to determine if the size of forage ranges varied among years. Forage range sizes of adult females in 1975 (delayed snowmelt, Fig. 1; and high density of residents, Fig. 3) were significantly larger than those of adult females in 1974 and 1976 ($K - W = 10.21$, $P < 0.001$).

The general pattern of foraging activity was one of foraging radially out from the home burrow, primarily to areas of open meadow vegetation; although marmots occasionally fed extensively among the willow thickets. Most marmots did not travel great distances to their foraging areas. In 1974 and 1976 (the years of early snowmelt) the mean distance from burrow to forage center for 28 female adults was 13 m (± 2 m). In 1975 the mean distance for 15 adult females was 25 m (± 3 m). These means were significantly different ($t = 12.5$, $P < 0.001$).

3. Forage Range Overlap. Overlap of forage range was measured between individuals (Table 5), and between burrow groups and harem groups (Table 6). For the latter two comparisons, data from all members of each burrow group were combined and new forage range CE's were calculated. These CE's were used to represent burrow-group and harem-group forage ranges (e.g., Fig. 5). Forage ranges of individuals overlapped extensively in all years (Fig. 4 and Table 5). The amount of total overlap varied from 54 to 100% with an average of 90% over three years. There was no appreciable difference between the amount that forage ranges of burrowmates overlapped (76% average) and the amount that forage ranges of nonburrowmates overlapped (75% average). Note that the preceding two averages do not sum to 90% (the average of total overlap), because areas of multiple overlap were treated as single areas. Overlap of burrow forage ranges varied from 13 to 100% with an average of 59% over three years (Fig. 5 and Table 6). Harem-group overlap ranged from 0 to 35% and averaged 12% over three years (Fig. 5 and Table 6). In terms of forage range exclusivity, the average for each level of organization is: individuals, 10%; burrow groups, 41%; harem groups, 88%.

IV. Social Dynamics

Social dynamics refers to the maintenance of or changes in social structure by processes of interindividual behavior (Crook and Goss-Custard, 1972).

1. Seasonal Distribution. The rate of amicable interactions was lowest through the first half of July, then reached a maximum in late July and early August (Fig. 6). Conversely, the rate of agonistic interactions was highest in early June

Table 5. Sizes of and amounts of overlap between individual marmot forage ranges, 1974–1976. Measures of overlap include: (1) percentage of forage range overlapped by the burrowmates of a given individual, (2) percentage overlapped by nonburrowmates, and (3) total percentage overlapped by all marmots. Areas of multiple overlap were treated as single areas. All forage range statistics were based on burrow occupancy as of July 1 each year

Identification no.	1974			1975			1976					
	Forage range size (ha)	Forage range overlap (%)		Forage range size (ha)	Forage range overlap (%)		Forage range size (ha)	Forage range overlap (%)				
		(1)	(2)	(3)		(1)	(2)	(3)		(1)	(2)	(3)
Male adults												
163	0.9	31	65	82								
230					2.1	23	97	92	2.2	27	50	70
239	0.5	100	82	100								
405	0.6	44	63	83	1.3	30	93	99	0.9	36	88	99
408	0.8	12	50	55	0.8	83	48	97				
435									0.5	48	45	57
Female adults												
42	0.1	*	54	54								
139	0.2	98	79	100	1.5	62	82	89				
141	0.2	68	42	68	0.4	99	58	99	0.3	95	81	100
143	0.8	73	23	81	0.6	61	98	98	0.3	67	91	91
173	0.5	100	100	100	0.5	100	98	100	0.3	99	63	100
175	0.4	53	67	80	0.9	94	86	98	0.6	*	69	69
183	0.6	61	84	99	0.7	54	88	88				
184	0.3	78	49	88	0.8	66	49	86	0.5	80	78	89
185	0.5	*	99	99	0.6	100	97	100	0.7	70	69	70
187	0.5	74	80	96	0.5	79	99	99				
192	0.6	97	22	95	0.5	80	97	97	0.5	50	93	97
248	0.8	73	96	96	1.1	75	89	93	0.7	*	56	56
257	0.5	*	85	85	0.7	61	81	89	0.3	94	62	94
401	0.2	100	81	100	0.7	93	97	100				
406	0.4	78	80	80	0.7	95	96	99	0.5	76	86	89
431	0.4	*	100	100	0.4	*	88	88				
489									0.1	99	63	100
491									0.3	49	66	82
509									0.3	81	81	92
Male yearlings												
433					0.6	99	31	99				
435					0.4	100	29	100				
467					1.0	60	84	89				
483					0.6	100	100	100				
533					0.8	98	97	98				
Female yearlings												
437					0.4	100	34	100				
477					0.7	83	84	84				
489					0.6	100	99	100				
491					0.8	99	100	100				
507					0.7	100	98	100				
509					0.6	88	63	99				
	Mean	71	70	87		82	81	96		69	71	85

