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Author(s): Kenneth B. Armitage

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POPULATION CHANGES AND SOCIAL BEHAVIOR FOLLOWING COLONIZATION BY THE YELLOW-BELLIED MARMOT

KENNETH B. ARMITAGE

ABSTRACT.—In most years, the population of a colony of yellow-bellied marmots (*Marmota flaviventris*) was fluid because of dispersal of yearlings and addition of young; the adult population remained relatively stable within any year. Recruitment to the adult population occurred solely from animals born in the colony. Total number of young produced was closely correlated with the number of females of reproductive age; the number of young per female decreased at higher population densities because of a greater percentage of nonbreeding 2-year-old females in the population. There was no density-dependent relationship between numbers and survival of young or between number of yearlings and number of adults. The rate of social interactions was generally highest in June and decreased thereafter. Year-to-year and seasonal variations in rates of social interactions are interpreted in relation to the social structure of the population. Rates of social interaction were not directly correlated with population density. The dispersion of the population increased as the population increased. Adult males attempted to obtain exclusive use of the area and directed most of their agonistic behavior toward other males, both adults and yearlings. Agonistic behavior among females exceeded amicable behavior in only one of the five years of study. The growth of the harem may be possible because of mutual tolerance among females. Play fighting occurred only among yearlings. A complex interaction occurs between the behavioral characteristics of the individual animals and density effects related to the number, age, and sex of the animals.

Downhower and Armitage (1971) proposed a model describing the development of polygynous mating systems, derived from an analysis of demographic data on yellow-bellied marmots (*Marmota flaviventris*). The model indicated that males should be territorial toward other males, but should recruit females. Females, on the other hand, should attempt to exclude other females as females are most fit when they are monogamous.

It follows from the model that as harem size increases, agonistic behavior should increase as the females attempt to exclude one another from the harem. However, agonistic behavior and population density were not directly related in a colony of marmots studied for 4 years in Wyoming (Armitage, 1962). Armitage suggested that both the number of animals and the behavioral characteristics of animals interacted in complex ways to produce the observed rates of agonistic behavior.

In the previous studies of marmots (Armitage, 1962, 1964), the analysis of social dynamics was based on a sampling of events from a larger on-going behavior-population system. In effect, the sampling over a short segment of time did not permit an interpretation of observed events to be influenced by the history of the animals present. The ontogeny of a population can be known only by studying it long enough so that the history of each animal is known or by studying a population from its inception. This paper presents



FIG. 1.—View of localities 1 and 2 from the west. Burrows at locality 1 were mainly in the face of the steep river bank; those at locality 2 were mainly under the buildings. Hills to the east of the localities contain many burrows under exposed rocks, but no marmots have lived more than a few days in the hill area.

an analysis of behavioral patterns associated with population growth in a colony of marmots from its inception to its elimination and interprets these patterns in light of the polygyny model.

METHODS

The area chosen for study was locality 2 (Downhower and Armitage, 1971; Shirer and Downhower, 1968), 0.8 kilometers south of the Rocky Mountain Biological Laboratory, Gothic, Colorado. Activity of *Marmota flaviventris* centered on a group of buildings (Fig. 1) on the east side of the East River. Locality 2 is 255 meters by the most direct route from locality 1, which centers on a shale cliff along the East River (Fig. 1). The intervening area is a rolling meadowland of grasses and mixed forbs. Low hills lie to the northeast, east, and southeast of locality 2.

In 1963, all marmots at locality 2 were trapped and introduced into other areas; none returned. In 1964 through 1969, animals appearing at this locality were live-trapped and marked (Armitage, 1962). Subsequent field observations indicated that every animal was trapped and marked each year. In 1969, all remaining animals were removed at the request of the owner of the cabin complex and the study was terminated.

