14. Marmot Polygyny Revisited: Determinants of Male and Female Reproductive Strategies

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MUCH OF THE FOCUS on the nature of mating systems has centered on determining the conditions under which polygyny evolves. One model, the polygyny threshold, states that a female should choose to mate with an already mated male when she can expect greater reproductive success than if she mated with a remaining unmated male (Verner and Willson, 1966; Orians, 1969). In this model, both males and females benefit. The underlying assumption in the study of mating systems is that individuals attempt to maximize fitness. An analysis of the mating system of the yellow-bellied marmot revealed that the fitness of individual females, measured as reproductive output, decreased as harem size increased (Downhower and Armitage, 1971). Downhower and Armitage emphasized that the reproductive interests of males and females conflict; such conflict is now widely regarded as fundamental (Wittenberger, 1979, p. 272). Additional studies of marmots have necessitated a revision of the Downhower-Armitage model. Before describing the current model, based on twenty-two years of data, some of the assumptions underlying the development of polygyny models must be examined. The assumptions led us astray in the past and I hope an examination of these assumptions and a clear statement of the assumptions underlying the present interpretation of the marmot mating system will at least clarify the issues.

Most studies of polygyny focused on birds. Because most bird species are monogamous, theory centered on why some birds are polygynous. But a student of mammals, noting that most mammals are polygynous, might try to find models to explain monogamy. Implicit in the polygyny threshold model is the assumption that females operate independently, make choices based on potential reproductive success, and do not interfere with the decisions of later-arriving females. Yet, among mammals, females may be bonded to other females and cooperation or competition among females may decide the size of the mating group. Two recent papers made major efforts to broaden perspectives on the evolution of polygyny. Greenwood (1980) emphasized the relationships among philopatry, dispersal, and mating systems. In many mammals, males defend females (mate defense); in many birds, males defend resources (resource defense). Female mammals and male birds are philopatric. Futhermore, philopatry should favor the evolution of cooperative traits among members of the sedentary sex. Emlen and Oring (1977) integrated ecology, sexual selection, and mating systems. They argued that polygamous mating systems occur when multiple mates, or resources sufficient to attract multiple mates, are energetically defendable and when animals have the ability to exploit this potential. Females independently choose whether to become polygynous (e.g., Emlen and Oring, 1977; Wittenberger, 1979); in resource defense polygyny, males determine the dispersion of females. However, Greenwood (1980) rightly pointed out that females may determine the dispersion of males, especially in harem defense polygyny (Emlen and Oring, 1977).

Female mammals, because of gestation and lactation, invest more in reproduction than males. Therefore, females should selectively choose a mate (Trivers, 1972). But there may be realistic constraints on female choice. Because of the greater reproductive investment of female mammals, females must satisfy their physiological and ecological requirements and males must adjust their strategies to the realities of what females must do. I hope to demonstrate that for yellow-bellied marmots, and probably many species of mammals, females determine the spacing patterns that make polygyny possible and males attempt to associate with clumped females.

BIOLOGY OF THE YELLOW-BELLIED MARMOT

The yellow-bellied marmot (*Marmota flaviventris*) is one of six species of marmots living in North America. Marmots are typical ground squirrels, along with prairie dogs, spermophiles, and chipmunks (Moore, 1959), of the subfamily Marmotinae of the family Sciuridae, order Rodentia. The yellow-bellied marmot is widely distributed in the western United States, especially in forest clearings and the alpine of the Cascade, Rocky, and Sierra Mountains (Frase and Hoffmann, 1980).

M. flaviventris occupies open areas, dominated by perennial forbs and grasses (Svendsen, 1974; Kilgore and Armitage, 1978), in which rock outcrops, boulders, or talus occur. Marmots excavate burrows at what appears to be every suitable site; where rock and/or soil structure do not permit burrowing, marmots are absent (Svendsen, 1974). Areas occupied by marmots become snow-free earlier in the year than adjacent forest areas do.

