

## **Kinship, Reproductive Strategies and Social Dynamics of Yellow-Bellied Marmots**

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**Summary.** Social behavior of yellow-bellied marmots was observed for three years in colonies where kinship was known and for one year in a high elevation colony where harems were contiguous. Social dynamics of yellow-bellied marmots is dependent on kinship, group composition, and age-sex classes. This pattern is a consequence of the reproductive strategies of males and females. Females behave cohesively toward sisters or daughters, but not with sons and agonistically toward other females. Males generally behave amicably toward females and agonistically toward males, including their sons. Thus, reproductive strategies limit nepotism. This behavior is consistent with a population process in which sons typically disperse as yearlings. At least some of the variation in the expected patterns of social behaviors is attributable to individual differences. Because male and female reproductive strategies differ, a marmot population consists of two social subsystems. The female unit is the closely-related kin group which may also be a burrow group. The male unit is a harem which usually consists of two or more competing female kin groups.

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### **Introduction**

Among social organisms, group living includes both costs and benefits (Hoogland and Sherman 1976). One possible cost is increased aggression (Hoogland 1979) or some other form of competition. The costs of aggression will be determined by the patterns of population dispersion, grouping,

and ranging which form the social structure (Crook et al. 1976). Social structure is maintained or modified by interindividual behaviors known as social dynamics (Crook and Goss-Custard 1972). Kin selection theory suggests that an animal may increase its inclusive fitness by behaving differentially toward other members of the group (Hamilton 1964, West Eberhard 1975). Close relatives should be favored by behaviors which increase the benefits of social grouping and non-relatives should be avoided or treated in such a way as to increase their costs. Thus aggressive behavior should be directed toward non-kin.

The primary cost of aggression may be demographic. Aggressive behavior may cause subordinates to disperse (Watson and Moss 1970, Armitage 1975, Lidicker 1975, Downhower and Armitage 1981). Presumably, the fitness of dispersers is less than that of residents as dispersers generally suffer high mortality (Gaines and McClenaghan 1980). Dispersal resulting from spacing behaviors may be the mechanism whereby the populations of voles and other small mammals are self-regulated (Krebs 1978). Self-regulatory behavior can occur through kin selection (Lomnicki 1980), and Charnov and Finerty (1980) postulated that behavior mediated by kinship may drive population cycles of voles. Therefore, it is important to establish if social dynamics is kin-related and ultimately to determine the demographic consequences of kin-preference behaviors.

Yellow-bellied marmots are diurnal, semi-fossorial mammals living in harems consisting of an adult male, one or more adult females, yearlings, and juveniles (Armitage 1962, 1974). Dispersal of yearlings is important in regulating population density (Armitage and Downhower 1974). Furthermore, most resident females are recruited from their natal colony (Schwartz and Armitage 1980).

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Thus these social animals have the characteristics for determining the relationships among social dynamics, relatedness, and demography.

In this paper an analysis of social dynamics of yellow-bellied marmots focuses on two categories of social interactions, amicable and agonistic. Amicable behavior is cohesive and may be viewed as a benefit in the sense that animals behaving amicably share resources; e.g., food and burrows, predator defense. Conversely, agonistic behavior is dispersive and may be viewed as a cost.

Three null hypotheses will be tested. The first hypothesis is based on the prediction that benefits should favor close relatives (Hamilton 1964; Alexander 1974). This null hypothesis states that there are no differences in frequencies of amicable or agonistic behavior between close and distant relatives.

The second hypothesis was prompted by the observation that several marmots may occupy the same burrow system (Armitage 1962) and that burrowmates often are close kin, whereas harem members living in separate burrows are usually distantly related (Johns and Armitage 1979). Because a burrow group shares a resource, the social interactions of burrowmates should be primarily amicable. By extension of this reasoning, social interactions among members of different burrows should be primarily agonistic. This null hypothesis states that there are no differences in frequencies of amicable or agonistic behavior between burrowmates and non-burrowmates within a harem.

The third hypothesis is derived from observations that social interactions may vary according to the age-sex structure of the population (Armitage 1977). This null hypothesis states that the frequency of amicable or agonistic behaviors between members of various age-sex classes does not differ from that expected from the class composition of the population to which the interactants belong. Rejection of this hypothesis indicates that social dynamics is at least partially a function of some characteristic associated with age or sex.

## Materials and Methods

Data for the yellow-bellied marmot (*Marmota flaviventris*) were chosen from three localities. Two localities are in the East River Valley (ERV), near Gothic, Colorado at an elevation of 2,900 m. Marmot Meadow (locality 4) contained one harem. Picnic (locality 5) usually contained two harems: Upper (upper half of slope) and Lower (lower half of slope); in some years the entire locality contained one harem (Armitage 1974). The third locality is in North Pole Basin (NPB) in Gunnison County, Colorado, at an elevation of 3,400 m (Johns and Armitage 1979). Three harems were contiguous which made social

interactions between members of different harems more likely. In 1974, an adult female and three female yearlings were introduced into Marmot Meadow to test the first hypothesis.