Animals were observed with a spotting scope from an automobile approximately 350 meters distant. There was no indication that observation affected the animals' activities. Behavioral interactions were recorded in a notebook and the locations of active animals were marked on a map of the locality. Observation occurred in the morning and evening,

the periods when animals are most active (Armitage, 1962). Most interactions were placed in the general classification of amicable or agnostic. Amicable behavior (Ewer, 1968:186) includes those activities, such as greeting and social grooming (Armitage, 1962), that lead to socialization or affiliation (Zajonc, 1971). Agnostic behavior includes those activities, such as chase, flight, "ready alert," that represent conflict between individuals (Scott, 1956). Previously, I (Armitage, 1962) considered social grooming to be agonistic because it occurred in dominance-subordination relationships in which the dominant animal groomed the subordinate. However, many additional observations of this behavior in several colonies of marmots revealed that subordinate animals may groom dominant animals and that the interaction did not result in chases or flight behavior. Grooming, therefore, apparently is a form of appeasement (Eibl-Eibesfeldt, 1970:127) enabling a subordinate animal to coexist with one or more dominant animals.

Play fighting is reported as a third type of interaction. This behavior consists of one animal leaping at another, striking another with the forefeet, wrestling, chasing, dashing about; all typical of this behavior in mammals (Ewer, 1968:291). Because the function of this behavior is unclear, it cannot be categorized as amicable or agonistic. Behavior categorized as play fighting occurred only among yearlings. Behavior of juveniles is not included.

POPULATION CHANGES

In 1964, an adult male and adult female formed a colony. Five yearlings were present in June; two of these were young at locality 1 (Fig. 1) in 1963. Only one yearling, a female, remained at locality 2 beyond 1 July. One young appeared above ground in early July. None of these individuals were identified in succeeding years.

In 1965, ♀649 occupied the main burrow system under cabin 1. She was born at locality 1 in 1962 and was retrapped there as a yearling in 1963 and in 1964 when 2 years old. An adult male was present, but was driven out in late June by the male at locality 1. From this time through 1968, localities 1 and 2 were technically one harem because the territory of one male included both localities. About the middle of July, ♀91 from locality 1 moved with her young to locality 2. Eight young were present in two litters, five in the litter of ♀649 and three in the litter of ♀91.

In 1966, ♀649 was the only adult residing at locality 2, although the male from locality 1 occasionally visited. Five yearlings, all born at locality 2 in 1965, were present in June; the two male yearlings dispersed by early July. One litter of six young was observed.

In 1967, there were five adults, ♀649, three 2-year-old females who were the yearling females of 1966, and a male. The male was chased out by the adult male from locality 1 in early July. Five yearlings were present in June; all were from the litter of the previous year. By early July only one yearling, a female, remained. Three litters, totaling 15 young, appeared above ground on 10 July.

In 1968, ♀649 returned to locality 1. The adults remaining at locality 2 were two 3-year-old females and one 2 years old. A 2-year-old male was present until he was driven out by the male from locality 1 in the middle of June. The 2-year-old male returned in late June and was driven away again in early July. A third male appeared in the middle of July, but departed by late July. Of the eight yearlings present in June, four remained throughout the summer. Three of these were males and all were gone the following year. Eight young from two litters were trapped.

In 1969, ♀649 remained at locality 1 with a yearling female who was at locality 2 in 1968. At locality 2, one of the males who was driven away in 1968 was present along with two 4-year-old females. Four yearlings were in the vicinity, but these had dispersed to River Bend (Fig. 1). The two 4-year-old females apparently were not lactating and probably did not have litters. All animals were removed.

From the foregoing it is clear that in most years the marmot population was fluid rather than stable. The fluidity resulted primarily from the dispersal of yearlings and birth of