Marmot populations are clumped on habitat patches that range widely in size. Larger patches (total open area, $\bar{x} = 58$ ha) that typically harbor three or more adults and variable numbers of yearlings are designated colonial sites. Smaller sites ($\bar{x} = 6.6$ ha), where typically only one or two animals live, are called satellite sites (Armitage and Downhower, 1974; Svendsen, 1974). Some satellite sites are within 100 meters of a colonial site, but most are more distant. Although marmot habitats may be classified into these two types, they form an almost continuous range of sizes from a single boulder in an area of about 0.01 hectare to a rocky slope and meadow of 70 hectares or more. Mean population density is correlated with habitat area (Svendsen, 1974).

The annual cycle of marmots consists of two phases: heterothermal and homeothermal (Morrison and Galster, 1975). The annual cycle is a circannual rhythm of metabolism, body mass, and food consumption (D. E. Davis, 1976) that persists in yellow-bellied marmots maintained in the laboratory (J. M. Ward and Armitage, 1981). Because the phases of the circannual rhythm are tightly locked, emergence, reproduction, growth, and maintenance and preparation for immergence are sequentially programmed. Emergence patterns follow an age-sex sequence. For example, at North Pole Basin in 1976, 50 percent of adult male marmots emerged by 16 May; 50 percent of adult females, by 25 May; 50 percent of yearling males, by 28 May; and 50 percent of yearling females, by 5 June. Immergence is reversed: adult males and nonreproductive females immerge first, usually between mid- and late August; reproductive females immerge in early September and juveniles immerge about mid–September. Two or more marmots commonly occupy the same hibernaculum (Johns and Armitage, 1979).

Emergence typically occurs through the snow. At colonial sites, there is no marmot activity into or out of a site; marmots are vulnerable to coyote predation when crossing snow. During the first two weeks there is little activity; females remain near their burrows. The adult male is most active and is especially attentive to females. As females become receptive, they are increasingly active and consort with the male from one to several hours. Reproductive activity ceases after two weeks (Armitage, 1965; Nee, 1969). Subsequent to mating, females may shift burrows; home ranges overlap less. The synchrony of reproduction into a short period early in the homeothermal period is critical for survival of the young; young weaned late in the period have a very low rate of survival through their first hibernation (Armitage et al., 1976). When lactation begins, marmot habitats are rich in food resources (Svendsen, 1974; Kilgore and Armitage, 1978; Frase, 1983). Marmots are generalist herbivores (Frase, 1983), feeding on leaves and flowers of a wide variety of forbs and grasses, but avoid eating plants with known defensive compounds (Armitage, 1979). Juveniles appear above ground between three and four weeks of age; weaning occurs at this time (Armitage, 1981). Marmots use less than 4 percent of the aboveground primary production available to them (Kilgore and Armitage, 1978). Although marmot population density apparently is not food-limited, the number of offspring weaned by a female was significantly associated with food resources in a high-altitude population (D. C. Andersen et al., 1976).

Yellow-bellied marmots live as solitary individuals or as members of social groups, consisting characteristically of one adult male, one or more adult females, yearlings of both sexes, and juveniles (Armitage, 1962; Armitage and Downhower, 1974; Svendsen, 1974; Johns and Armitage, 1979). Members of social groups are called colonial. Peripheral animals live near colonial animals, but their home ranges lie outside the home ranges of the colonial residents. Peripheral animals, especially males, occasionally venture into the colony. Female residents attempt to exclude female intruders, but are dominated by male intruders. Males rebuff male intruders, but accept females. Solitary females may be associated with juveniles, but rarely with yearlings. Virtually all male yearlings disperse (Armitage and Downhower, 1974; Downhower and Armitage, 1981), but 72 of 135 female yearlings became resident in their natal populations (Armitage, 1984). Home ranges of resident yearlings overlap by 50 percent or more those of the resident adult females (Armitage, 1975).