Each year, all resident marmots were live-trapped and marked with non-toxic fur dye for individual recognition. Numbered, self-piercing tags placed in each ear provided permanent identification. Observations were concentrated in the morning and afternoon when marmots are most active; each population was censused at 10 to 20 min intervals during each observation period (Armitage 1962, 1974; Johns and Armitage 1979). For each social interaction we recorded the identity of the interactions and the date, time, location and type of interaction. Later, the age and sex of the interactants, their degree of relatedness, and their burrow group membership were added to the record. Changes in burrow occupancy were monitored in order to update burrow group membership. Six kinds of social interactions were recorded. Greeting and allo-grooming were combined in the analyses as amicable interactions; chase, fight, flight, and avoidance were lumped as agonistic. These interactions were described previously (Armitage 1962, 1973, 1974). In addition, play-fighting (Nowicki and Armitage 1979) was recorded in two years. In total, nine colony-years (a colony-year is one colony studied for one year) of data were collected from 1974 through 1977.

The relatedness of animals in the East River Valley (ERV) was determined from pedigrees maintained annually since 1962. We assumed that the resident territorial male sired all offspring. This assumption was supported by genetic studies (Schwartz and Armitage 1980). The kinship of many marmots in North Pole Basin (NPB) was unknown; therefore, such animals were excluded from analyses involving relatedness. Because in the ERV we established that immigrants are, at best, distantly related to the other residents, we assumed that immigrants into the NPB colony were less than one-eighth related to other harem members.

For the analysis of social behavior among age-sex classes, four age-sex classes were established: male adult, female adult, male yearling, female yearling. A yearling is a marmot in its second summer of life and is non-reproductive (Armitage and Downhower 1974). These four classes formed ten age-sex pairs of interactants. Expected values of interactions were calculated by using equation (7) from Altmann and Altmann (1977):

$$E_{xz} = \frac{N \sum_j t_j m_{xj} m_{zj}}{\sum_{\substack{i,k \\ i < k}} \sum_j t_j m_{ij} m_{kj} + \frac{1}{2} \sum_i \sum_j t_j m_{ij} (m_{ij} - 1)}$$

for each unlike-class pair. The same equation is used for each same-class pairs except the numerator is multiplied by  $1/2$ . An important feature of this equation is that it accounts for differences or changes in the class composition of the groups being assessed. This feature is essential because changes in group composition alter the relative probabilities of paired encounters. Two assumptions underlie this analysis: (1) all social interactions are sampled without bias and (2) all interactions take place between individuals at a constant rate independent of the classes to which they belong. Significant violations of assumption (2) will be detected as large differences between observed and expected rates of interactions among one or more pair classes. The differences summed over all pairs are tested against the  $\chi^2$  distribution. Mean population composition was calculated by multiplying the number of animals in a class by the number of hours of observation for each observation period and dividing the total for all observation periods by the total number of hours of observation.

## Results

### 1. Social Interactions and Kinship

For both the ERV and NPB populations, social interactions were distributed non-randomly according to average relatedness (Table 1). Amicable; i.e., cohesive, interactions predominated among close kin; agonistic, i.e., dispersive, interactions predominated among marmots of more distant relatedness. Therefore, the first hypothesis that there are no differences in frequencies of amicable or agonistic behavior between close and distant relatives is rejected.

### 2. Social Interactions and Group Membership

For both the ERV and NPB populations, social interactions were distributed non-randomly according to group membership (Table 2). Social interactions among burrowmates were overwhelmingly amicable, especially if the marmots also were closely related. By contrast, social interactions of non-burrowmates were characteristically agonistic, especially if the marmots were distantly related. Therefore, the second hypothesis that there are no differences in the frequencies of amicable or agonistic behavior according to group membership is rejected.

### 3. Social Interactions and Age-Sex Classes

Frequency of social interactions by age-sex pairs was analyzed for four ERV harems and three NPB harems. Additionally, between-harem social interactions were analyzed for three contiguous NPB harems. These harems encompassed a variety of population structures and the number of social interactions were adequate for analysis. The ERV Picnic data permit a between-years comparison on the same site whereas the NPB observations constitute a between sites (contiguous harems) comparison in the same year.

