Chapter 7
RESOURCES AND SOCIAL ORGANIZATION OF GROUND-DWELLING SQUIRRELS

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I. INTRODUCTION

Animals form many kinds of groups, ranging from temporary fish schools to highly integrated honeybee colonies (Wilson 1975). Much of the focus on the evolution of groups has centered on the costs and benefits of group living (Alexander 1974). Benefits of group living may include increased defense against predation and more effective exploitation of resources. Costs of group living include increased competition for resources, higher parasite loads and transmission, greater probability of misdirected parental care and infanticide, and increased conspicuousness to predators (Alexander 1974; Hoogland 1979a).

Costs and benefits are important only as they affect reproductive success. Thus increased parasite loads are not in themselves evidence of cost; the cost must be measured in terms of its effects on fitness, generally estimated from some measure of reproductive output. Likewise, increased vigilance behavior (Hoogland 1979b; Holmes 1984a) or modification of patch use (Holmes 1984a; Carey 1985) as antipredator strategies do not necessarily entail reproductive costs. A species or an individual's behavior may be modified by predation pressure, but the cost may be trivial compared to the benefit (death vs. survival). Many animals spend time apparently doing nothing (Herbers 1981); thus a simple demonstration that time is spent on an activity (e.g., vigilance behavior) does not demonstrate a cost. However, the reproductive suppression of some females by other females in the group (Wasser and Barash 1983; Armitage 1986a) does entail a cost; i.e., loss of reproductive output. Any analysis of the role of resources on social organization should focus on reproductive success. One may predict that an individual should be a member of a group when membership increases the probability of leaving reproductive descendants but should leave the group when membership decreases that probability.

Groups are so diverse in structure and function that it seems unlikely that, except in the broadest sense, the same pressures select for group living. For example, male groups of white-tailed deer may form because of the added vigilance of group living but female groups may form because of direct reproductive investment by mothers in daughters (Ozoga et al. 1982). In the former instance, the group may form because each individual has a lower probability of becoming prey; in a sense, the group is based on reciprocity and genetic relatedness is unnecessary for group formation to evolve. In the latter instance, an adult female forms a group only with daughters; genetic relatedness is a necessary condition for the evolution of the group.

This distinction among kinds of groups is critical when looking at groups of ground-dwelling squirrels. Ground-dwelling squirrels are typically described as living in colonies. The word colony connotes some type of group living. But in reality, many species are highly individualistic (Armitage 1981); five grades of sociality may be recognized (Michener 1983). The idea of colonial living stems from the aggregation of these species on patches of favorable habitat (Armitage 1981). Within these aggregations social groups may form. I have argued elsewhere that sociality occurs when body size combined with a relatively short active season results in reproductive maturity being delayed to age two or later (Armitage 1981). Sociality is viewed as a life-history trait in which females continue reproductive investment beyond weaning as a mechanism for increasing the probability of producing reproductive offspring.

It seems obvious that different selection pressures have acted on group formation and the development of sociality in these animals. Groups occur whenever resources are adequate. The interesting questions are what happens to sociality when resources on a patch are varied.
or when resources differ among patches and what is the likely role of kin selection in the formation of the more highly social groups.

In this paper I will examine the relationship of habitat variability to sociality in yellow-bellied marmots. Because sociality is part of a population-behavioral system (Armitage 1977), the effects of habitat variability on population processes will be considered. Second, I will review the effects of resource manipulation on the social systems of ground-dwelling squirrels. Third, I will discuss whether direct or indirect selection predominates in these systems. Parental investment is considered a component of direct fitness; indirect fitness (= kin selection) includes effects on non-descendant relatives (Brown 1980).

II. HABITAT QUALITY AND SOCIETY IN MARMOTS

Yellow-bellied marmots (Marmota flaviventris) are large, diurnal, burrow-dwelling ground squirrels that occupy forest openings and the alpine of the Cascade, Sierra, and Rocky Mountains (Fraser and Hoffman 1980). The populations are clumped on habitat patches consisting of an open area dominated by grasses and perennial forbs and in which talus, boulders, or rock outcrops occur (Svensen 1974; Kilgore and Armitage 1978). Habitat patches range widely in size; larger patches that normally harbor three or more adults are designated as colonial sites; smaller sites that typically support one or two adults are called satellite sites (Armitage and Downhower 1974; Svensen 1974). This report will emphasize colonial sites.

The annual cycle of marmots is a circannual rhythm that characterizes the Marmotini (Davis 1976). Marmots in our study area in the upper East River Valley, Gunnison County, Colorado, elevation 2900 m, emerge from hibernation in early May. Mating occurs soon after and young are weaned usually by mid July. Body weights are minimal after emergence and all age classes gain weight during the summer (Armitage et al. 1976). Immersion begins in late August; young immerge last and rarely are animals active past mid September. Marmots, as well as all the hibernating ground-dwelling squirrels, are annual breeders. Reproduction must begin early in the year to ensure that young have sufficient time to achieve a body size and fat storage that will carry them through eight months of hibernation and that parous females have time to prepare for hibernation. Litters that are weaned late in the year have virtually no survivors through their first hibernation (Armitage et al. 1976). Yellow-bellied marmots are generalist herbivores (Fraser 1983). Feeding preferences are unrelated to protein or water content of plants. Marmots use less than 4 percent of the above-ground primary production available to them (Kilgore and Armitage 1978). Population density apparently is not food limited; however, individual reproductive success may be related to food availability during pregnancy and lactation (Andersen et al. 1976).

