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# Social Dynamics of Juvenile Marmots: Role of Kinship and Individual Variability

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**Summary.** A population of eight juvenile female yellow-bellied marmots (*Marmota flaviventris*) was introduced into a marmot locality from which all other marmots were removed. Social interactions were monitored in the field and the individual behavioral profile of each animal was determined by mirror image stimulation. Social interactions were unequally distributed among the eight juveniles. Neither body size nor kinship were significantly related to frequencies of social interactions. Social interactions were significantly related to individual differences.

important in sibling interactions and in decreasing agonistic behavior among mammalian conspecifics (see review by Bekoff 1981 b). Another factor which may influence behavioral dynamics is individual behavioral variability.

In view of the arguments raised by Charnov and Finerty (1980) and Bekoff (1981 a, b), the results of the following experiment should be of interest. I believe the results suggest that individual behavioral differences markedly affect social dynamics (also see Bekoff 1977).

## Introduction

Emigration is the usual response to increased density in natural populations (Archer 1970). The proximal factors initiating dispersal, which is density-independent, are unknown (Gaines and McClenaghan 1980).

Charnov and Finerty (1980) suggested that kin-selection may contribute to vole population dynamics. In brief, they argue that when the population density is low, the coefficient of relatedness,  $r$ , is probably high among nearest neighbors, and aggressive interactions among neighbors are few. As the population increases,  $r$  among nearest neighbors decreases and aggressive interactions with their consequent effects on population dynamics increase. Thus, average  $r$  may drive the behavioral changes associated with population dynamics. Bekoff (1981 a) argued that familiarity among individuals and not  $r$  is more important in mediating social interactions and is more likely than  $r$  to be the proximal factor affecting population dynamics. The possibility that kin-selection is a factor in population dynamics is attractive because of the prominent role social behavior plays in theories that populations in nature are self-regulating (Krebs 1978).

Available data suggest familiarity and not  $r$  is

## Materials and Methods

Eight female, weaned, juvenile yellow-bellied marmots (*Marmota flaviventris*) were live-trapped over an 8 day period in late July and early August. Each animal was identified by means of placing numbered tags in each ear and dyeing the fur with individual marks of stripes or blots. Animals were housed in a common cage in the laboratory until all eight were trapped. The number of female young used in this experiment equals the largest number of female young I have ever trapped in a harem. Each animal was submitted to mirror-image stimulation (Svendsen and Armitage 1973). Then they were introduced into marmot locality 4 (Armitage 1974) from which all other marmots were removed. Animals were about 10 weeks old.

The eight female young were observed for 12 h during a 12 day period. Observations were concentrated in morning and evening hours when marmots are most active (Armitage 1962). All social interactions were recorded and every 10 min the location of each animal was recorded on a map of the locality. The locations were later converted to grid coordinates and space-use was plotted as a perspective block diagram (Sampson 1975). The data from mirror-image stimulation (MIS) were combined with those of other juveniles and the entire data set was analyzed by factor analysis (Svendsen and Armitage 1973; Svendsen 1974).

## Results

No agonistic behaviors were observed nor have I ever observed agonistic behavior among juvenile marmots. Social interactions were greetings and allo-grooming (Armitage 1962) and play (Nowicki and Armitage

1979). A possible relationship between number of social interactions for each individual and the order in which the animals were trapped (hence, the amount of time spent in the common cage) was tested by the Spearman rank-order correlation. The relationship was not significant ( $r_s = -0.428$ ,  $P > 0.05$ ). Therefore, the variable time animals were housed together before being released did not affect their subsequent social behavior.

The number of social interactions per individual ranged from 5 to 31. Because all eight young lived in the same burrow, I assumed that each young had equal probability of engaging in social interaction. The distribution of observed social interactions was compared with the expected. For both total social interactions (play, greeting, and allo-grooming combined) and greetings, the number of observed interactions differed significantly from the expected (total:  $\chi^2 = 43.7$ ,  $df = 7$ ,  $P < 0.005$ ; greeting:  $\chi^2 = 16.2$ ,  $df = 7$ ,  $P = 0.025$ ).