For Picnic in 1975, the observed frequency of both amicable and agonistic interactions summed over seven age-sex pairs differed significantly from the expected (Table 3). Therefore, hypothesis three – that the frequency of amicable or agonistic behaviors between members of various age-sex classes does not differ from that expected from the class composition of the population to which the interactants belong – is rejected. For amicable behavior, yearling females interacted with yearling females more frequently than expected and with adult females less than expected; adult females interacted with adult females much more than expected

**Table 1.** The number of observations of amicable and agonistic behavior according to kinship. ERV=East River Valley; NPB=North Pole Basin. Relatedness includes both descendent and collateral kin and both males and females. Five colony-years are represented for ERV. Data were collected from three contiguous harems for three years at NPB. Because social interactions between animals with average relatedness between  $1/8$  and  $1/2$  are too few to analyze, they are lumped.  $\chi^2=90.4$ ,  $P<0.001$  for ERV; 194.7,  $P<0.001$  for NPB

| Average relatedness | Amicable |     | Agonistic |     |
|---------------------|----------|-----|-----------|-----|
|                     | ERV      | NPB | ERV       | NPB |
| $1/2$               | 162      | 142 | 21        | 13  |
| $<1/2$              | 52       | 53  | 85        | 203 |

**Table 2.** The number of observations of amicable and agonistic behavior according to burrow-group composition for closely and distantly related marmots for all East River Valley and North Pole Basin populations. Relatedness and testing as in Table 1

|                   | Closely related $>1/4$ |           | Distantly related $<1/4$ |           |
|-------------------|------------------------|-----------|--------------------------|-----------|
|                   | Amicable               | Agonistic | Amicable                 | Agonistic |
| East River Valley | $\geq 1/4$             |           | $<1/4$                   |           |
| Burrowmates       | 138                    | 3         | 16                       | 1         |
| Non-burrowmates   | 31                     | 22        | 29                       | 80        |
|                   | $\chi^2=53.2, P<0.001$ |           | $29.2, P<0.001$          |           |
| North Pole Basin  | $1/2$                  |           | $<1/2$                   |           |
| Burrowmates       | 116                    | 3         | 44                       | 67        |
| Non-burrowmates   | 12                     | 10        | 23                       | 136       |
|                   | $\chi^2=37.8, P<0.001$ |           | $22.2, P<0.001$          |           |

(Table 3). Yearling females:adult females interacted more agonistically and adult females:adult males interacted less agonistically than expected.

Only one adult male resided at Picnic in 1976. Thus, the entire colony was one harem. Agonistic interactions were too few to analyze. The single encounter between a transient adult male and the resident adult male was sufficient to cause the transient male to leave. In contrast to 1975, amicable behavior between yearling females and adult females was greater than expected and that between adult females was as expected (Table 3). In addition, yearling females and yearling males were more amicable and yearling males and adult females were less amicable than expected. Therefore, for amicable behavior, hypothesis three is rejected.

Although only one male resided at Picnic in 1977, data were adequate only for the animals living in the lower harem. Hypothesis three is rejected for both amicable and agonistic behavior

**Table 3.** Frequency analysis of amicable and agonistic interactions by age-sex classes for the lower harem of Picnic Colony. Although there is no test of significance for individual rows, those values that contributed markedly to the total  $\chi^2$  are marked with <sup>a</sup>. Mean population composition was: 1975, 1.0 adult male, 2.0 adult females, 0.57 yearling males, 1.34 yearling females; 1976, 1.1 adult males, 5.9 adult females, 1.0 yearling males, 2.0 yearling females; 1977, 1.0 adult males, 3.0 adult females, 0.5 yearling males, 1.0 yearling females. Ylg=yearling, Ad=adult, O=observed interactions, E=expected interactions. –indicates the age-sex pair was not possible