* Indicates marmots without burrowmates at time of censusing

Table 6. Overlap of burrow-group and harem-group forage ranges, measured as percentages of the group forage ranges

Burrow	Forage range overlap (%)						
	Between burrow groups			Harem	Between harem groups		
	1974	1975	1976		1974	1975	1976
A	57	25	16	I	15	*	*
B	100	40	58	II	26	5	0
C	13	56	53	III	0	12	12
D	75	100	65	IV	0	14	35
E	72	91	76	Mean	10	10	16
F	76	*	*				
G	58	30	42				
H	24	*	*				
I	43	71	34				
J	*	86	*				
K	71	76	84				
L	48	*	*				
Mean	60	64	54				

* Indicates unoccupied burrows or absence of harem

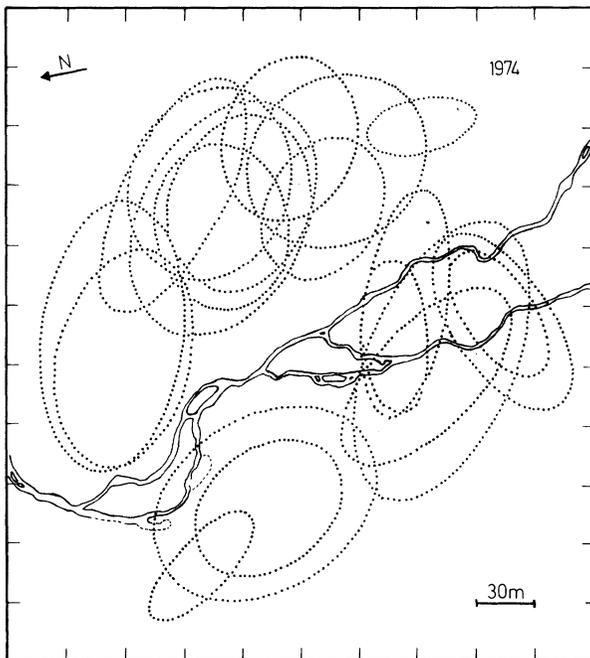


Fig. 4. Forage ranges of yearling and adult residents of the North Pole Basin study site, 1974. Forage range boundaries are depicted by 75% confidence ellipses (dotted lines) computed by a bivariate home range program. The stream bed is outlined for reference to study site features in Fig. 2