One explanation for the unequal distribution of social behavior is that kin preferentially interacted. The eight young were placed in three categories: full-sibs, half-sibs, and unrelated. The category of half-sibs was established because four of the females were trapped from the same harem and had the same father, but I was unable to be certain that they came from one litter. Frequently, two or more female marmots occupy the same burrow system. When the young emerge above ground, they intermingle with each other and with the adult females to form one large social group. The animals designated half-sibs were at least members of such a group. Two animals were known sisters and two animals were known to be unrelated to any other animal. Therefore, the probability of encounters was calculated as follows:

$$\text{Full-sibs} = \frac{2 \text{ animals} \times 1 \text{ encounter}}{2} = 1.$$

$$\text{Half-sibs} = \frac{4 \text{ animals} \times 3 \text{ encounters}}{2} = 6.$$

$$\text{Unrelated} = \frac{2 \text{ an} \times 6 \text{ en} + 4 \text{ an} \times 4 \text{ en} + 2 \text{ an} \times 7 \text{ en}}{2} = 21.$$

$$\text{Total} = \frac{8 \text{ animals} \times 7 \text{ encounters}}{2} = 28.$$

Thus, full-sibs were expected to engage in 1/28 of the social interactions; half-sibs, 6/28; and unrelated, 21/28.

The following null hypothesis was tested: there is no difference between the observed pattern of social interactions and that expected on the basis of the number of animals in each group. The null hypothesis

was accepted for each category of social interaction (greeting:  $\chi^2 = 3.2$ ,  $P > 0.1$ ; play:  $\chi^2 = 1.2$ ,  $P > 0.5$ ; total:  $\chi^2 = 3.0$ ,  $P > 0.1$ ;  $df = 2$  in each case).

All animals were trapped and weighed at the end of the observations. Because body size could mediate social interactions, the relationship between body weight and the number of social interactions was tested by Spearman rank-order correlation. There was no significant relationship ( $r_s = -0.33$ ,  $P > 0.05$ ).

The factor analysis of the MIS data produced three axes which explained 85% of the variance. The rank order of the eight females on each axis was compared with their rank order of total social interactions observed in the field. There was no significant relationship with axis I ( $r_s = 0.285$ ,  $P > 0.05$ ). Animals scoring high on axis I were characterized by spending most of their time in the front of the arena, nosed and pawed at the image, but engaged in few other activities. This factor was designated 'approach'; this group included both social and aggressive animals (Svendsen 1974). There was no significant relationship with axis II ( $r_s = 0.334$ ,  $P > 0.05$ ). Animals scoring high on axis II made no contact with the image, did not engage in other activities, but tended to sit in the back of the arena. This factor was designated 'avoidance' because the marmots avoided social contact (Svendsen 1974). The relationship with axis III was significant ( $r_s = -0.857$ ,  $0.05 > P > 0.01$ ). Animals scoring high on this axis nosed and pawed at the image, tail-wagged, were likely to spend time in either the front or the back of the arena, and engaged in other activities such as eating and investigating the arena. Therefore, axis III was designated the 'sociability' factor (Svendsen 1974). Interestingly, the number of social interactions observed in the field was inversely related to the sociability ranking; animals ranking high on Factor II (avoidance) had more social contacts than animals ranking high on Factor III (sociability).

For further analysis, the juveniles were classified into aggressive, avoider, and sociable behavioral profiles by step-wise discriminant analysis with the option for classification of new cases (Svendsen 1974). This multivariate technique classified the young on the basis of known groups from factor analysis of MIS data. Three young were classified as sociable, two as aggressive, and three as avoider. The following null hypothesis was tested: there is no difference between the pattern of social interactions observed in the field and that expected on the basis of the number of animals in each behavioral category. The null hypothesis was rejected for play ( $\chi^2 = 22.8$ ,  $df = 2$ ,  $P < 0.005$ ). None of the sociable animals was observed to participate in a play bout; the aggressive animals participated in twice as many play bouts as expected

and avoider young were in 40% more play bouts than expected. The null hypothesis also was rejected for greeting ( $\chi^2 = 11.2$ ,  $df = 2$ ,  $P < 0.005$ ). Sociable animals greeted much less than expected, aggressive animals greeted slightly more and avoider animals greeted about 60% more than expected. For 25 greetings, the animal initiating the contact was known; sociable animals initiated a greeting less often than expected, aggressive animals initiated a greeting as often as expected and avoider animals initiated greetings about 50% more often than expected ( $\chi^2 = 4.33$ ,  $df = 2$ ,  $P \approx 0.1$ ).