| Age-sex pairs | 1975            |     |                 |     | 1976            |      |           |                 | 1977     |                 |           |   |
|---------------|-----------------|-----|-----------------|-----|-----------------|------|-----------|-----------------|----------|-----------------|-----------|---|
|               | Amicable        |     | Agonistic       |     | Amicable        |      | Agonistic |                 | Amicable |                 | Agonistic |   |
|               | O               | E   | O               | E   | O               | E    | O         |                 | O        | E               | O         | E |
| Ylg♀:Ylg♀     | 5 <sup>a</sup>  | 1.5 | 0               | 1.9 | 0               | 1.7  | 0         | –               | –        | –               | –         | – |
| Ylg♀:Ad♀      | 0 <sup>a</sup>  | 7.2 | 28 <sup>a</sup> | 9.0 | 29 <sup>a</sup> | 19.7 | 0         | 22 <sup>a</sup> | 12.3     | 3               | 4.5       |   |
| Ylg♀:Ad♂      | 1               | 3.6 | 1               | 4.5 | 0               | 3.8  | 1         | 1               | 4.1      | 0               | 1.5       |   |
| Ylg♂:Ylg♂     | 2               | 3.1 | 0               | 3.8 | 11 <sup>a</sup> | 3.4  | 0         | 5 <sup>a</sup>  | 2.0      | 0               | 0.7       |   |
| Ylg♂:Ad♂      | 0               | 1.5 | 0               | 1.9 | 0               | 1.9  | 1         | 0               | 2.0      | 1               | 0.7       |   |
| Ylg♂:Ylg♀     | –               | –   | –               | –   | –               | –    | –         | 5               | 1.0      | 0               | 0.4       |   |
| Ylg♂:Ad♀      | 0               | 3.1 | 6               | 3.8 | 3 <sup>a</sup>  | 9.9  | 0         | 0 <sup>a</sup>  | 6.0      | 2               | 2.2       |   |
| Ad♀:Ad♀       | 12 <sup>a</sup> | 2.7 | 0               | 3.3 | 22              | 24.2 | 1         | 9               | 12.3     | 12 <sup>a</sup> | 4.5       |   |
| Ad♀:Ad♂       | 8               | 5.3 | 0 <sup>a</sup>  | 6.7 | 11              | 11.2 | 5         | 10              | 12.3     | 1               | 4.5       |   |
| Ad♂:Ad♂       | –               | –   | –               | –   | 0               | 0.2  | 1         | –               | –        | –               | –         |   |
|               | $\chi^2=55.7$   |     | $\chi^2=61.7$   |     | $\chi^2=34.0$   |      |           | $\chi^2=39.7$   |          | $\chi^2=18.4$   |           |   |
|               | $P<0.001$       |     | $P<0.001$       |     | $P<0.001$       |      |           | $P<0.001$       |          | $P=0.01$        |           |   |

(Table 3). Agonistic behavior among adult females was much higher than expected. As in 1976, amicable behavior between yearling and adult females was higher than expected and as in 1975 and 1976, amicable behavior between yearling males and adult females was lower than expected. Additionally, amicable behavior among yearling males was greater than expected.

The composition of the marmot population at Marmot Meadow in 1976 was the simplest of the populations analyzed because only four of the ten possible age-sex pairs were present (Table 4). Even so, hypothesis three is rejected for both amicable and agonistic behavior. Yearling males and the adult male were agonistic more frequently than expected. All patterns of amicable behavior departed from the expected (Table 4). Especially noteworthy is the continuation of the trends that yearling males were less amicable with adult females and more amicable with other yearling males than expected. Also, yearling males were less amicable with adult males than expected. Interestingly, no amicable interaction was observed between yearling and adult males (Tables 3, 4), but only in Marmot Meadow in 1976 was there a notable difference between expected and observed.

Early in 1975, when adult male 405 expanded his territory to include that of an adult male which vanished, four NPB harems were reduced to three. For harem 405, hypothesis three is rejected for both amicable and agonistic interactions (Table 5).

**Table 4.** Frequency analysis of amicable and agonistic interactions by age-sex classes for Marmot Meadow Colony in 1976. Mean population composition was 1.0 adult males, 1.1 adult females, and 4.0 yearling males. Other symbols as in Table 3

| Age-sex pairs | Amicable        |      | Agonistic      |     |
|---------------|-----------------|------|----------------|-----|
|               | O               | E    | O              | E   |
| Ylg♂:Ad♂      | 0 <sup>a</sup>  | 6.1  | 8 <sup>a</sup> | 3.1 |
| Ylg♂:Ylg♂     | 21 <sup>a</sup> | 11.1 | 2              | 5.5 |
| Ylg♂:Ad♀      | 1 <sup>a</sup>  | 7.4  | 3              | 3.7 |
| Ad♀:Ad♂       | 4 <sup>a</sup>  | 1.4  | 0              | 0.7 |
|               | $\chi^2=25.2$   |      | $\chi^2=10.7$  |     |
|               | $P<0.001$       |      | $P<0.025$      |     |

Yearling males behaved more amicably than expected toward other yearlings. Adult males behaved more agonistically toward adult females and all yearlings than expected, yearling males behaved less agonistically toward yearling females than expected, and yearling females were less agonistic with other females than expected.