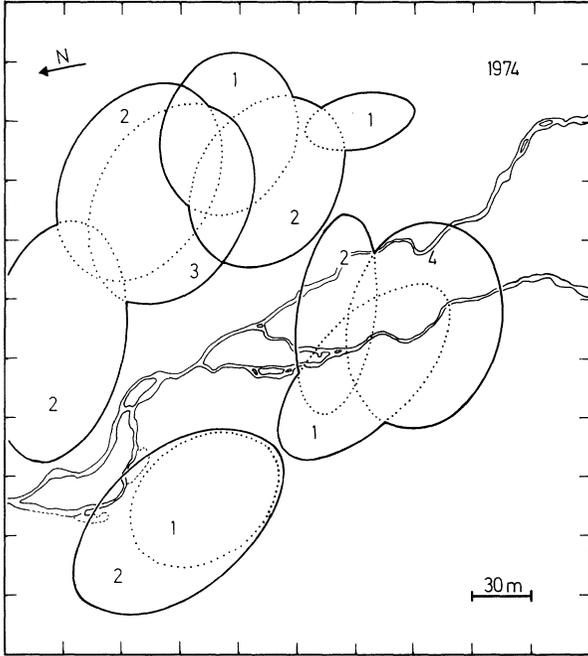


Fig. 5. Forage ranges of burrow groups (*dotted+solid lines*) and harem groups (*solid lines only*) composed of yearling and adult residents, 1974. Forage range boundaries are depicted by 75% confidence ellipses computed by a bivariate home range program. Values within ellipses indicate burrow-group size; sums of values within solid lines indicate harem-group size. The stream bed is outlined for reference to study-site features in Fig. 2

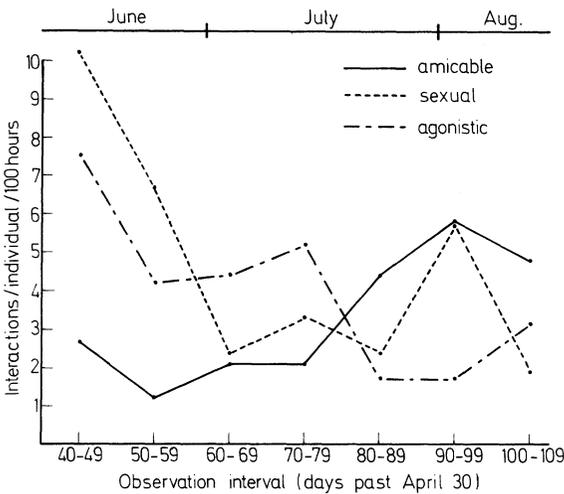


Fig. 6. Seasonal distribution of rates of intraharem social interactions (intraburrow and interburrow combined) involving three adult male and thirteen adult female members of three harems in 1974

Table 7. Amicable (AM) and agonistic (AG) interactions at various levels of social organization: intraburrow (between burrowmates), interburrow (between nonburrowmate harem members), and interharem (between members of separate harems). Values are summed over three years of observations, 1974–1976

Age–sex pair AD = adult YL = yearling	Interaction frequency					
	Intraburrow		Interburrow		Interharem	
	AM	AG	AM	AG	AM	AG
♀ YL : ♀ YL	10	0	0	0	0	0
♀ YL : ♂ YL	50	0	0	0	0	3
♀ YL : ♀ AD	46	12	4	31	2	4
♀ YL : ♂ AD	10	4	6	16	0	0
♂ YL : ♂ YL	23	2	*	*	0	8
♂ YL : ♀ AD	34	10	2	31	0	6
♂ YL : ♂ AD	12	6	2	19	0	9
♀ AD : ♀ AD	114	14	10	139	20	65
♀ AD : ♂ AD	66	78	32	136	8	69
♂ AD : ♂ AD	*	*	*	*	0	17
Total	364	126	56	372	30	181

* Some paired encounters were not possible due to age–sex composition of the groups involved

and lowest in late July and early August. The rates of agonistic interactions of parous females were also calculated separately. The pattern was almost identical to that for all individuals, and therefore is not depicted in Fig. 6. The rate of sexual interactions was highest in mid-June, dropped to a low level that was maintained throughout July, reached a second peak in early August, then dropped to its lowest level in mid-August. At least 95% of the sexual behavior was initiated by the adult male.

2. *Spatial Distribution.* Agonistic encounters tended to occur with high frequency near occupied burrows, but were also widely dispersed throughout the study area.