Although the age of first reproduction is two years for both sexes, most marmots do not breed before age three or older (Armitage and Downhower, 1974; Armitage, 1981). Yearlings have a greater probability of living to age three than juveniles (Armitage and Downhower, 1974); therefore, the number of yearlings produced by an adult is a more critical measurement of reproductive success than the number of young.

The adult male is territorial (Armitage, 1974). Many habitat patches support only one male, but larger patches may have two or more. Virtually all of the variation in the population density of adults results from changes in the number of resident females. Changes in population density are not density-dependent (Armitage and Downhower, 1974; Armitage, 1975).

Predation is rarely detected (Armitage, 1982a). Marmots of all age classes gain weight normally (Armitage et al., 1976); diseased animals have not been detected. The loss of residents, which occurs over winter, is assumed to be mortality. This assumption is supported by the higher survival of young and adults when winter terminated earlier and by the higher survival of females that produced a litter when the onset of winter was later or the length of winter was shorter (Armitage and Downhower, 1974).

Immigration is significantly more likely to produce residents when the previous residents fail to return (Armitage, 1984). Recruitment of yearling females is highly variable. A recruit is an animal who becomes resident in its natal population; recruitment is defined as retention of yearling offspring in the parent's population without implying any particular proximal mechanism whereby it occurs. Social structure and recruitment are highly philopatric among closely related ($r = 0.5$) females (Armitage, 1984). Adult females that are successful recruiters produce more yearling females than nonrecruiters (Armitage, 1984). Sociable females (Svendsen and Armitage, 1973) have greater lifetime reproductive success as measured by the number of female yearlings produced, the number of daughters recruited, and the number of two-year-old daughters who were residents (Armitage, 1983). Recruitment is not affected when a new adult male replaces a previous resident.

Social behavior is highly variable (Armitage, 1975, 1977). This variability is partly attributable to individuality (Armitage, 1982b, 1983) and to the age-sex composition of the population (Armitage and Johns, 1982). The major variable affecting social interactions is kinship: behavior among females related by 0.5 is amicable (greetings, allogrooming) but is agonistic (chase, fleeing) when relatedness is 0.25 or less (Armitage and Johns, 1982). Although adult females generally behave amicably to their daughters, they behave neutrally to their yearling sons. Adult males behave cohesively toward females and agonistically toward males (Armitage, 1974; Armitage and Johns, 1982).

METHODS

Yellow-bellied marmots were studied every year since 1962 in the East River Valley, Gunnison County, Colorado, at an elevation of 2,900 meters. Each year at each study site virtually all animals are trapped, sexed, and permanently marked for identification. Each time an animal is trapped, it is weighed and its reproductive status noted. At various periods during the study, blood samples were collected for genetic studies. Juveniles were trapped as soon as possible after their first appearance above ground. In this way, maternity could be assigned except in seven instances (16 of 158 litters) when adult females occupied the same burrow system and young intermingled from the time they were first observed.

Usually our field season extended from about the first of June to late August. Consequently, in most years we missed mating and the last two or three weeks prior to immergence. Paternity was assigned to the male resident in early June. In those years when we were present early in the season, no male was replaced by another during the reproductive period. Genetic analyses verified that the June resident was the probable father of juveniles produced at a particular study site (O. A. Schwartz and Armitage, 1980).

Marmot populations were observed in excess of 250 hours each summer. Because of low population densities, all animals at a study site are monitored. Observation hours are concentrated in the morning, late afternoon, and evening when marmots are most active (Armitage, 1962). All social interactions are recorded. At regular intervals the position of each animal is recorded from a transparent numbered grid overlying a map of the study site. These census data are plotted by the Surface II computer program (Sampson, 1975) as three-dimensional block diagrams.