Also in 1975, 3-year-old male 230 moved into the NPB territory vacated by male 163. In this harem, the observed frequencies of amicable and agonistic interactions summed over seven age-sex pairs differed significantly from the expected (Table 5); therefore, hypothesis three is rejected. There were no large deviations of observed from expected amicable interactions for any one of the seven age-sex pairs. However, adult males behaved

**Table 5.** Frequency analysis of amicable and agonistic interactions by age-sex classes for North Pole Basin harems in 1975. Symbols as in Table 3. Mean population composition was: harem 405, 1.0 adult males, 6.2 adult females, 2.0 yearling males, 3.7 yearling females; harem 408, 1.0 adult males, 2.6 adult females, 2.0 yearling males, 1.0 yearling females; harem 230, 1.0 adult males, 5.4 adult females, 0.8 yearling males, 1.0 yearling females

| Age-sex pairs | Harem 405       |      |                  |      | Harem 230       |     |                 |     | Harem 408       |     |                 |      |
|---------------|-----------------|------|------------------|------|-----------------|-----|-----------------|-----|-----------------|-----|-----------------|------|
|               | Amicable        |      | Agonistic        |      | Amicable        |     | Agonistic       |     | Amicable        |     | Agonistic       |      |
|               | O               | E    | O                | E    | O               | E   | O               | E   | O               | E   | O               | E    |
| Ylg♀:Ylg♀     | 4               | 5.2  | 0 <sup>a</sup>   | 10.5 | —               | —   | —               | —   | —               | —   | —               | —    |
| Ylg♀:Ad♀      | 18              | 23.2 | 31 <sup>a</sup>  | 47.3 | 8               | 4.2 | 3               | 3.0 | 1               | 3.3 | 4               | 5.7  |
| Ylg♀:Ad♂      | 4               | 3.7  | 14 <sup>a</sup>  | 7.6  | 2               | 0.8 | 3 <sup>a</sup>  | 0.6 | 2               | 1.3 | 1               | 2.2  |
| Ylg♀:Ylg♂     | 19 <sup>a</sup> | 7.4  | 0 <sup>a</sup>   | 15.2 | 0               | 0.7 | 0               | 0.6 | 2               | 2.6 | 0 <sup>a</sup>  | 4.5  |
| Ylg♂:Ad♂      | 0               | 2.0  | 16 <sup>a</sup>  | 4.1  | 2               | 0.6 | 1               | 0.4 | 5               | 2.6 | 0 <sup>a</sup>  | 4.5  |
| Ylg♂:Ylg♂     | 3 <sup>a</sup>  | 1.0  | 1                | 2.1  | —               | —   | —               | —   | 6 <sup>a</sup>  | 1.3 | 0               | 2.2  |
| Ylg♂:Ad♀      | 12              | 12.6 | 21               | 25.7 | 0               | 3.0 | 2               | 2.2 | 7               | 6.7 | 12              | 11.4 |
| Ad♀:Ad♀       | 13              | 16.5 | 34               | 33.7 | 9               | 8.6 | 0 <sup>a</sup>  | 6.2 | 0               | 3.9 | 20 <sup>a</sup> | 6.8  |
| Ad♀:Ad♂       | 5               | 6.3  | 42 <sup>a</sup>  | 12.8 | 1               | 4.2 | 7 <sup>a</sup>  | 3.0 | 2               | 3.3 | 6               | 5.7  |
|               | $\chi^2 = 26.7$ |      | $\chi^2 = 139.3$ |      | $\chi^2 = 14.6$ |     | $\chi^2 = 22.6$ |     | $\chi^2 = 25.7$ |     | $\chi^2 = 38.0$ |      |
|               | $P < 0.001$     |      | $P < 0.001$      |      | $P < 0.05$      |     | $P < 0.001$     |     | $P < 0.001$     |     | $P < 0.001$     |      |

**Table 6.** Frequency analysis of agonistic inter-harem interactions by age-sex classes for North Pole Basin harems 405, 230, and 408. No amicable behaviors were observed. Symbols as in Table 3. Mean population composition of the three harems was 3.0 adult males, 13.0 adult females, 4.8 yearling males, and 5.4 yearling females

| Age-sex pairs | Agonistic        |      |
|---------------|------------------|------|
|               | O                | E    |
| Ylg♀:Ylg♀     | 0                | 1.3  |
| Ylg♀:Ad♀      | 0 <sup>a</sup>   | 14.2 |
| Ylg♀:Ad♂      | 0                | 3.8  |
| Ylg♀:Ylg♂     | 2                | 5.9  |
| Ylg♂:Ad♂      | 6                | 3.4  |
| Ylg♂:Ylg♂     | 8 <sup>a</sup>   | 1.2  |
| Ylg♂:Ad♀      | 6                | 7.6  |
| Ad♀:Ad♀       | 16 <sup>a</sup>  | 8.8  |
| Ad♀:Ad♂       | 10               | 9.2  |
| Ad♂:Ad♂       | 8 <sup>a</sup>   | 0.5  |
|               | $\chi^2 = 181.2$ |      |
|               | $P < 0.001$      |      |

more agonistically than expected with both yearling and adult females, whereas observed agonistic behavior between adult females was less than expected.