Marmots form two kinds of social groups. Females establish matrilines of one or more closely related (motherdaughter or sistersister)

adults; males attach to one or more matrilines to form harems. Per capita reproductive output is unrelated to the number of females living in a matriline, but is inversely related to harem size (Armitage 1986a). The reduction in per capita output is attributable in part to reproductive suppression of females in one matriline by females in an adjoining matriline. The mechanism of suppression is unknown. Matrilines share space and members of a matriline may cooperate to defend against conspecific intruders (Armitage 1984, 1986a).

Although food usually comes to mind when thinking about social organization and resources, burrows are a critical resource for ground-dwelling squirrels. Burrows are usually of three types: (1) nest or home burrows where an animal lives during the active season; (2) auxiliary or flight burrows that usually are located near foraging areas and to which an animal can retreat when threatened (Armitage 1962); and (3) the hibernaculum, the burrow in which one or more animals hibernates. The hibernaculum may also be the nest burrow. Burrows in marmot habitats that are used as a hibernaculum are a small subset of the total number of burrows present. Unfortunately, no one has devised a means of evaluating burrow quality, but several lines of evidence suggest that burrows vary in quality. The same summer burrows are used year after year; some burrows have been used for each of the 24 years that I've studied marmots. Only a few burrows are used as hibernacula; the same hibernaculum are used in successive years. Reproductive success may depend on access to a quality burrow. Reproductive success of the Wyoming ground squirrel (Spermophilus belli) was related to maternity-burrow sites (Pfeifer 1982) and adult female S. columbianus may relinquish nest sites to the yearling daughters (Harris and Murie 1984). To conclude, burrows and food are the critical resources that are expected to affect social organization in marmots and other ground-dwelling squirrels.

A. A Measure of Habitat Quality

Marmots prefer to use some parts of their habitat more than others (Armitage 1984; Fraser and Armitage 1984). Because we have no objective way to evaluate burrow quality and other parameters of habitat quality are extremely difficult to measure (e.g., energy, nutrition, predator defense, avoidance of conspecifics), an indirect method of measuring habitat quality was developed. Because an animal's fitness depends on its reproductive success, marmots should use their habitat patches so as to maximize their reproductive success. Reproductive success is measured as:

\[ RS = \frac{\text{number of yearlings}}{\text{number of young weaned}} \]

This ratio integrates overall habitat quality into one measure. For example, the production of young measures the ability of females to obtain needed energy and nutrients, to avoid predators, and to occupy a burrow in which the young can be nursed and sheltered. The number of yearlings measures the capacity of the habitat to provide to the young energy and
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nutrients for growth and hibernation, a burrow to serve as a hibernaculum, and defense against predators; e.g., flight burrows, good visibility. Because this measure is a ratio, it is independent of the size of the habitat patch and the number of females present.

RS was calculated for each year for each sex habitat (= colonies). Yearly values, ranging from 0 to 1.0, were not normally distributed; therefore, differences among habitats were tested by the Kruskal-Wallis analysis of variance by ranks (Siegel 1956, p. 184). RS differed among habitats (Table I). The smallest habitat, Boulder, is characteristic of a satellite site and the lowest RS occurred there. The second-lowest RS occurred at the largest habitat patch. This relationship suggests that area is not related to RS; a rank correlation between area and RS was insignificant (rs = 0.03, p > 0.1).

Habitat quality could affect survivorship (S) of adult females. Survivorship was measured as:

\[
S = \frac{\text{number of adult females}}{\text{number of adult females the previous year}}
\]

Annual survivorship ranged from 0 to 1.0; mean survivorship varied from 0.569 to 0.782 (Table I). Survivorship did not differ among habitats nor were RS and S correlated among habitats (rs = -0.31, p > 0.1). However, RS and S were correlated within colonies in three habitats but not in three others (Table II). The significant values of rs are not particularly large. These low correlations, the lack of significant correlations in three colonies, and the lack of significant correlations among habitats suggest that survivorship and reproductive success are not tightly coupled, but that there is some trend for habitats that favor survivorship to favor reproduction also. The areas where marmots live probably represent long-term selection for habitat choice by female marmots. Any tendency to occupy sites with low survivorship probabilities should receive strong negative selection. Doubtless we have chosen study sites

where marmots are successful; thus our results likely are biased toward the upper end of survivorship. Calculations of survivorship of two additional satellite sites produced rates of 0.439 and 0.50. These rates are lower than those of any of the long-term sites (Table I), but may be misleading. Satellite females may seek a new habitat and be erroneously recorded as dead. We have had females return to a satellite site after one or more year's absence; therefore, these survivorship values are minimal. RS values for these two sites were 0.397 and 0.38, respectively. Both values are in the range of the two low values from the long-term study sites (Table I). A tentative conclusion is that the places where female yellow-bellied marmots reside do not differ much in survivorship, but vary considerably in reproductive success. Female marmots commonly live to five or more years of age; thus a female has several opportunities to breed and may be able to locate a better habitat patch in a subsequent year. Our experience is that the better habitat patches are quickly occupied; thus many females have no alternative but to occupy a patch that promises little in the way of RS. However, her fitness is likely to be higher if she reproduces even if the probability of RS is low, than if she does not reproduce at all (RS = 0). In effect, a female may have to make the best she can of a poor situation.