3. *Degree of Association.* Most of the amicable interactions occurred between burrowmates (i.e., under the intraburrow category), the most closely associated interactants (Table 7). When amicable and agonistic encounters were summed for all age–sex pairs under the intraburrow category, amicable interactions accounted for 74.3%. Amicable encounters outnumbered agonistic in all age–sex pairs, except the ♀AD : ♂AD pair. This exception possibly is a result of the difficulty in distinguishing between some agonistic and sexual encounters among male and female adults. Most of the interactions for this pair involved the avoidance of a male by a female. All avoidance behavior was routinely classified as submissive agonistic behavior, but in cases of females avoiding males, the avoidance might also have been categorized under sexual behavior. If avoidance behaviors are excluded from tabulation for the ♀AD : ♂AD category, the ago-

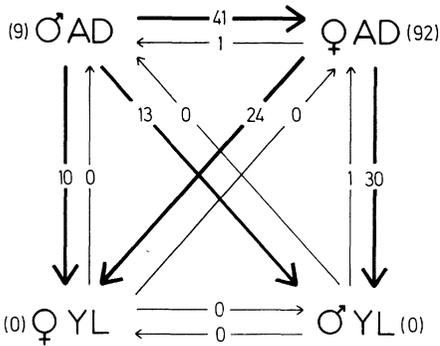


Fig. 7. Dominance relations involving members of four age–sex classes in the North Pole Basin study area, 1974–1976. Numbers represent observations of unambiguous fights, chases, and avoidance behavior that occurred between marked members of the same harem. *AD*, adult; *YL*, yearling. Values in parentheses are interactions between members of the same age–sex class. Direction of arrows indicates dominance: dominant → subordinate

Table 8. Amicable (AM) and agonistic (AG) interactions between yearlings and their parents or other adults in 1975. Values in parentheses represent numbers of potential interactants in each category. Yearlings were subordinate in all agonistic categories

Yearling interactants	Adult interactants							
	♀ Parent (3)		Other ♀ (8)		♂ Parent ^a (2)		Other ♂ (1)	
	AM	AG	AM	AG	AM	AG	AM	AG
♀♀ (5)	17	1	5	15	6	0	1	4
♂♂ (5)	18	2	0	18	6	0	0	6

^a Male parentage was highly probable, but not confirmable

nistic count drops from 78 to 26 and amicable behavior occurs more frequently than agonistic behavior for this pair also.

Agonistic encounters outnumbered amicable ones in all age–sex categories for both interburrow and interharem levels (Table 7). Among interburrow encounters, 86.9% were agonistic; among interharem encounters, 85.8% were agonistic.

4. Age–Sex Classes. Within harems male adults were dominant over all other age–sex classes, female adults were dominant over yearlings, and yearlings exhibited no dominance (Fig. 7). Territorial males maintained dominance over younger males in the few instances in which male offspring remained in the harem area as two-year-olds. Dominance among adult females appeared to be spatially determined; that is, the victor of an agonistic encounter between adult females was nearly always closer to its home burrow at the time of the encounter. Observations were insufficient to determine this relationship for other age–sex classes. Occasional dominance between burrowmates followed typical age–sex patterns (Fig. 7).

5. Relatedness. Both male and female yearlings who remained resident throughout the summer had predominantly amicable encounters with their parents (Table 8).

Conversely, the majority of encounters between yearlings and nonparent adults were agonistic.

Discussion

1. Marmot Dispersion and Density

The clumped spatial distribution of yellow-bellied marmots conforms closely to the mosaic of forested and meadow habitat (Svendsen, 1974). Marmots also are clumped within suitable habitat (Table 9). In the ERV, marmots were usually clumped in a single centralized area, whereas NPB marmots were clustered in at least three widely separated areas. When measured within such localities, marmot ecological density (Odum, 1971) varied from 0.6 to 8.6 residents per hectare with a mean of 1.3 (Table 9).