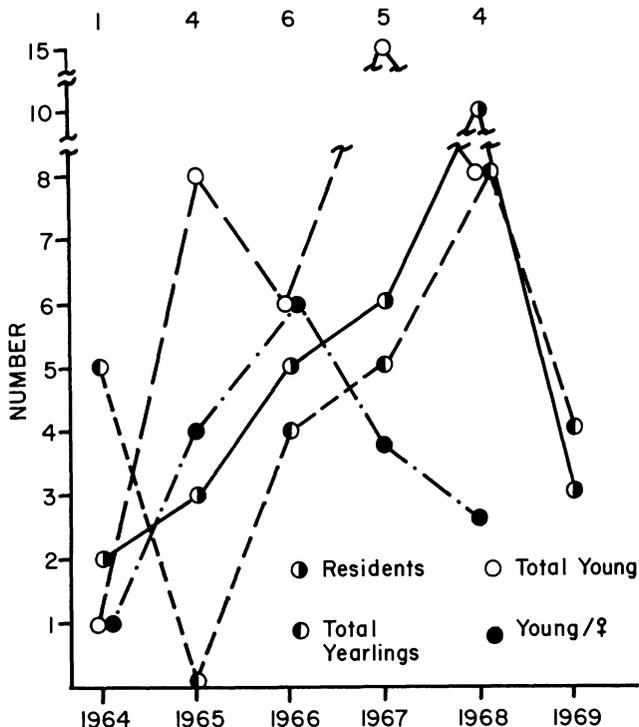


FIG. 2.—Population and reproduction at locality 2. Numbers across the top are mean litter sizes for the years 1964 through 1968. Total yearlings refers to the number present at the start of the summer and includes those yearlings that emigrated during the summer. Residents include the adults and those yearlings that remained throughout the summer. Young per female is the total number of young that appear above ground divided by the total number of resident adult females.

young. The adult population remained relatively stable in any year. Recruitment to the adult population occurred solely as a result of survival of animals born in the population. The number of resident marmots (adults and yearlings) varied from two to 10 (Fig. 2). The number of young varied from one to 15. The total number of yearlings varied from none to eight (Fig. 2).

The curves for total number of yearlings and total number of young paralleled the curve for residents (Fig. 2). Thus the production of new marmots is related to total population size. The number of young is more closely correlated with the number of females of reproductive age. The Spearman rank correlation coefficient was 0.95 (Siegel, 1956: 202). However, the number of young per female increased in each year from 1964 through 1966, then decreased in 1967 and 1968. This relationship indicates a reduction in the production of young per female at higher population densities. The mean litter size was essentially the same in all years except the first (Fig. 2). Thus, the reduction in the number of young per female must have resulted from some females not reproducing at the higher population densities. In 1967 and 1968, one female in each year did not produce young. In each case the female was 2 years old. Of a total of 25 known 2-year-old marmots in the East River Valley, 17 did not produce young. The decrease in the number of young per female in 1967 and 1968 may be attributed mainly to the proportion of non-

breeding 2-year-old females in the population, 25 per cent in 1967 and 33 per cent in 1968. These data are similar to those for *M. monax* in which a shift of the age structure of the population toward younger animals results in the production of fewer young (Snyder, 1962).

The proportion of young recaptured as yearlings was 50 to 62 per cent except in 1967 when five yearlings from a litter of six were recaptured and in 1965 when there was no recovery of the single young of 1964. The 37 to 50 per cent loss of young may occur through emigration as young, overwinter mortality, predation, or early emigration as yearlings. Trapping records revealed the loss of only four young in 1965, one in 1967, and none in 1968 by late August or early September just prior to hibernation. Thus, there is no relationship between population density and loss of young. The loss of young most probably occurred as winter mortality or emigration as yearlings prior to our arrival on the study area. In 1969, trapping was begun by the middle of May and animals were dispersing at that time, but were still within the general locality. Most of them dispersed from the area by mid-June, thus supporting early dispersal as a possible source of loss of numbers between young and yearlings. Because only four yearlings were present in 1969, there was a loss of four young over winter, thus supporting winter mortality as a source of loss of animals. There is no relationship between the number of yearlings and the number of adults. In conclusion, the available data do not support any density-dependent relationship between numbers and survival of young or between number of yearlings and number of adults.

SOCIAL INTERACTIONS

The rate of all social interactions generally was highest in June and decreased thereafter (Table 1), a pattern apparently common to ground squirrels (Armitage, 1962; Bronson, 1964; Yeaton, 1972). The major exception to the pattern occurred in 1968 when social interactions increased in the second half of July. The total rates in any time block varied considerably among years and the rates of the three categories of behavior did not always vary alike (Table 1). The year-to-year and time-block-to-time-block variations in rates of behavior are interpretable only in relation to the social structure of the population.