A female's fitness requires leaving reproductive offspring. One estimate of fitness is recruitment, the retention of daughters in their natal area. Recruitment was measured as:

\[
\text{Recruitment} = \frac{\text{number of 2-year-old daughters added}}{\text{number of adult females resident the previous year}}
\]

RS is significantly correlated with recruitment in all habitats except one. RS and recruitment are highly correlated among colonies (rs = 0.943, p = 0.01). Both results are consistent with an analysis of recruitment that revealed that the production of yearling daughters was the single most important demographic factor affecting recruitment (Armitage 1984).

<table>
<thead>
<tr>
<th>Colony</th>
<th>N</th>
<th>RS</th>
<th>S</th>
<th>Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>River</td>
<td>23</td>
<td>0.477</td>
<td>0.569</td>
<td>2.73</td>
</tr>
<tr>
<td>Marmot Meadow</td>
<td>21</td>
<td>0.458</td>
<td>0.672</td>
<td>2.39</td>
</tr>
<tr>
<td>Cliff</td>
<td>8</td>
<td>0.467</td>
<td>0.713</td>
<td>1.88</td>
</tr>
<tr>
<td>Picnic</td>
<td>23</td>
<td>0.405</td>
<td>0.782</td>
<td>5.27</td>
</tr>
<tr>
<td>Boulder</td>
<td>22</td>
<td>0.170</td>
<td>0.673</td>
<td>0.02</td>
</tr>
<tr>
<td>North Picnic</td>
<td>20</td>
<td>0.329</td>
<td>0.688</td>
<td>7.24</td>
</tr>
</tbody>
</table>

TABLE II. Spearman rank correlations between reproductive success (RS) and other population parameters within habitats (= colonies). Significance levels: 0.1*, 0.05**, 0.01***.

<table>
<thead>
<tr>
<th>Colony</th>
<th>Adult Female</th>
<th>Per Capita RS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Survivorship</td>
<td>Recruitment</td>
</tr>
<tr>
<td>River</td>
<td>0.331*</td>
<td>0.358**</td>
</tr>
<tr>
<td>Marmot Meadow</td>
<td>0.489**</td>
<td>0.352**</td>
</tr>
<tr>
<td>Cliff</td>
<td>0.521*</td>
<td>0.428*</td>
</tr>
<tr>
<td>Picnic</td>
<td>0.167</td>
<td>0.143</td>
</tr>
<tr>
<td>Boulder</td>
<td>0.223</td>
<td>0.431**</td>
</tr>
<tr>
<td>North Picnic</td>
<td>-0.048</td>
<td>0.326*</td>
</tr>
</tbody>
</table>
TABLE III. Spearman rank correlations between demographic parameters within colonies (= habitats). \( p = 0.1^* \) or \( 0.05^*\).

<table>
<thead>
<tr>
<th>Colony (Habitat)</th>
<th>Survivorship vs Replacement</th>
<th>Survivorship vs Recruitment</th>
<th>Number of Females Returning vs Replacement</th>
<th>Number of Females Returning vs Immigration</th>
<th>Number of Females Returning vs Recruitment</th>
</tr>
</thead>
<tbody>
<tr>
<td>River</td>
<td>-0.456**</td>
<td>0.116</td>
<td>-0.353**</td>
<td>-0.246</td>
<td>0.290</td>
</tr>
<tr>
<td>Marmot Meadow</td>
<td>-0.039</td>
<td>-0.115</td>
<td>-0.058</td>
<td>0.456**</td>
<td>0.045</td>
</tr>
<tr>
<td>Cliff</td>
<td>-0.296</td>
<td>-0.023</td>
<td>-0.673**</td>
<td>-0.083</td>
<td>-0.167</td>
</tr>
<tr>
<td>Picnic</td>
<td>0.025</td>
<td>-0.100</td>
<td>-0.474**</td>
<td>0.195</td>
<td>-0.406**</td>
</tr>
<tr>
<td>Boulder</td>
<td>-0.172</td>
<td>0.296</td>
<td>-0.340*</td>
<td>-0.084</td>
<td>0.294</td>
</tr>
<tr>
<td>North Picnic</td>
<td>0.179</td>
<td>0.220</td>
<td>-0.112</td>
<td>-0.094</td>
<td>0.319*</td>
</tr>
</tbody>
</table>
females ($r_s = 0.771, p < .01$). Therefore, the mean number of females could affect replacement; however, replacement and the mean number of females are not correlated among habitats ($r_s = 0.257, p > 0.1$).