One likely determinant of population density is the location of sites for construction of good quality burrows. Marmots spend up to 80% of their lives in burrows (Kilgore and Armitage, 1978). The need to return frequently to a refuge that is fixed in space places constraints on animals in terms of mobility and patterns of resource exploitation and defense (Hamilton and Watt, 1970). Other things being equal, marmots that forage out of a centralized refuge area (as in ERV) would exploit their forage resources less efficiently than an equal number of marmots that forage from decentralized refugia (as in NPB). Centralized animals must travel further (on the average) from the refuge to obtain food as a result of extensive biodeterioration around the refuge area (Hamilton and Watt, 1970). Because the optimal distance for a consumer to travel is that which minimizes risk to predation while maximizing resource yield (Covich, 1976), centralized marmots should have larger optimal distances than decentralized marmots. Since optimal distance would increase with the number of marmots utilizing a centralized refuge area, the resulting increase both in foraging cost and in predator risk would eventually operate against large group size. In addition, spatial packing of marmots at centralized sites is correlated with high rates of agonistic behavior (Armitage, 1977), which may act as a constraint against high density. Therefore, the higher population density in NPB may result from the availability of a greater number of decentralized sites for construction of good quality burrows.

Another resource variable potentially affecting population density is the availability of food resources. Because size of forage range was greater in the year of low food availability in NPB, marmots appear to compensate for seasonal reductions in food resources by foraging over wider areas. However, this observation does not demonstrate that food availability in NPB placed constraints on the numbers of marmots occupying the study site. Furthermore, basing their argument on the low proportion of primary production consumed by marmots in ERV localities, Kilgore and Armitage (1978) concluded that food availability alone does not affect marmot population density.

Table 9. Comparison of habitat and population parameters of the North Pole Basin and East River Valley study sites

Habitat and population parameters	North Pole Basin	East River Valley
Forage vegetation		
Distribution	Somewhat patchy	Probably uniform ^a
Abundance	Probably in excess ^b	In excess ^c
Home burrows		
Distribution	Random	Clumped ^d
Abundance	Possibly limited	Variable ^d
Relation to other habitat features	Among rocky structures; near meadow and cover vegetation; on 15–35° slope	Among rocky structures; near meadow vegetation; on 20–45° slope ^e
Unoccupied burrows		
Distribution	Random	Probably random ^d
Abundance	In excess	In excess
Marmot dispersion		
Among burrows	Clumped	Probably clumped ^d
Over habitat	Clustered in three widely separated areas	Clustered in one centralized area ^d
Ecological density (number of yearlings and adults per ha)	High (mean = 3.7, range = 3.3–4.2)	Low (mean = 1.3, range = 0.6–8.6) ^f

^a Armitage (1974, Plate 1)

^b Andersen et al. (1976): vegetation was abundant in overall habitat, but was restricted in parts of the study area

^c Kilgore and Armitage (1978)

^d Armitage (unpublished data)

^e Svendsen (1974)

^f Armitage and Downhower (1974, Table 1) and Armitage (unpublished data): averaged for three colony sites: # 1 (1.4 ha), # 4 (1.6 ha), and # 5 (10.1 ha)

2. Social Dynamics and Resource Exploitation

In marmot social systems, competition among individuals for the best food and burrow resources is counteracted by the advantages of group living. The high rate of amicable behavior (Table 7) and close relatedness (Table 4) of burrowmates suggest that kin selection (Hamilton, 1964, 1972) would favor the inhibition of aggressive competition among burrowmates. The relatively high levels of agonistic behavior among nonburrowmates suggest behavioral competition occurs primarily between members of different burrowgroups who are likely to be unrelated or only distantly related.

The seasonal rise in intraharem amicable behavior (Fig. 6) primarily reflects an increase in the rate of intraburrow amicable interactions. Nine litters were born in June–July and weaned in July–August of 1974. Therefore, the seasonal rise in amicable behavior may have facilitated increased burrow-group cohesive and cooperative behavior that would enhance the survival of developing young.

Because aggressive competition would be pointless unless some proximate or ultimate resource were gained (MacArthur, 1972), the agonistic behavior observed among NPB marmots is assumed to be directed primarily toward monopolizing food or burrows, either or both of which could be potentially limited in supply. Because the quantity of food and burrows increases as snow-pack gradually diminishes, these resources become less limited as the season progresses. If there is aggressive competition for food and/or burrows, it should decrease as resource availability increases. The general seasonal decline in agonistic behavior is consistent with the contention that aggressive competition declines as resource availability increases. This decline is also consistent with the hypothesis that agonistic behavior should decline in response to diminishing reproductive activity and spatial packing of marmots as the season progresses.