Differences in reproductive success among groups were assessed by analysis of variance or linear regression; differences among means were tested

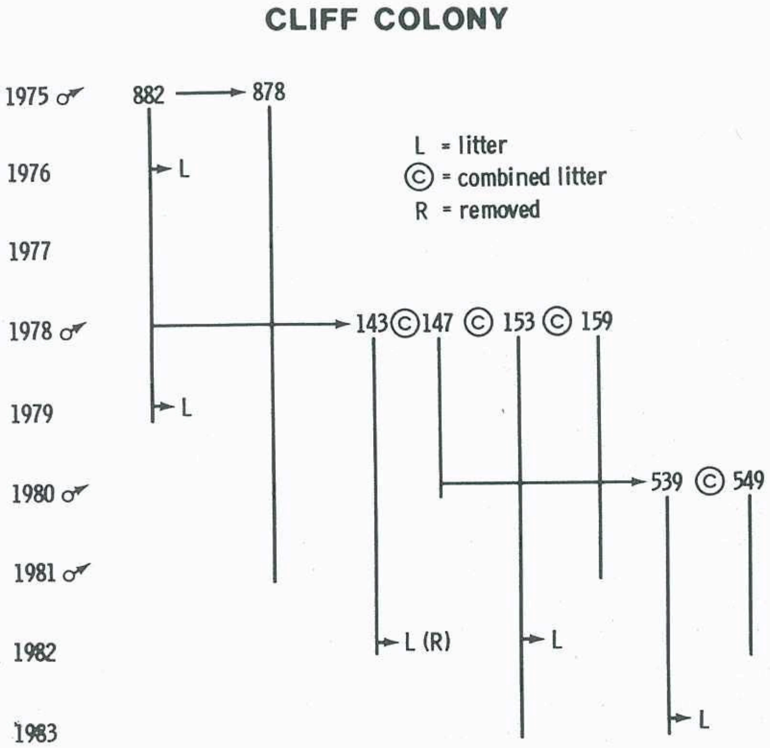

Fig. 14.1. An example of a matriline. The ♂ symbols indicate when a new male became resident. Note that not all litters (L) produce recruits, that females fail to breed in many years, and that some litters are intermingled (horizontal line crossing two or more vertical lines). An animal's number is recorded in the year of its birth (except ♀882, who was a resident adult in 1975). The vertical line indicates the years of residency.

by the *t* method of SNK; and the distribution of social interactions was tested by χ^2 (Sokal and Rohlf, 1981).

RELATIONSHIPS AMONG ADULT FEMALES

Matrilines

Females form groups of one to five ($\bar{x} = 1.47$). A group of two or more animals consists of closely related animals who usually are full-sister or mother–daughter pairs (Fig. 14.1). Larger groups occur when a female recruits several daughters from the same litter; within these, average relatedness is 0.5. Females in these kin groups may produce litters in common, such that maternity cannot be assigned (Fig. 14.1). Larger groups also occur when nieces, granddaughters, and so on are added to the group and average relatedness decreases. Female kin-groups continue through space and time as matrilines (Armitage, 1984). Known lineages have persisted for eleven, twelve, and twenty-three years. Such lineages may undergo fission to form daughter matrilines. For purposes of analysis, I define a matriline as any number of females known to be related by descent that occupy a common home range. When home ranges diverge and females no longer share burrows or foraging areas, a single matriline is considered to have undergone fission.