Replacement has two components, immigration and recruitment. Within colonies, only three of 12 correlations between immigration or recruitment and the number of females returning were significant (Table III). These results suggest considerable variation among habitats. The correlations are low, again suggesting that factors other than population density affect replacement. Further evidence supporting the lack of simple density dependence are the low and insignificant correlations between survivorship and recruitment within colonies (Table III), and the low correlations among colonies between recruitment and the mean number of adult females ($r_s = 0.381, p > 0.1$), RS and the mean number of adult females ($r_s = 0.257, p > 0.1$), and RS and area of the habitat ($r_s = 0.03, p > 0.1$).

The production of young per female could be affected by the number of resident females. All rank correlations between per capita production of young and the number of resident females within colonies were insignificant (Table V). Among colonies the per capita production of young was negatively, but insignificantly related to the mean number of females ($r_s = -0.6, p > 0.1$). RS was not related to the per capita production of young ($r_s = 0.029, p > 0.1$), but adult survivorship was ($r_s = -0.714, p = 0.1$). This result suggests a tradeoff between adult survivorship and the production of young. Those habitats of poor quality apparently cannot sustain both high productivity and survivorship. For the two colonies with the highest mean rates of RS, adult survivorship was significantly positively correlated with the per capita production of young (Tables I and V). As indicated previously, good habitat supports both a high RS and adult survivorship.

In conclusion, differences in reproductive success, survivorship, replacement, and recruitment are partly attributable to habitat differences, and partly to population density. But much of the variation

<table>
<thead>
<tr>
<th>Colony</th>
<th>Number of Resident Females</th>
<th>Survivorship</th>
</tr>
</thead>
<tbody>
<tr>
<td>River</td>
<td>0.069</td>
<td>0.541**</td>
</tr>
<tr>
<td>Marmot Meadow</td>
<td>0.159</td>
<td>0.222</td>
</tr>
<tr>
<td>Cliff</td>
<td>-0.196</td>
<td>0.551*</td>
</tr>
<tr>
<td>Picnic</td>
<td>-0.022</td>
<td>0.256</td>
</tr>
<tr>
<td>Boulder</td>
<td>0.245</td>
<td>0.090</td>
</tr>
<tr>
<td>North Picnic</td>
<td>-0.092</td>
<td>0.159</td>
</tr>
</tbody>
</table>
remains unexplained. This unexplained variation could be a consequence of social organization.

III. SOCIAL ORGANIZATION, REPRODUCTIVE SUCCESS, AND DEMOGRAPHY

Two demographic relationships suggest that social organization may be critically important to population processes. First, among colonies, replacement is significantly correlated with recruitment ($r_s = 0.943, p = 0.01$). Because recruitment is the retention of yearling daughters in their natal colony, the high correlation between rates of replacement and recruitment suggests the social system makes it possible for recruits to be preferred over immigrants as replacements. Second, the percentage of replacement that is recruitment (hereafter referred to as percent recruitment) varies widely among colonies (Table IV) and is not significantly related to replacement ($r_s = 0.486, p > 0.1$). But percent recruitment is significantly related to the mean number of resident females ($r_s = 0.771, p = 0.1$). Therefore, replacement is more likely to be recruitment when more adult females are present. This relationship can be interpreted to mean that females associating in a matriline can exclude immigrants and increase the probability that replacement will be relative.

Percent recruitment is low at the two habitats where RS is low (Tables I and IV). However, the correlation among habitats between RS and percent recruitment is low ($r_s = 0.486, p > 0.1$), primarily because Picnic, with the highest percent recruitment, ranked fourth in RS and River, with the number one ranking in RS, ranked fourth in percent recruitment. The other habitats had identical rankings for both parameters. This relationship further suggests that habitat quality and demographic effects are influenced by some other factor, such as social organization.

Social organization varies among the habitats. There is little difference in the mean size of matrilines, but considerable variation in the mean number of matrilines among the six habitats (Table VI). None of the following habitat characteristics are significantly correlated among colonies with either the mean number or mean size of matrilines: RS, S, per capita production of young, replacement, recruitment, and percent recruitment (Table VII).

A. Habitat and Matrilineal Organization

The mean size of matrilines is negatively correlated with habitat area (Table VII). The mean number of matrilines is positively correlated with habitat area and the mean number of resident females. Thus, as habitat area increases, the number of resident females increases, but the high number of females is subdivided into more matrilines rather than increasing the size of individual matrilines. In smaller habitats, there is no space for matrilineal subdivision and all resident females must be compressed into a single matriline. Also, in larger habitats, immigrants may successfully establish a new matriline in the presence of residents, but immigration occurs in the smaller habitats only in the absence of residents.

The process of matrilineal formation and subdivision may be illustrated by comparing Picnic and Boulder, the habitats with the largest and smallest numbers of matrilines, respectively, but with similar mean size of matrilines (Table VI).