One question then remains, are burrows and/or food defended? It is advantageous to defend an area only if an adequate supply of a limited resource is found in an area small enough to defend economically (Brown, 1964). An important characteristic of defense of a fixed area is range exclusivity (Brown and Orians, 1970). The lack of forage range exclusivity at the individual and burrow-group levels (Tables 5 and 6) suggests that either food resources were unlimited (and thus required no competitive exclusion) or food resources were limited in availability, but were not defended as exclusive areas. If burrows were the only resource that marmots defended, the location of agonistic encounters should be strongly clumped around occupied burrows. Although many agonistic encounters were clustered around burrow sites, a substantial proportion of agonistic encounters occurred in foraging areas. This spatial distribution of agonistic encounters suggests that NPB marmots defended resources by maintaining an individual distance (Hediger, 1941). The scatter of locations of agonistic encounters indicates that this individual distance of intolerance moves with the marmot. Because marmots spend a large proportion of above-ground time near their burrows (Armitage, 1962; Travis and Armitage, 1972), the clustering of agonistic encounters around burrows may reflect activity patterns, and not specific burrow defense. Individual distance was maintained by Uinta ground squirrels (*Spermophilus armatus*), which do not defend home ranges (Balph and Stokes, 1963).

3. Social Dynamics, Natality, and Parent–Offspring Relations

A parent may attempt to maximize its inclusive fitness at the possible expense of the fitnesses of some of its offspring (Trivers, 1974). Yellow-bellied marmots may disperse as yearlings, as two-year-olds, or not at all. The major benefit of an extended period of juvenile residency is timing dispersal so that survival risks are minimal. Although an extra year of juvenile residency may appear contrary to parental interests, marmots appear to have adaptations that resolve this conflict.

The length of the parent–offspring bond is often determined by the period of nutritional dependence of the young (Crook et al., 1976). In habitats where food becomes scarce for part of the year, the period of dependence may extend

beyond one season. This dependence occurs among yellow-bellied marmots that inhabit areas where snowpack covers most vegetation for up to eight months each year. By sharing summer burrows, foraging areas, and hibernacula with young of the year, adult marmots maintain the parent-offspring bond for several months beyond the time of weaning. In the ERV colonies, most offspring emigrate in their second summer of life; only 5% of the male yearlings and 46% of the female yearlings were trapped in their natal localities as two-year-olds (Armitage and Downhower, 1974). NPB marmots had a greater tendency toward delayed dispersal: 24% of the male yearlings and 64% of the female yearlings were trapped in their natal areas as two-year-olds.

A number of factors may promote a greater tendency among NPB marmots to extend the parent-offspring bond long after weaning. Barash (1973b) postulated that Olympic marmots (*M. olympus*) delay dispersal until the age of two because of retarded growth rates and the need to approach adult size before dispersing. This hypothesis is rejected for yellow-bellied marmots in NPB; juvenile and yearling growth rates often exceeded those of marmots in ERV (Andersen et al., 1976; Armitage et al., 1976). The prolonged parent-offspring bond among many NPB marmots may best be explained in terms of parental investment theory (Trivers, 1972). Although delayed dispersal may enhance an offspring's chances of survival, the offspring's continued dependence may adversely affect parental ability to invest in other young, and therefore operate against delayed dispersal. However, if little or no additional investment is incurred by parents of offspring that stay, delayed dispersal should be favored by natural selection.