In 1964, a new harem was in the process of formation. All amicable behavior occurred between the adult male and the adult female or yearling female. All agonistic behavior involved yearlings. The emigration of most of the yearlings by early July was associated with the absence of agonistic behavior and play fighting. However, the rate of amicable behavior remained high, particularly because of interactions between the adult male and the remaining female yearling.

All social interactions in 1965 were agonistic. Two adult males were contesting the area and half the interactions in June were between the males. The adult female tended to flee at the approach of a male. By early July one male was gone, but the female still displayed some agonistic reaction to the remaining male who, however, spent most of his time at locality 1. The rate of agonistic behavior decreased along with this change in social structure and was not observed after the first part of early July.

In 1966, all agonistic behavior occurred between a male yearling and a female yearling. Only 9 per cent of the amicable behavior was between a male yearling and a female yearling. By contrast, 45 percent of the amicable behavior was among female yearlings and 45 per cent was between an adult and a female yearling. The small amount of play fighting occurred among female yearlings. The male yearlings emigrated and the female yearlings became members of the colony.

In 1967, all amicable behavior was among adults. Male yearlings took part in every observed play fighting, half the time with female yearlings. All agonistic behavior involved adults. About three-fourths of the agonistic behavior was between adults and male yearlings. Adult male-yearling male agonistic behavior accounted for 65 per cent of the

TABLE 1.—Rates of social interactions among adults and yearlings. Rates are calculated as number per animal per hour and are summarized in four time blocks. A = agonistic, Am = amicable, P = play fighting, T = total (sum of A + Am + P), — no observations.

Year	June 1–June 15				June 16–June 30				July 1–July 15				July 16–July 31			
	A	Am	P	T	A	Am	P	T	A	Am	P	T	A	Am	P	T
1964	—	—	—	—	.19	.10	.10	.39	0	.37	0	.37	—	—	—	—
1965	—	—	—	—	.17	0	0	.17	.07	0	0	.07	0	0	0	0
1966	0	.02	0	.02	.07	.10	0	.17	.02	.02	.02	.06	0	.03	0	.03
1967	.07	0	.1	.17	.09	.01	.01	.11	.03	.03	0	.06	0	0	0	0
1968	.11	.03	.12	.26	.10	.05	.09	.21	.09	.03	0	.12	.21	.13	0	.34

total. Adult male-adult female conflict accounted for 12 per cent of the agonistic interactions. Conflict between two adult males and between an adult male and yearling female accounted for 6 per cent each. The interactions of female adults and yearlings with an adult male were all attributable to the avoidance of a strange male by females. Most of the interactions occurred during June. By early July, only one yearling, a female, remained. The other yearlings apparently emigrated because of the agonistic behavior directed toward them. Indeed, one male yearling was seen leaving immediately at the end of being chased by an adult male. The low rate of amicable behavior is attributed to two factors: the three 2-year-old females were incorporated into the colony in the previous year and there seemingly is no sustained reinforcement of social bonds once they are formed, and neither of the female yearlings was successfully joining the harem as the one who remained spent much of her time on the periphery of the colony (Fig. 5).

In 1968, play fighting among yearlings was most frequent in early June and ceased by early July (Table 1). Male-male interactions accounted for 73 per cent of those instances of play fighting when the yearlings were identified. Patterns of agonistic behavior were more complex. About 7 per cent of the agonistic interactions occurred between the resident male and two intruder males. About 6 per cent of the conflicts occurred between an adult male and an adult female, and all of these were within a 5-day period in the middle of June when the level of conflict was high among the adult males. Only 2 per cent of the agonistic behavior was among adult females and only 1 per cent was among yearlings. Thus, 84 per cent of the agonistic behavior was between an adult and a yearling. About half of all agonistic interactions were between an adult male and a yearling male. By contrast only one twenty-fifth of the agonistic behavior was between an adult male and a yearling female. Adult female-yearling interactions accounted for 32 per cent of the agonistic behavior, of this 32 per cent, 30 per cent was between females and 70 per cent was between male and females.