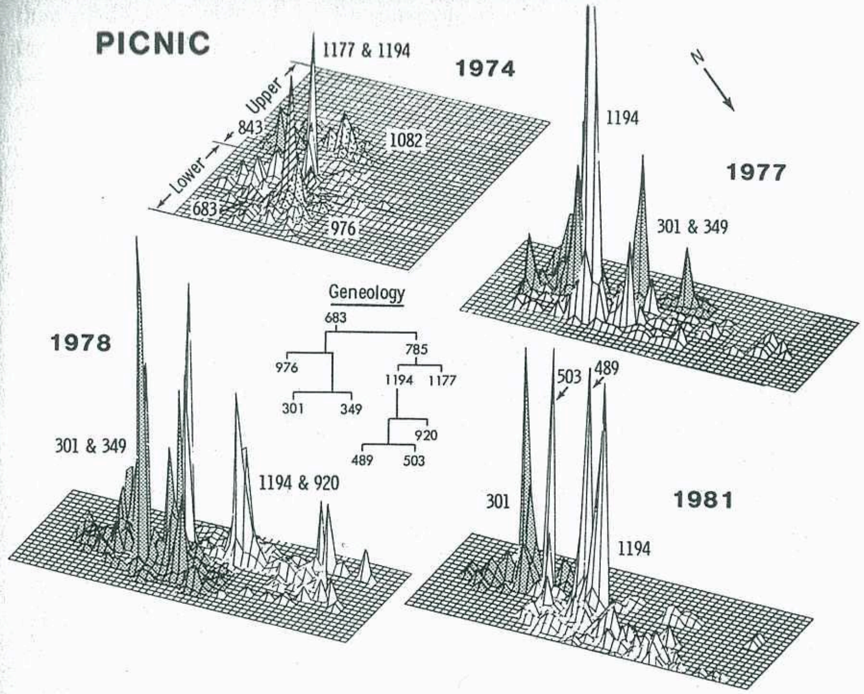

Fig. 14.2. Patterns of space use at Picnic Colony. The plots are oriented as if one were standing at the foot of the slope and looking uphill. The grids are 9 × 5 m. For 1974, the right side of the habitat was not plotted as no animals were using that area. For the other three years, only the lower half (Lower Picnic) is included. For each year, all resident adult females are shown. The height of each peak is a function of the number of times the animal was censused in that area. The genealogy of the residents of Lower Picnic begins with ♀683. The horizontal position of each animal on the chart indicates order of birth. Except for paired sisters, all births occurred in different years. In any year, different matrilines are distinguished by patterns of shading.

Matrilines occupy space exclusively. There was no overlap of home ranges among members of three different matrilines at Picnic Colony in

TABLE 14.1
Frequency analysis of amicable and agonistic interactions by kinship for adult females at Picnic Colony

Kinship group	Amicable		Agonistic		Amicable		Agonistic	
	1974				1977			
	E	O	E	O	E	O	E	O
Sisters	3.3	10*	1.2	0	3.3	10*	4	0*
Mother:daughter	3.3	2	1.2	0	—	—	—	—
Grandmother:granddaughter	6.7	6	2.3	1	—	—	—	—
Aunt:nieces	6.7	2*	2.3	6*	6.7	0*	8	12*
χ^2	17.5		8.9		20.3		6.0	
p	<0.001		<0.05		<0.001		<0.02	
	1978				1981			
	E	O	E	O	E	O	E	O
Sisters	3.5	13*	1.8	3	2.5	10*	—	0
Mother:daughter	3.5	8	1.8	0	7.5	5	—	1
Grandmother:granddaughter	—	—	—	—	—	—	—	—
Aunt:nieces	14	0*	7.3	8	5.0	0*	—	0
χ^2	45.6		2.7		28.3			
p	<0.001		>0.2		<0.001			

NOTE: Although there is no test of significance for individual rows, those values that contributed markedly to the total χ^2 are marked with an asterisk. O = observed interactions, E = expected interactions, — indicates the kinship group was not possible. In some instances, aunt:nieces also included grandnieces.

1974 (Fig. 14.2). At Upper Picnic, ♀843 represented the sole survivor of a matriline initiated at Lower Picnic in 1967; ♀1082 was descended from a matriline initiated at North Picnic, 300 meters distant. These females illustrate that matrilines may persist across space. Both animals died by 1980; thus the matrilines became extinct, the fate of most matrilines (Armitage, 1984). At Lower Picnic in 1974, the home ranges of the kin group overlapped (Fig. 14.2), but matrilineal fission was beginning. The peaks of major activity of ♀1177 and ♀1194 overlapped directly and were displaced from those of their grandmother and aunt.