Female yellow-bellied marmots inhabiting ERV sites (2,900 m) often reproduce annually (Downhower and Armitage, 1971). The failure of females in NPB (3,400 m) to produce litters in consecutive years is reflected in the mean numbers of young produced per adult female per year in each of the two areas. The average of 0.94 for NPB females was only half that (1.99) reported for ERV colonial females (Armitage and Downhower, 1974). Because the number of young produced per litter was almost identical for the two areas (NPB=4.07, ERV=4.15), the difference in fecundity is accounted for entirely by differences in frequency of litter production (NPB=0.23/adult female/year; ERV=0.48/adult female/year). The low rate of litter production in NPB is probably associated with the poor success rate of pregnancies; only half of the NPB adult females presumed to be pregnant produced litters above ground. At high elevations the postweaning growth period may not be sufficient to allow postpartum females to both survive hibernation and reproduce the following spring (Andersen et al., 1976).

The litter-free year allows offspring an additional year of residency in their natal harem areas without directly interfering with the production of another litter by their mother. However, their prolonged presence may interfere with the litter production of other harem females. Because no yearling occupied a burrow in which young were weaned, the most likely source of interference by yearlings would be competition for food resources. Parent-offspring amicability and agonistic behavior between yearlings and nonparent adults characterized adult-yearling behavior (Table 8).¹ Cohesive behavior between parents and year-

ling offspring would facilitate delayed dispersal. However, since yearlings are subordinate to adults (Fig. 7), agonistic behavior by nonparent adults would promote early dispersal.

Young males have a greater tendency to disperse than females in both NPB and the ERV. Male yearlings are potential rivals of the territorial male. Dispersal of yearling males is promoted by the territorial male who frequently drives them off (Armitage, 1974). However, male yearlings disperse in the absence of overt aggression. They may view their prospects of mating as being highly improbable if they stay where a larger male controls the territory.

4. Social Dynamics and Male Territoriality

The continuous association of the harem male with the harem may indirectly aid in rearing young. Crook et al. (1976) postulated that only if the male's presence significantly enhances the survival of his offspring will he be tolerated by and stay with the female(s) through gestation and rearing. Among hoary marmots (*M. caligata*) the male may enhance survival of his progeny by facilitating their social integration prior to hibernation and/or by increasing alertness to predators (Barash, 1975). In addition, the male's maintenance of a territory would prevent conspecifics from exploiting resources that his own young might require (Crook et al., 1976). However, territory maintenance may be part of the male mating strategy. A male may continuously maintain a territory in order to increase his fitness beyond that gained by exclusive insemination of the resident females (Trivers, 1972). This additional fitness could be gained as a result of female mate selection. Female mate selection may be based on the morphologic and/or behavioral traits that reflect male fitness and on the quality of the male's territory (Orians, 1969; Emlen and Oring, 1977). The second seasonal peak of sexual encounters in August (Fig. 6) may be interpreted as a well-timed announcement of male fitness to females that are selecting hibernacula. The occurrence of the majority of shifts in residency by adult females after the breeding season (Table 2) is consistent with the contention that females may select between territories of varying quality. A male may indirectly advertise his fitness by continuously controlling access to the resources within his territory.

Although female mate selection is possible, it is unlikely the major selective pressure causing territorial maintenance. A female cannot travel between widely spaced localities in order to assess either the male or the habitat quality. Furthermore, strange females are usually excluded by the residents (Armitage, 1975). A female is more likely to be better off where she is than to risk the uncertainties of seeking a 'better' male and of gaining residency. Therefore, territorial control may be necessary because of male competition for better quality territories (Orians, 1969). Peripheral or transient males represent potential competitors for colonial sites; six of twenty such males trapped in the ERV became colonial in the area in which they were trapped (Armitage, 1974).

Marmots are long-lived; males commonly attain the age of six to eight years and may be resident, colonial males for three years or more. Thus the

maintenance of territories can be viewed as a strategy of prospective parental investment (Dawkins and Carlisle, 1976; Maynard Smith, 1977), since natural selection will favor the strategy that maximizes future genetic contribution, regardless of past expenditures. The continued defense of the territory assures that the male and associated females will have one or more hibernacula which, in turn, facilitates their overwinter survival and association during breeding following emergence in the next year.

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