In NPB harem 408, amicable interactions among yearling males were much greater than expected (Table 5). Additionally, yearling males behaved less agonistically than expected with yearling females and adult males; adult females were more agonistic toward one another than expected. Therefore, hypothesis three is rejected.

No amicable interactions were observed between individuals who were members of separate

but contiguous NPB harems. However, the distribution of the frequent agonistic interactions differed significantly from the expected (Table 6); thus, hypothesis three is rejected for the inter-harem frequency analysis. Agonistic interactions among adult territorial males occurred more frequently than expected. Adult females behaved more agonistically among themselves and less agonistically with yearling females. Agonistic behavior among yearling males was greater than expected.

#### 4. Introduction Experiments

A yearling female was introduced on June 15 into Marmot Meadow where a non-reproductive adult female and an adult male resided. The yearling occupied a burrow on the periphery of the home range of the adults. The seven observed social interactions between the residents and the yearling were all agonistic whereas the residents had eleven amicable interactions. The yearling departed 12 d after her release.

A female adult and four young were introduced on July 9. She occupied a burrow well beyond the home ranges of the residents. The only observed interaction with the resident female was agonistic. The introduced female remained throughout the summer and dispersed the following June. During the remainder of the summer, the two residents were observed to have seven amicable interactions.

Two female yearlings were introduced on July 22. They occupied a burrow about halfway between the burrows occupied by the two resident

adults and the introduced adult and young. In the next two days the yearlings had one amicable and three agonistic interactions with the introduced female and five agonistic interactions with the resident adults. Both yearlings departed by the end of the second day. Thus, social interactions among strangers, i.e., introduced vs residents, was overwhelmingly agonistic whereas the interactions among familiars, i.e., the unrelated resident male and female, was entirely amicable.

## Discussion

### 1. Kinship, Burrow Groups, and Age-Sex Classes

Clearly, social dynamics of yellow-bellied marmots are dependent on kinship, group composition, and age-sex classes (Tables 1–6). To what degree can differences in the behavior of age-sex pairs and burrow groups be explained by kinship? In the ERV populations, all members of a burrow-group were either sib or mother-offspring groups except when an adult male shared a burrow with adult females with whom he was unrelated. Where kinship was known, similar patterns occurred in NPB.

Of the 31 instances of amicable behavior among closely related non-burrowmates in the ERV (Table 2), 27 were mother: yearling daughter, three were grandmother: adult granddaughter, and one was putative father: yearling daughter. Similar relationships occurred among known kin in the NPB colony.

Most of the significant differences in the frequency analysis of amicable and agonistic interactions among age-sex classes can be interpreted in terms of kinship. At Picnic in 1975, amicable behavior characterized the social interactions between two adult sisters who were burrowmates, and between yearling sisters who also were burrowmates (Table 3). However, only agonistic behavior occurred between yearling (aunts) and adult females (half-nieces), non-burrowmates related by only 0.125. By contrast, in 1976, when two burrow groups each consisted of an adult female and her yearling daughter amicable behavior among adult and female yearlings was greater than expected (Table 3). In 1977, the yearling female, although living in a separate burrow, interacted amicably with her mother and agonistically with two adult females (half grand aunts) to whom she was related by 0.0625. The pair of adult sisters interacted amicably whereas they behaved agonistically with the third female (their half-niece, to whom they were related by 0.125). In NPB (Tables 5, 6), yearlings generally interacted amicably with siblings and

parents and agonistically with others (see also Table 8, Johns and Armitage 1979).

The treatment of introduced strangers by residents also may be interpreted in terms of kinship. None of the strangers was related to the residents and the behavior between residents and strangers was agonistic. Possibly, familiarity is one basis of kin recognition, as in Beldings (Sherman 1980a) and Richardson's (Michener 1974) ground squirrels. Mother and daughters and sisters share burrows and home ranges. Thus, kin have the opportunity to become familiar with one another while avoiding extensive contact with members of other kin groups occupying different burrow systems and utilizing different home ranges.

Although 38 agonistic interactions were observed between yearling and adult females living in different burrows at NPB, 70 were expected (Tables 5, 6). The less than expected frequency of agonistic interactions may be explained primarily by the tendency of female yearlings to avoid interactions with other than close kin or members of their burrow group. By using space so as to avoid contact with agonistic adults, social interactions are reduced (Armitage 1977). Avoidance of agonistic interactions may be an important strategy for achieving residency. Yearlings are much smaller than adults (Armitage et al. 1976) and always lose when agonistic encounters occur. If the yearling female can remain until she is two years old, she will be at a much less size disadvantage plus there is some probability that the hostile adult female may not have survived.