Patterns of amicable behavior also were complex in 1968. Thirty-four per cent of all amicable behavior was among yearlings and 32 per cent was between yearlings and adults. Most of the adult-yearling amicable behavior was between an adult female and a yearling male and usually involved social grooming. Two observations of amicable behavior between a male yearling and a male adult were greetings; the adult male was the 2-year-old intruder. Amicable behavior among adult females accounted for 9 per cent of the total. Adult male-adult female interactions accounted for 25 per cent of the observed amicable behavior. All except one of these interactions were between one of the intruder males and a resident female.

POPULATION DENSITY AND SOCIAL INTERACTIONS

Behavioral interaction as a density-dependent regulator of population has been proposed in several forms (Wynne-Edwards, 1965; Christian and Davis, 1964; Chitty, 1967). Wynne-

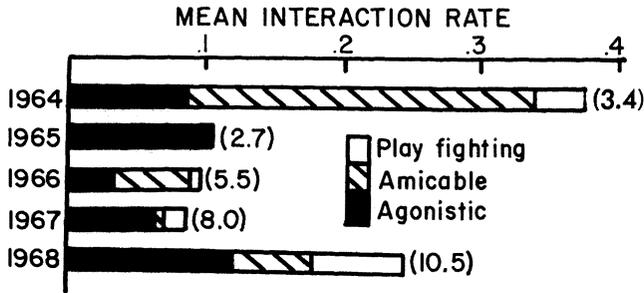


FIG. 3.—Mean interaction rate (MIR) among yearlings and adults at locality 2. MIR was determined by multiplying the number of hours of observation times the number of residents in each time period (Table 1) to derive animal-hours, summing the animal-hours from each time period to form total animal-hours, and dividing the total number of social interactions observed throughout the summer by total animal-hours. The final value (MIR) is the number of social interactions per animal per hour of observation. The number at the end of each bar is the mean number of residents and is derived by summing the number of residents in each time block and dividing by the number of time blocks.

Edwards especially has emphasized that the homeostatic system operates through feedback. If a feedback homeostatic system were operating to control the number of marmots in a colony, amicable behavior should decrease and agonistic behavior increase as the number of marmots increases. Unless there are lag effects in the system, rates of social interactions should be directly correlated with population density. However, no such relationship exists between mean interaction rate and mean number of residents or between either the rates of amicable or agonistic behavior and mean number of residents (Fig. 3). The rate of play fighting, however, is related to the mean number of residents. A recalculation of rates of play fighting as number per yearling present in the colony per hour reveals that the rate of play fighting is directly related to the number of yearlings present, but is not related to the number of adults present. Thus the relationship between the rate of play fighting and mean number of residents (Fig. 3) occurs because the variation in the mean number of residents was strongly influenced by the number of yearlings present.

Both agonistic behavior and mean number of residents increased from 1966 through 1968 (Fig. 3). This trend is consistent with the hypothesis of density-dependent regulation. This regulation seemed to affect primarily recruitment and dispersion. Yearlings present in 1966 and 1967 were added to the adult population in 1967 and 1968. Their addition to the population was the sole cause of population growth as no adults born outside the colony were added. The peak of population in 1968 occurred because of the presence of six yearlings, because two adults present in 1967 were not present in 1968. One of them, ♀649, returned to locality 1 (Fig. 1) where she displaced two 2-year-old females and two yearling females. The other adult female apparently died over winter. In 1969, the drop in population is attributed to no recruitment of yearlings into the adult class, the presumed overwinter death of a 2-year-old female and the absence of yearlings. Thus the major cause of population decline of adults was insufficient recruitment to replace adult losses (most of which were presumed mortality).