Only in 1975 and 1976 did Boulder have two matrilines. Each female immigrated into the habitat in the same year; one of the females emigrated and the other established a matriline continuing through 1985 (Fig. 1). By contrast, as many as six matrilines occurred in the same year at Picnic (e.g., 1965, 1968, Fig. 1) and in only six of the 22 years were there as few as two matrilines. At both habitats, new matrilines were initiated by immigrants, but matrilines persisted through time only by incorporating daughters. In both habitats, the average relatedness of members of a matriline usually was 0.5. When average relatedness decreased, matrilines generally subdivided (e.g., Picnic 1974, 1976, 1983).

| TABLE VII. Spearman rank correlations between the mean number or mean size of matrilines and habitat characteristics, $p = 0.1^*, 0.05^{**}$. |
|-------------------------------|----------------|----------------|
| Habitat Characteristics       | Mean Number of Matrilines | Mean Size of Matrilines |
| Survivorship (S)              | 0.486            | 0.457          |
| Reproduction success (RS)     | 0.143            | -0.029         |
| Per capita production of young| -0.314           | -0.657         |
| Replacement                   | 0.143            | -0.029         |
| Recruitment                   | 0.363            | 0.2            |
| Percent recruitment           | 0.563            | 0.314          |
| Area                          | 0.886**          | -0.771*        |
| Mean number of females        | 0.829**          | 0.086          |
Boulder has only one major burrow system and all residents share it. Because of competition between members of different matrilines (Armitage 1986a), it is unlikely that matrilines can subdivide and coexist. Matrilines larger than two occurred only three times in 22 years; a Picnic, matrilines larger than two occurred only four times in the same time frame despite a three-fold greater mean number of residents. Thus females tend to form a matriline with only one other female, a daughter or a sister. The larger area at Picnic includes many more burrow sites and foraging areas and provides the opportunity for females to dissociate themselves from individuals related by <0.05 and to initiate their own matriline. The formation of a new matriline is characterized by the lack of overlap in space use between members of different matrilines (Armitage 1984). Furthermore, social behavior among females related by 0.5 is mainly amicable whereas social behavior among more distantly related females is characteristically agonistic (Armitage 1986b; Armitage and Johns 1982).

B. Matrilines as a Mechanism for Increasing Direct Fitness

Matrilines are family units; specifically, mother-daughter units. In a sense, marmot sociality follows a familial pathway (Slobodchikoff 1984). Fifty-five matrilines can be distinguished in the six colonies during the period of study. Of these, 35 were established as mother-daughter matrilines and 20 as sister-sister matrilines. Of the 20 sister-sister matrilines, eight were derived from mother-daughter matrilines after the mother presumably died. Only 22 percent of the matrilines were formed in the absence of the mother; even in these 12 cases the mother usually was present the previous year, but died before her daughters became residents (e.g., Fig. 1, Picnic 1968, 1973; Boulder 1974).

The formation of matrilines is a form of parental investment. It is generally accepted that mortality is higher among dispersers than among residents (Gaines and McClenaghan 1980). A female's evolutionary fitness will be greater the larger her number of reproductive descendants. Therefore, she should act to increase the probability that her daughters will live long enough to be reproductive. One way to increase that probability is to retain daughters in their natal area. The natal area has proven successful; marmots have survived and reproduced there. The adult female can protect her daughters against conspecifics; daughters are highly philopatric (Armitage 1984). When a daughter reaches adulthood, she may form a coalition with her mother. A numerically dominant matriline can defend its space against conspecifics and can cause the numerically inferior matriline to abandon space (Armitage 1986a). Thus, both the mother and daughter can increase their potential fitness by gaining resources and cooperating in defense.

However, there are costs to the formation of a matriline. The reproduction of two-year-old females living with their mothers is significantly less than the population average (Armitage 1986a). These females fail to produce litters. The failure of these females to disperse...
in order to increase their likelihood of reproduction suggests that the survivorship of recruits is sufficiently greater than that of dispersers so that lifetime reproductive success compensates for any short-term annual loss.

Competition among females probably is the ultimate cause of matrilineal subdivision. A female will gain more in direct fitness by producing more daughters than by helping her daughters produce her grandchildren (Rubenstein and Wrangham 1980). The mother's offspring will be related to her by 0.5; her grandchildren likely will be related by 0.25. The mother can increase her direct fitness by being the only reproductive female and using her daughter(s) to help defend the matrilineal resources. Conversely, the daughter should try to maximize their direct fitness by producing offspring rather than maximizing their indirect fitness by assisting her mother. Thus, the daughter should avoid reproductive suppression either by becoming codominant with her mother or by forming an independent matriline. This competition is a clear example of parent-offspring conflict (Trivers 1974). The same arguments apply to sisters; they should remain together when the direct fitness of each is enhanced. But a sister whose direct fitness is lowered by competition with her sister should form her own matriline if that will increase her direct fitness. However, in many situations a subordinate sister may lose both direct and indirect fitness if the only choice she has is to emigrate. Therefore, she should make the best of her situation and gain as much inclusive fitness as possible.