### 2. Male Reproductive Strategy

Amicable behavior among distantly related burrowmates and non-burrowmates suggests possible reciprocal altruism (Trivers 1971). However, male reproductive strategy must be excluded as a possible alternative explanation. The model of marmot polygyny predicts that males should recruit females by treating them cohesively (Downhower and Armitage 1971). All 16 amicable interactions among distantly related burrowmates and 26 of the 29 amicable interactions among distantly related non-burrowmates in the ERV (Table 2) were among adult males and females. The other three amicable interactions among unrelated non-burrowmates were: adult male: yearling female, one; yearling male: yearling female, two. Thus, all amicable interactions among unrelated ERV marmots is consistent with the model of polygyny and male reproductive strategy and there is no necessity to invoke reciprocal altruism.

In the NPB colony, 31 of 44 amicable interactions among distantly related burrowmates (Table 2) were between adult males and females. Seventeen of 23 amicable interactions among distantly related non-burrowmates were among adult males and females, one was between an adult male and yearling female and one was between a yearling male and an adult female. About 25% (17 of 67) of the amicable interactions among presumed distantly related animals at NPB cannot be explained by male reproductive strategy. Ten of these were amicable interactions of female yearlings with other females, primarily adults. This behavior possibly represents attempts by the subordinate yearling to appease the dominant adult (Wilson 1975, p. 181). One observed amicable interaction between an adult male and a yearling male could also be appeasement. Such behavior is not uncommon (Armitage 1974). The remaining six instances of amicable behavior occurred among adult females. We cannot exclude the possibility that these marmots could have been close relatives. However, these behaviors might represent reciprocal altruism. Social tolerance may permit females to share burrows and foraging areas. This behavioral situation is rare among marmots and reciprocal altruism is potentially far less important than kinship and male reproductive strategy as a mediator of social dynamics.

Agonistic behavior between adult males and adult or yearling females seems to be contradictory. This apparent contradiction can be explained by two phenomena. First, males resident in their first year establish dominance over females; females often react by fleeing from the male or snapping at him. In harems 405 and 230 (Table 5) in 1975, a new male established residence in each harem and the agonistic conflict between adult males and females was greater than expected. Second, males normally approach females sexually throughout the summer (Armitage 1965). The typical female response is to flee or snap at the male. Most of our observations of male: female agonistic behavior was fleeing by the female; therefore, this behavior more properly is sexual rather than agonistic.

Adult male marmots are territorial (Armitage 1974) and should view other males, including yearlings, as potential rivals. Therefore, behavior among males should be predominantly agonistic. This pattern prevailed (Tables 3–6) except among burrowmates in harem 408 when amicable behavior predominated between an adult male and his yearling sons (Table 5).

The behavior of yearling males is consistent

with the polygyny model which states that males should obtain exclusive domain over a group of reproductive females through territoriality (Downhower and Armitage 1971). Territorial males usually are highly aggressive, socially dominant animals (Svendsen and Armitage 1973). Dominance may be achieved through a developmental process including social behavior among sibs (Bekoff 1977); social play may be one of the social mechanisms in the developmental process (Nowicki and Armitage 1979). Yearling males behaved amicably with female yearlings (Tables 3, 5) and other male yearlings (Tables 3, 4, 5) unless the male yearlings were from a different harem (Table 6). The higher than expected amicable behavior among male yearlings occurred among brothers, primarily as a greeting, which usually precedes a play bout. Probably, the high frequency of greetings represents potential play bouts that did not develop. The low frequency of agonistic behavior among these yearling males may also be explained by play. In 1977 at Picnic, play among male yearlings was higher than expected and between female and male yearlings was lower than expected ( $\chi^2 = 11.3$ ,  $P < 0.001$ ). Thus play seems to substitute for agonistic behavior among yearling males and may be the social mechanism whereby dominance develops.

### 3. Limits to Nepotism

Nepotism (Sherman 1980a), as evidenced by amicable behavior, was limited to close relatives in the marmots. A similar pattern occurs in Belding's ground squirrels (Sherman 1980b). Sherman (1981) suggested that in *S. beldingi* the extent of cooperation was limited by demography; that is, mortality produced a discontinuity in kin co-occurrence such that the likelihood of their co-occurrence was sufficiently low to preclude the development of recognition mechanisms and cooperative behaviors. Sherman considered only females because males disperse from their natal areas as juveniles (females are more sedentary).

Demography does not adequately explain the limits of nepotism in the longer-lived marmots. At Picnic, females related by 0.125 were present all four years of the study. The average frequency of these female pairs was 0.27; the average frequency of female pairs related by 0.5 was 0.19. All 24 social interactions among females related by 0.125 were agonistic. Animals related by 0.25 occurred at a frequency of 0.2. Four interactions occurred between an adult female and her grand-daughter; three of these were amicable and occurred on one day. The grand-daughter was classified as a social:

non-aggressive behavioral type (Svendsen 1974). Her behavior supports the suggestion that individual variability is one factor determining social dynamics (Armitage 1977). The other two interactions were agonistic and occurred between an aunt:nephew pair.