As the population increased, the dispersion of the population increased. In 1966, the home range of ♀649 centered in the area around cabins 1 and 2 (Fig. 4) with a few excursions beyond this core area. This same area was the home range of the resident adult female in 1964 and 1965. The home ranges of the yearling females overlapped that of the adult female, but activity centered on the wall area and much activity occurred in the area

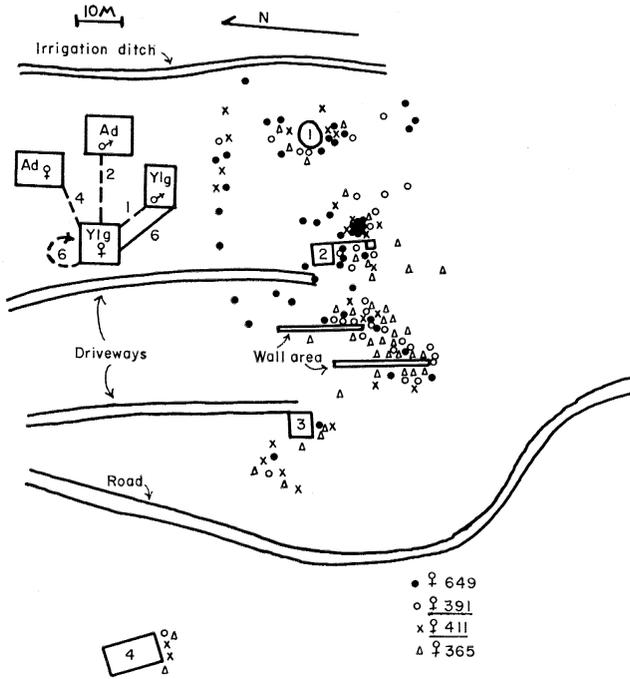


FIG. 4.—Home ranges of female residents in 1966. Yearlings are underlined. Main buildings are numbered. Home range is indicated by placing a symbol on the map of locality 2 where the animal was observed to be active. Thus, the map shows areas of use and not the total area through which the animals moved. The diagram in the upper left shows the absolute number of social interactions among the major categories of sex and age. A line connects the age-sex categories between which social interactions were observed and the number of interactions is placed by the line. Ylg = yearling; Ad = adult; — represents agonistic behavior; - - - represents amicable behavior. Social interactions within a sex-age category are shown by an arrow forming a loop from and to that category.

around cabins 3 and 4. In addition, the yearlings in late June and early July made excursions to the hill area to the east (Fig. 1).

In 1967, home range of ♀649 was essentially the same as it was the previous 2 years. However, dispersion of adults was clearly evident as the home ranges of the 2-year-old females occupied much of the area from the wall to cabin 4 (Fig. 5). The home range of one of these females was highly unstable and she made frequent excursions to an area south on the west side of the river and sometimes remained in this area for several days. There are fewer observations of this animal because she spent most of her time around cabin 4 where she could not be seen. The one yearling established a home range around cabin 1 where there was little adult activity. The overall dispersion of the resident animals resulted in use of all of locality 1 close-in to the burrow sites under the cabins and in the wall area.

In 1968, the two 3-year-old females occupied the area previously used by ♀649. The home ranges of these two marmots were larger than that of ♀649 in previous years. The 2-year-old female now occupied the area centering on cabin 4 (Fig. 6). The home ranges of the yearlings essentially were in the area from the wall to cabin 4. The total area used

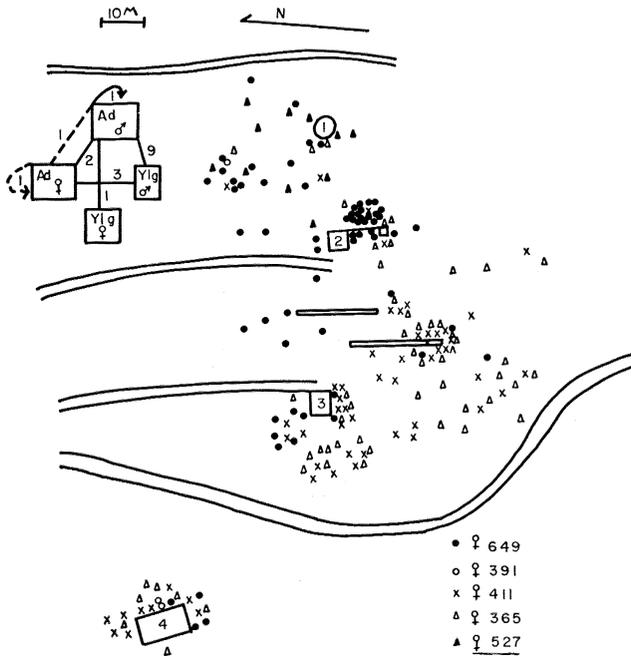


FIG. 5.—Home range of female residents and absolute number of social interactions in 1967. Symbols as in Fig. 4.

by the residents was slightly expanded over that used in 1967. The yearlings also made excursions beyond the colony area along both sides of the river and frequently spent several days in the river bend area. The 2-year-old female also went to the south area on the west side of the river, although she established her litter of young at cabin 4.