Social Behavior

Social behavior is strongly related to matrilineal structure. Both amicable and agonistic behavior occur nonrandomly (Table 14.1; Armitage and Johns, 1982). Mother:daughter and grandmother:granddaughter amicable behavior occurs at a frequency predicted from the frequency of these kin pairs in the population. Amicable behavior between sisters occurs more frequently then predicted, and between aunts and nieces, much less frequently than predicted (Table 14.1). By contrast, agonistic behavior between sisters, mother and daughters, and grandmother and granddaughters occurs less than or about as expected whereas agonistic behavior between aunts and nieces occurs more frequently than expected.

Social and Spatial Dynamics of Matrilines

Sister pairs in 1974, 1977, 1978, and 1981 behaved amicably (Table 14.1) and had similar patterns of space use (Fig. 14.2). Social behavior of aunts and nieces was either more agonistic or less amicable than expected (Table 14.1). Home ranges of aunts and nieces (or grandnieces) either overlapped slightly (e.g., 976 vs. 1177, 1194 in 1974) or not at all (e.g., 301, 349 vs. 1194, 920 in 1978; 301 vs. 503, 489, 1194 in 1981). Both home range patterns and social interactions must be considered because social interactions between individuals who have lived in the same colony for more than one year typically decline over the period of joint residency (Armitage, 1977). For example, agonistic behavior was frequent between females 1194 and 301 in 1977, but never observed in 1981.

The shifting home range patterns suggest that a matriline attempts to exclude members of other matrilines from resources; e.g., preferred burrows, foraging areas, and rocks used for sitting or lying. In 1977, ♀1194 was dominant to either ♀301 or ♀349 alone, but when both 301 and 349 were present simultaneously ♀1194 retreated. As a result, ♀1194 moved downslope away from a primary burrow site which 301 and 349 used and extended her foraging area to the northwest (Fig. 14.2). In 1978, ♀s 301 and 349 occupied the prime talus and foraging areas of Lower Picnic, ♀1194 and her two-year-old daughter 920 maintained residency, but avoided space used by the other matriline. By 1981, ♀s 349 and 920 had died, but ♀1194 had two new two-year-old daughters. The matriline of three now occupied the prime resource area and 301 was displaced to the southeast edge of the habitat (Fig. 14.2). The space-use patterns of 1981 suggest that an animal in a subordinate position may avoid contact with dominant animals of a different matriline. This avoidance pattern may be a consequence of the behavioral interactions in previous years. For example, 301 was alone in 1979. She was subordinate in all encounters with 1194 and 920. Her space-use pattern of 1981 resembled that of 1979 (Armitage, 1984), despite no observed agonistic behavior between ♀301 and ♀1194 and her daughters. These results suggest that a major advantage of a matriline of two or more females is that resources are more readily obtained and defended and that the presence of several matrilineal associates may deter potential competitors.

Why does not one matriline with clear advantage drive out all members of another matriline? Two possible reasons come to mind. One, they may not be capable. Two, they may have garnered the necessary resources for

TABLE 14.2
The number of amicable behaviors between adult female and juvenile yellow-bellied marmots

	Marmot meadow					Picnic	
	1978	1979	1980	1981		1974	1976
♀911	24*	1	6*	15*	♀1177	4	20*
♀918	18	6*	9*	20*	♀1194	8*	54*
♀179	—	—	3*	0*			
χ^2	0.8	3.6	3.0	18.5		1.3	17.0
p	>0.3	>0.05	>0.2	<0.001		>0.2	<0.001

NOTE: Females with litters are indicated with an asterisk. Because females and juveniles shared the same burrow system, it was assumed that social interactions occurred with equal probability between any adult female and any juvenile. A dash indicates an animal was not present. Sister pairs are 1177–1194 and 911–918; ♀179 is the daughter of ♀911.

growth and reproduction and the costs of attempting to gain more space may exceed any potential benefits. The benefits would come in future years when new offspring are produced to move into and occupy the space. I never observed any group of females cooperatively seek out and attempt to drive out competitors.