In all of our sister-sister matrilines, one sister was dominant. The subordinate sister(s) were never known to disperse to form a new matriline. One subordinate female, whose sister died, was forced to move by an immigrant to a marginal habitat at the edge of Picnic Colony where she produced one litter in six years and failed to recruit any daughters. In River Colony, a subordinate female moved to a peripheral location when an aggressive immigrant became resident, returned when the immigrant died, again became peripheral when new adults appeared, returned another year as the only adult present, but never reproduced. These examples suggest that subordinate females have little chance of success as immigrants to other habitats or to form and defend an independent matriline in the natal habitat. Only sisters of the same year class form a matrilineal group; full sisters from different year-classes and maternal half-sisters are treated as strangers; i.e., they are treated agonistically and space (with its food and burrow resources) is not shared.

The small size of matrilines, the subdivision of matrilines when average relatedness increases, the preponderance of mother-daughter matrilines, the patterns of cooperative and competitive behavior, and reproductive suppression (Armitage 1986a) indicate that female yellow-bellied marmots attempt to maximize direct fitness. Post-weaning reproductive investment in which offspring are retained in their natal habitat for an additional growing season leads to the subsequent residency of some daughters and the formation of matrilines. Matrilines should be considered a result of direct reproductive investment and not a form of kin selection. Regardless of the resource level, the only sociality evidenced by yellow-bellied marmots is the matriline. Matrilines rarely form in small habitat patches where the quantity of resources does not typically allow more than one adult female resident.

IV. SOCIAL SYSTEMS OF GROUND-DWELLING SQUIRRELS

The fundamental social system of the ground-dwelling squirrels is based on female associations. Females must locate sufficient resources for growth, gestation, lactation, and fattening. These needs are especially critical during lactation (Kiehl and Millar 1980). Thus, the primary issue of residency is set by the females whose fitnesses will be zero if they do not obtain sufficient resources to meet all their needs. Males associate with females in a variety of mating systems ranging from male-dominance polygyny in a resource-based lek in Spermophilus beldingi (Sherman and Morton 1984) to the highly territorial systems of marmots (Armitage 1974; Barash 1973, 1981) and prairie dogs (King 1955; Hoogland 1981a; Rayor 1985; also see reviewed by Michener 1983 and Dobson 1984). Males usually disperse from their natal area the year before reaching reproductive maturity (Holker 1984). My analysis of behavior of male yellow-bellied marmots concluded that males seek out females. Where females are clumped, such as on habitat patches like Picnic or Cliff, a male may form a harem that is defended against intruding males. The harem consists of more than one matriline (Armitage 1986). This mating system, from the male viewpoint, is female-defense polygyny (Emlen and Oring 1977).

On small habitat patches, such as Boulder, the male may be monogamous. Monogamy probably characterizes the mating system at widely separated satellite sites. However, we recently discovered through the use of radiotelemetry that some males may travel widely among two or more satellite sites and defend a dispersed harem (Van Vuren, pers. comm.). A population of 11 colonies of hoary marmots (M. caligata) in south-central Alaska was monogamous (Holmes 1985b). Food supported only one adult female and her young at each site and hibernacula were too far apart for a male to defend more than one. Litters were produced infrequently and movement of subadults to the periphery of the colony seemed to coincide with the appearance of groundhogs of a new litter juviniles. Thus, resources would not allow the development of a social group consisting of at least two adult females.

Female kin associations occur among several species of Spermophilus. These associations, or kin clusters, occur in S. tridecemlineatus (Vestal and McCarley 1984), S. beldingi (Sherman 1981), S. terrestris (Dunford 1977), S. richardsonii (Michener 1979), S. parryii (McLean 1982), S. columbia (Festa-Bianchet 1981; Harris and Murie 1984) and probably in S. beecheyi (Owings et al. 1977) and S. armatus (Slade and Balph 1974). It seems likely that female kin associations are universal in this genus.
Among *Cynomys*, female groups consist of descendent and collateral kin in *C. ludovicianus* (Hoogland 1985) and probably also in *C. gunnisoni* (Rayor, pers. comm.). For both species, the female assemblages are consistent with the interpretation that adult females increase their direct fitness by retaining daughters in their natal home range. Demography would then be expected to produce kin groups consisting of cousins, nieces, daughters, and sisters. The social organization of *C. leucurus* is poorly known, but females probably form kin clusters (Clark 1977).

Both *M. olympus* (Barash 1973) and *M. caligata* (Barash 1974) form female social groups that evidence sociality, i.e., several adult females with their offspring share burrow and foraging resources, although parous females tend to defend their burrows against conspecific intruders. It is very likely that these female groups are derived from mother-daughter matrilines. Among woodchucks (*M. monax*), some daughters gain access to a portion of their mother's home range (Meier 1985). This pattern is reminiscent of the kin clusters of speromophiles, but on an expanded scale. Home range of marmots is related to body size (Lindstedt et al. 1986); therefore, neighboring kin should be much further apart in the larger species. When adult females are not so dispersed, but share highly overlapping home ranges, sociality is indicated.

I conclude that there is a general trend among the ground-dwelling squirrels for some daughters to settle near their mothers. The tolerance of the adult for the juvenile is a form of parental investment that increases the likelihood that an adult will produce descendants that survive and reproduce. This association of kin may be expressed as sociality, especially in those species where reproductive maturity is delayed to age two or later and resources are clumped (Armitage 1981).