DISCUSSION

Social interactions are related both to density of marmots and social structure of the population. Rates of agonistic behavior were highest when the mean population density was highest and second highest when mean population density was lowest (Fig. 3). In 1965, the high rate of agonistic behavior was related to conflict among territorial males (such conflict is relatively uncommon—Armitage, 1973); in 1968, most of the conflict was adult:yearling. The highest total mean interaction rate occurred in 1964 when a new population was invading the locality; the lowest mean interaction rate occurred in 1967 when the number of adults was the highest of the 6 years of the study. Therefore, any assessment of the role of social behavior as a density-dependent regulator of population density must take into account the age and sex of the interacting animals.

Behavioral relationships apparently are more subtle than the observation of overt interactions indicates. In 1966, the agonistic interactions were be-

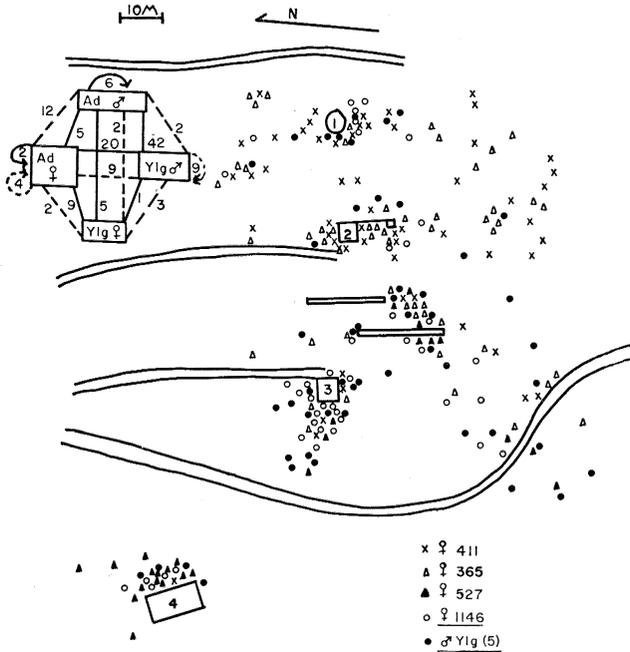


FIG. 6.—Home ranges of female residents and male yearlings and absolute number of social interactions in 1968. Symbols as in Fig. 5 except there are 18 additional observations of male yearlings at cabin 4, 27 additional observations of male yearlings at cabin 3, 27 additional observations of male yearlings and nine additional observations of the female yearling at the wall area, nine additional observations of ♀ 411 and 18 additional observations of ♀ 365 around cabin 2. Home ranges of the five yearling males are lumped together.

tween yearling males and yearling females (Fig. 4). Most of these were avoidance of the males by the females. The male yearlings dispersed. In 1967, the adult male was highly agonistic to the male yearlings and the male yearlings dispersed (Fig. 5). In 1968, the adult males were highly agonistic to the male yearlings, but most of the male yearlings remained throughout the summer, although spending much time in peripheral areas (Fig. 6). Thus among marmots, as among Richardson's ground squirrels (Yeaton, 1972), there is no consistent direct correlation between agonistic behavior and dispersal. The lack of such direct correlation likely results from the behavioral diversity among the individuals of a population. Svendsen and Armitage (1973), using factor analysis of behavioral patterns measured during mirror image stimulation, found a broad continuum of behavioral profiles. Some animals were highly social, whereas others were characterized by avoidance. Some were aggressive, others, amicable. The continuum of behavioral profiles is evident in young marmots (G. A. Svendsen, personal communication). Thus, a population of marmots, and probably other mammals as well, contains a broad behavioral substrate upon which social interactions occur. Given this

behavioral diversity, it follows that some animals may disperse as a response to the presence of others; some may disperse only when harassed, and some may remain in a locality despite agonistic conflict.