Space-use patterns were either clumped or dispersed. There was no clear relationship between behavioral profiles and the space-use patterns. The more dispersed pattern was typical of one sociable, one aggressive, and one avoider animal. Rates of social interactions were not clearly related to space-use. One of the dispersed animals, an avoider, had the highest number of social interactions and another, a social animal, had the lowest. However, two of the three animals with the dispersed pattern were not recovered as yearlings the following year.

A seeming incongruity is that animals classified as avoider had the highest rates of social interactions and tended to initiate greetings. The behavioral profiles of avoider, sociable, and aggressive were based on the animals' responses to MIS. Under these conditions each animal encounters a stranger in an unfamiliar location. An animal with the avoider profile does not socialize with strangers in either field or laboratory, but may form social bonds with littermates and/or their mother (Svendsen and Armitage 1973; Armitage, unpublished data). The avoider is a submissive animal who might better be categorized as 'socially unsure'. The high number of social interactions by these animals likely represents their attempt to maintain familiarity with burrowmates and to form social bonds.

## Discussion

The results do not indicate that kin could not recognize each other but that kinship was not the major determinant of observed social behavior. Because sib groupings and length of association groupings were identical, length of association probably did not confound results. For example, full-sibs had lived together for 11 weeks; half-sibs, for at least 8 weeks; and the unrelated associated for 3 weeks. Kin preference may require continued exposure to kin over relatively long time periods (Porter and Wyrick 1979). If juvenile marmots require long exposure learning in order to discriminate kin, these results may indicate that such learning was in process and that social en-

counters occurring on the basis of chance is the mechanism by which familiarity develops. Possibly the brief period the animals were housed in the common cage provided sufficient time to establish familiarity and to override any influence of  $r$  on subsequent social interactions in the field. Only future experiments can discriminate between these possibilities.

Most importantly these results suggest that the individual behavioral profile is the proximal mechanism mediating social behavior. This individuality coupled with differences in patterns of space use provides a mechanism for determining recruitment and dispersal in natural populations. The results of a social encounter differ depending on whether an animal is a stranger or whether it is in its natal area. For example, an avoider profile probably would disperse from an area if it encountered a stranger whereas an aggressive profile probably would attempt to exclude other animals. We have observed these patterns in the field. For example, ♀ 843 frequently engaged in social interactions with her littermates as a sub-adult. But as a 2-year old she moved to a new location in the colony and had frequent social contacts with the adult male. As a 3-year old, she had a few amicable social interactions with her sister who moved with her litter into the same area. The next year, at age five, ♀ 843, living alone (her sister died in mid summer the year before) produced her first litter. The next year, immigrant ♀ 1082 (a stranger) moved in and ♀ 843 moved to a peripheral location where she lived alone for the last 5 years of her life. Although she produced 2 more litters while living as an isolate, she did not recruit any of her offspring into a social group. When 6-year old ♀ 649 moved from a nearby colony into River Colony, ♀ 690 and ♀ 685, both avoider animals, promptly emigrated. Three adult females were introduced into North Picnic Colony where aggressive ♀ 622 lived. None of the introduced females remained more than 2 days. By contrast, aggressive ♀ 755 successfully immigrated into the colony in the same year. These examples demonstrate the demographic consequences of individual behavioral variability. Further examples are described in Svendsen and Armitage (1973) and Svendsen (1974). Obviously the results of the behavioral acts of the aggressive and sociable profiles depend in part on the profile of the stranger. Therefore, population dynamics may be the consequence of the interaction of individuals of different behavioral profiles (i.e., phenotypes, see Bekoff 1977).

Familiarity decreases agonistic and increases amicable behavior; strangeness has opposite effects (Armitage 1977). Familiarity could be tightly coupled with relatedness (Bekoff 1981a; Charnov 1981); the population consequences would be kin-related. For

example, recruitment of kin occurs in marmot populations (Schwartz and Armitage 1980; Armitage, in preparation). A comprehensive model invoking kin-selection as an ultimate factor explaining population dynamics must also provide a mechanism whereby kin-selection operates. I conclude that the mechanism consists of three factors: familiarity, individuality, and dispersion. How these interact to determine recruitment or dispersal of individuals awaits further study in the field.

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