The major limitation to marmot nepotism is reproductive strategy. This limitation is evident in male behavior. Of the 22 instances of agonistic behavior among closely related non-burrowmates (ERV, Table 2), eight were between adult males and their yearling sons. Twelve agonistic behaviors were between adult females and their yearling sons. Five of six agonistic interactions among burrowmates were between yearling males who were brothers. Discrimination on the basis of sex is strongly supported by the frequency analysis of amicable behavior between yearling males and adult females. If the observed and expected are added over all populations (Tables 3–6), 48.7 amicable interactions were expected but 23 observed. This difference is highly significant ( $\chi^2 = 13.6$ ,  $P < 0.01$ ). By contrast, the observed number of agonistic interactions (46) between these age classes was about as expected (49). Therefore, adult females do not preferentially interact with yearling males either cohesively or dispersively as they do with yearling females. Rather, they fail to act cohesively. This failure to form social bonds apparently is related to dispersal strategy. Although virtually all male yearlings disperse, they disperse later when rates of amicable interactions are high (Downhower and Armitage 1981). Many female yearlings are recruited into their natal population (Armitage and Downhower 1974, Schwartz and Armitage 1980). This pattern prevails among ground-dwelling sciurids (Armitage 1981). Causes of dispersal are unknown (Gaines and McClenaghan 1980); our interpretation suggests that both overt agonistic behavior and the absence of cohesive behavior may combine to initiate dispersal.

Another factor limiting nepotism is that under most conditions greater return can be expected from investing in offspring rather than in other kin (Rubenstein and Wrangham 1980). Therefore, we should not be surprised that females may treat daughters or sisters agonistically. In NPB, eight of ten agonistic interactions among closely related non-burrowmates were among sisters and one was between a mother and her daughter. At Marmot Meadow in 1979, of 48 agonistic interactions, 34 were either between two sisters or between an aunt and her niece or nephew. Despite the agonistic behavior which continued in 1980 and 1981, the two sisters and daughter-niece remained in the colony

and all three raised litters in the same burrow system in 1980 and 1981. If an animal cannot obtain exclusive use of resources; e.g., burrows or food, its inclusive fitness is increased if resources are shared with close rather than distant kin (Hamilton 1964). Thus, in marmots, sisters or mother: daughter groups share burrows and/or home ranges (=food) (Armitage 1975, this paper and unpublished data). The occurrence of female kin clusters in other sciurids (reviewed by Armitage 1981) suggests that sociability in these animals evolved by kin selection.

#### 4. Social Structure

Social structure is a consequence of the different reproductive strategies of males and females. The female social structure is a closely-related kin group which may coincide with a burrow group. Members of a kin group may occupy separate burrows but have similar home ranges (like *S. beldingi* and *C. ludovicianus*). Members of a burrow group may cooperate in the detection of predators and defense of the home range against conspecifics. Such cooperation represents advantages of group living.

The male social structure is a harem which varies considerably in its composition. Large, multi-female harems may consist of two or more competing female kin groups e.g., Picnic 1977, NPB 1975. Therefore, the harem may be composed of both cooperative (within kin group) and competitive (between kin group) female units, all of which interact with the territorial male in the same manner. A given female kin line may increase in number or become extinct (Armitage, in preparation). The variation in the size of female kin groups produces changes in the size of the harem. The predominance of agonistic behavior between marmots from different harems is an extension of inter-burrow competition which results in the maintenance of the harem as a social unit. Thus, even in NPB where there were no physical barriers to restrict mobility among harems, harem structure remained intact.

The maintenance of the harem is a consequence of the individual strategies of males and females and not a cooperative venture. Females attempt to exclude non-closely related kin; males exclude other males. When possible, a male extends his territory to include additional females and thus enlarge the harem; e.g., Picnic 1976, NPB 1975 (Armitage 1974). Under these conditions, female behavior does not change; the basic kin group structure is retained. Furthermore, females may be



members of different harems in different years as male territories wax and wane; e.g., Picnic, 1975, 1976.

Both social dynamics and social structure support the view that individuals attempt to maximize their reproductive success. These attempts may be expressed by agonistic behavior toward closely related kin. The conditions which determine how a female will treat her kin are not understood. Nevertheless, the social biology of marmots is consistent with the hypothesis that population dynamics is a consequence of individual reproductive strategies which discriminate between closely related kin and other individuals.

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