V. RESOURCE VARIABILITY AND SOCIAL ORGANIZATION

Previously we demonstrated that whether male *M. flaviventris* and *M. caligata* are monogamous or polygamous depends on the resources available to support females. If resources are too scattered or too sparse to support more than one adult female in a habitat patch, males are monogamous. Conversely, scanty resources limit female sociality; in the three well-studied species of montane marmots, matrilineal groups rarely or never occur on small habitat patches. However, the resources may be inherited by a daughter from her mother. In this section I will discuss the results of resource manipulation on ground squirrels and prairie dogs.

A. Natural Experiments

Several field studies have compared populations living in habitats with observable differences in the abundance of food. Two populations of Gunnison's prairie dog (*C. gunnisoni*) were studied in south-central Colorado. One population occupied a dry, barren site and the other, a lush, irrigated site (Rayor 1985). No differences in social organization were observed. All differences were in life history traits; the prairie dogs in the lusher habitat were heavier, dispersed at an earlier age, reached sexual maturity more rapidly (some yearlings raised litters) and adult females produced larger litters. A young colony of black-tailed prairie dogs (*C. ludovicianus*) with access to abundant grasses exhibited earlier reproductive maturity, larger litters, a greater proportion of successful pregnancies, faster juvenile growth, and greater survivorship than an older colony whose habitat was characterized by plants of low palatability (Garrett et al. 1982). Again, all differences were in life history traits. No differences in social organization were reported.

Other evidence from field studies indicates that increased nutrition affects life history traits. Some female yearling *S. columbianus* reproduced in a favorable habitat (Festa-Bianchet 1981); normally, first reproduction is at age two. Better nutrition produced larger litters in *S. tereticaudus* (Reynolds and Turkowski 1972), *S. richardsonii* (Sheppard 1972), and *S. columbianus* (Murie et al. 1980). To summarize, all reports of differences in food resources indicate that individuals opt to initiate reproduction earlier or to produce more offspring. Each of these responses is a mechanism for potentially increasing the direct fitness of the individuals involved.

B. Manipulative Experiments

Manipulation experiments involve either removing food resources, e.g., by mowing, or enhancing food by distributing some supplement in the habitat. In a colony of Gunnison's prairie dogs, mowing produced an increase in territory size and shift toward monogamy from the previous polygynous mating systems. Adding food to the mowed patches decreased territory size, but no change in monogamy (Slobodchikoff 1984). This response is similar to that of yellow-bellied or hoary marmots living on small patches which is equivalent to reduced resources. Apparently the experiment was not continued long enough to determine effects on reproduction and other traits.

Two populations of Columbian ground squirrels (*S. columbianus*) received food supplements whereas two additional populations served as controls (Dobson and Kjelgaard 1985a,b). Age at maturity decreased (yearling females successfully weaned litters) and litter size, reproductive effort, survival of young, and spring body weight increased in the food supplemented populations in comparison with the reference populations. There was no evidence for changes in social behavior or organization.

VI. DIRECT FITNESS AND SOCIALITY

Throughout I have argued that sociality is a mechanism whereby a female ground squirrel attempts to maximize her direct fitness by increasing the probability that one or more daughters will survive to
maturity. The retention of daughters in the natal area implies that survivorship is lower in dispersers than in residents. Female recruits may lose at least one year of reproduction because their reproductive capacity is suppressed by older females, often their mothers. This apparent willingness to forego reproduction in order to be a resident further suggests that the costs of dispersing are considerable. No female should disperse from her birth site unless her fitness would be increased over what it would be if she attempted to become a resident. A juvenile female should "assign" the probability of achieving reproductive success as a resident and "decide" whether to emigrate or remain. The proximal mechanisms initiating this decision are incompletely known (Gaines and McClenghnan 1980; Holekamp 1984), but adult residents probably play a major role. When all adults were removed from a colony of yellow-bellied marmots, none of the yearling females dispersed (Brody and Armitage 1983). Possibly the proximal mechanisms are subtle, the mere presence of an adult who expresses dominant behavior may be sufficient to initiate dispersal of some juveniles. The benefits and costs of dispersal in comparison to recruitment must be determined if we are to understand the function of sociality as an evolutionary strategy for increasing fitness.

There is little evidence that resource manipulation changes the basic social structure of a species. Food supplementation has direct fitness consequences: the probability of producing reproductive offspring is increased by increasing litter size and decreasing the age of first reproduction. Both responses increase the lifetime reproductive output of an individual. This response has its physiological limitations; every species has an upper limit to the biomass of offspring a female can produce. In ground-dwelling squirrels, the age of first reproduction cannot be lower than one year of age because of the limitations imposed by hibernation or winter inactivity. If there are limits to maximizing fitness by increasing the probability of evolutionary success through the production of more offspring, then we would expect social mechanisms to evolve to increase that probability.