The complexity of the interaction between an individual with a particular behavioral profile and its population environment is well illustrated by ♀649. When ♀649 lived at locality 1 in 1964, she was involved in 23 per cent of all observed interactions, 78 per cent of which were agonistic. That year locality 1 was characterized by a high rate of agonistic behavior, 87 per cent of which was among adults. ♀649 was chased by another adult in one-third of her interactions. She had the largest home range of all the females with a diameter (as measured across the widest part of the area she utilized) of 200 meters. Her movements took her more than half way toward locality 2. Her behavior in 1964 characterized her as relatively subordinate. Her movement to locality 2 in 1965 is interpreted as avoidance of the social conflict associated with the marmots at locality 1. As a nonagonistic animal, her observed social interactions with yearling and adult females in 1966 and 1967 were amicable. These animals were her offspring and social bonds probably formed, in part, in 1965 when these animals were young. However, in 1968 she moved back to locality 1 and chased out two yearling and two 2-year-old females. Apparently she was an animal who could not tolerate crowding. If she could not tolerate crowding, why did she not drive away the yearlings in 1966? Possibly because the yearlings dispersed into areas not utilized by ♀649 (Fig. 4) and social conflict was avoided. In 1967, the dispersion of the residents would reduce social contact (Fig. 5). Not until 1968 were the social pressures great enough that ♀649 reacted. Evidently she could not exclude the other adults from locality 2 and she dispersed to an area where she could obtain exclusive use. Admittedly this interpretation is speculative, but it is consistent with the observed behavior and with our knowledge of the variability of behavioral profiles.

The analysis of the behavior and population changes of the marmots at locality 2 indicates that the factors determining harem size are related to the behavioral profiles of the residents. As predicted by the model (Downhower and Armitage, 1971), males did attempt to obtain exclusive use of an area. Adult males directed most of their agonistic behavior toward other males, both adults and yearlings (Figs. 5, 6) and their amicable behavior was primarily with yearling and adult females (Figs. 4 to 6). Most of the agonistic behavior between adult males and females was avoidance of the male by the female; most of the agonistic behavior among males was chasing. Thus, males did attempt to maintain harem size through amicable behavior with females and by refraining from aggressive acts toward females. However, there was no behavior that could be interpreted as overt recruitment of females into a harem. For example, a male did not attempt to prevent a female from dispersing. Thus, male behavior toward females may be categorized as acceptance of and amicable behavior toward whatever females are present in the area he

occupies. Because females are more fit when they are monogamous, they should try to exclude other females from a harem (Downhower and Armitage, 1971). However, agonistic behavior among females was rare until 1968 (Figs. 4 to 6). Only in that year did agonistic behavior between adult females and yearling females exceed amicable behavior. The growth of a harem may depend on the presence of one or more females whose behavioral profiles result in either the tolerance of other females or in the inability to exclude other females. This interpretation is consistent with the population growth described above for locality 2. Small harems probably occur when the resident female(s) can exclude other females. This pattern may have been developing in 1969 when only two adult females remained and the yearlings had dispersed by the middle of May. Unfortunately, the need to remove the population in 1969 prevented further analysis of this problem.

CONCLUSION

Analysis of data obtained from a marmot colony, beginning from one female, indicates a complex interaction between the behavioral characteristics of the individual animals and density effects related to the number, age, and sex of the animals. The population-behavior system is dynamic, and changes through time, both within a year and between years. Because this system is dynamic, there is no population level that is homeostatically maintained. Rather, the population grows or declines as a result of a complex of environmental factors, including behavior. Any attempt to relate social behavior to population dynamics or to environmental factors such as habitat, clearly requires long-term study and detailed knowledge of the individuals in the population.

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Department of Biology, The University of Kansas, Lawrence, 66045. Accepted 27 January 1973.