Cooperative Breeding

"Cooperative" and "communal" are applied to breeding units in which some members in a social unit behave as parents but are not the genetic parents of the juveniles they aid (J. L. Brown, 1978). W. D. Hamilton (1964) used "cooperative" for those situations in which the direct fitness of both actor and recipient is increased. In the discussion that follows, I will use "communal" in the sense of Brown and "cooperative" only in the sense of Hamilton. However, I will describe behaviors that appear to be cooperative, but measurements of fitness benefits are lacking.

Among rodents, only the naked mole rat breeds communally (Jarvis, 1981). Among the Marmotini, black-tailed prairie dogs breed cooperatively in the sense that members of the colony share territorial defense (Hoogland, 1981). Among yellow-bellied marmots, females may live in the same burrow system. If more than one female has a litter, the juveniles at weaning intermingle such that maternity cannot be assigned (Fig. 14.1; Armitage, 1984). Although some females forgo breeding, there is no evidence that these females act as helpers (Brown, 1978); thus, communal breeding is not known to occur. Cooperative breeding occurs because all females assist in the detection of predators and in the defense of the matrilinal space against conspecific intruders. If cohesive behaviors with juveniles are considered postweaning parental care, females share such care.

TABLE 14.3
The number of occurrences of amicable and agonistic behavior between adult females at Marmot Meadow

	1978	1979	1980	1981	
	♀918:♀911*	♀911:♀918*	♀911*:♀918*	♀911*:♀918*	♀179*:♀918*
Amicable	14	1	7	4	0
Agonistic	1	6	8	5	18
χ^2	11.2	3.6	0.06	0.1	18.0
p	<0.001	$0.1 > p > 0.05$	>0.8	>0.7	<0.001

NOTE: Expected values were calculated on the basis that a female had equal probability of behaving amicably or agonistically in any encounter. Reproductive females are indicated with an asterisk. 911 and 918 are sisters; 179 is the daughter of 911 and the niece of 918.

At both Marmot Meadow and Picnic, females sharing burrow systems usually interacted with all juveniles even if the female was not a mother (Table 14.2). Only amicable behaviors were observed between juveniles and adults. In two instances, the frequency of amicable behaviors of individual females was nonrandom; in 1981, ♀179 at Marmot Meadow was not observed to interact with any juvenile and ♀1177 at Picnic interacted with juveniles less frequently than expected. Social interactions were tested to determine if an adult female demonstrated preferential treatment to any young when litters intermingled. Generally no such preference was detected; ♀1177, $\chi^2 = 5.9, p > 0.3$; ♀1194, $\chi^2 = 6.6, p > 0.3$; ♀301 (Picnic, 1978), $\chi^2 = 9.9, p > 0.2$, ♀911 (1981), $\chi^2 = 21.7, p > 0.2$; ♀918 (1981), $\chi^2 = 35.1, p < 0.01$. Female 918 interacted three times more often with one of nineteen young than with any other. Except for this one instance, there is no evidence that adult-female juvenile amicable behavior (mostly greetings) is biased toward the mother's own offspring.

Although adult-juvenile postweaning, above-ground social behaviors suggest cooperative breeding, other behaviors indicate that adult females attempt to maximize direct fitness (J. L. Brown, 1980) and maximize indirect fitness as a second choice. In 1978, reproductive ♀911 interacted amicably with her nonreproductive sister ♀918 (Table 14.3). However, when ♀918 reproduced in 1979, she treated nonreproductive ♀911 agonistically. Social interactions were fewer because ♀911 extended her home range to avoid contact with ♀918 and occupied a different burrow system for part of the summer (Frase and Armitage, 1984). In 1980 and 1981, when both females had litters, social interactions were few even though they lived in the same burrow system, had similar home ranges, and often fed within a few meters of one another (Frase and Armitage, 1984). By contrast, ♀179 occupied a different burrow system and utilized a foraging area generally distinct from that of her mother and aunt (Frase and Armitage, 1984). Each year she