If sociality is such a successful mechanism for increasing fitness, why are not all ground-dwelling squirrels social? The answer seems to lie in mother-offspring conflict, in other words, in the costs of sociality. The costs are mediated through competition and expressed by loss of reproductive output or loss of space to distant kin (r < 0.25) that otherwise could be used by closely related kin (r = 0.5). Dispersal characteristically occurs in the summer before reproductive competition begins. This competition must make the costs of sociality too high for those species who are reproductively mature at age one. The establishment of separate home ranges in those species who do not form matrilineal groups is functionally similar to the subdivision of yellow-bellied marmot matriline and the generally small size (x = 1.47) of these matriline. Females attempt to occupy a resource base and live in a social environment that will increase their direct fitness.

Prairie dogs are an interesting example of this process. The Gunnison and black-tailed prairie dogs are highly social, but the white-tailed is much less so (Hoogland 1981b). White-tailed prairie dogs breed at age one; most black-tailed prairie dogs breed at age two. A comparative study of the two species hypothesized that reduced predation may be the most important benefit of prairie-dog sociality (Hoogland 1981b). However, I suggest that the benefits of sociality must be explained in terms of reproductive success. Various selective pressures can modify behavior without inducing sociality. Vigilance and alarm calling are common behaviors among ground-dwelling squirrels, but only a few species have developed sociality.

Sociality in prairie dogs can be explained in terms of reproductive benefits. In the not-too-distant past, black-tailed prairie dog populations extended for many miles and were (and still are) characterized by sparse vegetation (Koford 1938). The population is organized into female groups with one or two males called coteries (King 1955). Except for coterie on the periphery, all coterie are surrounded by competitors. Any disperser must enter hostile territory and the likelihood of finding a place to settle must be low. It does not matter whether a disperser would fail because of the inability to find a burrow site, or inability to obtain sufficient food, or by becoming prey; the key issue is that the likelihood of reaching reproductive maturity is very low. The probability of failure would be greater the younger and smaller the disperser. Thus, the probability of reproductive success would increase by retaining offspring in their natal area until they approach reproductive maturity. At the time of approaching maturity, decisions could be made. If mortality reduced coterie membership, the offspring could remain. If the coterie could not accept an additional member, the offspring could disperse. Because it would be older and larger, it would have some increased probability of survival.

It is critical to coterie success that new members be recruited. Coterie members defend their area against intruding conspecifics (King 1955; Hoogland 1981a). Small coteries may lose space (= resources) to larger, neighboring coterie. A female will maximize her fitness if all coterie members are her daughters. Demographic considerations suggest that situation would be difficult to achieve. In fact, coterie memberships may include half-sisters, full first cousins, half-aunt-nieces, etc. (Hoogland 1986). Thus, females probably are forced to accept less closely related kin in order to have assistance in coterie defense. However, coterie space is limited and only a few of the young that are produced can expect to achieve residency. A female should initiate behaviors that will increase the likelihood that her daughters will become residents rather than nieces, granddaughters, cousins, sisters, etc. One strategy is to kill offspring who would compete with one's own offspring for the limited space. Although female prairie dogs defend their burrows against coterie, infanticide is common (Hoogland 1985). Competition among female black-tailed prairie dogs is greatest during late pregnancy when the danger of infanticide is high (Hoogland 1986). Infanticide in this context is readily understood as an evolutionary strategy. Furthermore, amicable behavior among females is not distributed according to relatedness but varies inversely with competition (Hoogland 1986).
animals do not aid the reproduction of kin; they attempt to gain more by maximizing their direct fitness (see also Rubenstein and Wrangham 1980).

Sociality has both cooperative and competitive behaviors. Because social groups are frequently kin groups, too much attention has focused on cooperation under the assumption that individuals should assist kin. This assumption implies that indirect fitness is an important component of inclusive fitness. The blend of cooperation and competition suggest that ground-dwelling squirrels attempt to maximize direct fitness (see also Armitage 1986a). The indirect component of fitness is important only as it contributes to an animal's direct fitness. Thus, a female yellow-bellied marmot or a female black-tailed prairie dog tolerates a sister or daughter, not because of indirect fitness benefits, but because these individuals contribute to her direct fitness. Black-tailed prairie dogs are highly agonistic toward non-coterie members, and amicable behavior within the coterie is always greater than amicable behavior with non-coterie members (Hoogland 1986). Obviously, inclusive fitness is greater when sociality involves kin groups rather than unrelated individuals. That is not the issue. What is critical is whether an animal's behavior is directed toward maximizing direct fitness.

I suggest that the behavior of ground-dwelling squirrels is directed toward maximizing direct fitness. Social behavior is both cooperative and competitive. In most species, "competitive decisions" are made in the first year of life; dispersal occurs at this time and most species, including white-tailed prairie dogs, do not form matrilineal groups. When the competitive decisions come at age two or later, matrilineal groups are formed. But competition becomes a way of life as each individual plays its game of attempting to maximize direct fitness.

I have sketched a scenario. This scenario can be verified or rejected only by focusing on the lifetime reproductive success of individuals of known relatedness. And these studies must include learning the fate of dispersers. Only by documenting the reproductive success of dispersers and residents can we construct a logical story of the relative importance of direct and indirect selection in animal sociality. I predict that direct selection will be by far the most important.

REFERENCES