TABLE 14.4
Contingency table analyses of the number of occurrences of amicable and agonistic behavior between adult female and yearling yellow-bellied marmots at Marmot Meadow

	1978		1979	
	Amicable	Agonistic	Amicable	Agonistic
♀911	0	42	8	1
♀918	5	5	4	28
χ^2	23.2		19.8	
p	<0.001		<0.001	

NOTE: Female 911 was reproductive in 1978 and ♀918, in 1979.

moved with her litter just prior to weaning to the burrow system occupied by her kin. Although when ♀918 was reproductive her behavior toward the other adults was agonistic, she was unable to exclude either of them. Thus, her sharing of resources and cooperative breeding may be interpreted as obtaining the best fitness possible under the circumstances.

The behavior of adult females toward yearlings is affected by kinship (Armitage and Johns, 1982) and reproductive status. The patterns suggest females attempt to maximize the direct component of inclusive fitness (Brown, 1980). When reproductive, females 911 and 918 behaved agonistically toward yearlings (Table 14.4). In 1978, the yearlings were maternal sibs of the females, but a year younger. In 1979, ♀918 was agonistic to her niece and nephews, but 911 was amicable to her yearling offspring (Table 14.4). The daughter (♀179) of ♀911 was recruited into the population. In 1981, when the yearlings were descended from all the adult females, there was no difference in the frequency of amicable or agonistic behavior between the adult females and the yearlings ($\chi^2 = 0.3, p > 0.5$). Because all adult females were reproductive in 1981, reproductive status is insufficient to explain behavioral patterns. Presumably the females could not distinguish among the yearlings and may have opted under those conditions to maximize inclusive fitness. Thus, six of the thirteen yearlings were recruits.

Individual variability characterizes marmot behavior and complicates the interpretation of behavioral patterns (Svendsen and Armitage, 1973; Svendsen, 1974; Armitage, 1983). When amicable versus agonistic behavior is summed over all years of pregnancy, ♀179 was generally noninteractive, even with juveniles (Table 14.2); ♀911 was amicable ($\chi^2 = 3.9, p < 0.05$); and ♀918 was so agonistic ($\chi^2 = 12.7, p < 0.001$) that she contributed to the significant level of agonistic behavior ($\chi^2 = 7.0, p < 0.01$) directed by the adults toward her yearlings in 1980. At Picnic in 1976, the behavior between sisters 1177 and 1194 was entirely amicable, but ♀1177 interacted

TABLE 14.5
Frequency analysis of amicable and agonistic interactions between the adult females and the yearlings at Marmot Meadow in 1981

	Amicable		Agonistic	
	E	O	E	O
♀179	15	3*	13.3	3*
♀911	15	18	13.3	24*
♀918	15	24	13.3	13
χ^2	15.6		16.5	
p	<0.001		<0.001	

NOTE: All females were reproductive. O = observed interactions, E = expected interactions. Individual row values that are probably biologically significant are marked with an asterisk.

significantly less with juveniles than ♀1194 (Table 14.2). Adult females differed in their frequency of social interactions with yearlings. Female 179 had fewer amicable and agonistic interactions than predicted and ♀911 was more agonistic than expected (Table 14.5). These individual differences may be part of a strategy that emphasizes phenotypic plasticity in a variable and unpredictable environment (Armitage, 1983). Briefly, both the social, physical, and other biological environments of marmots vary across space and time. Any particular behavioral pattern may not be adaptive to all sets of environmental conditions, but a diversity of behavioral characteristics among an animals's descendants may produce a range of individuals adaptive to a range of environmental conditions.

Chance, such as unpredictable mass mortality, may significantly determine the outcome of female competition. By early August of 1981 the population at Marmot Meadow consisted of one adult male, three adult females, four yearling females, two yearling males, twelve juvenile males, and seven juvenile females. The three adult females moved off and were not seen thereafter. In 1982, only two of the female yearlings and one adult female were recovered. Similar mass disappearances occurred previously at Marmot Meadow and at two other colonies. Mortality is the suspected cause of the disappearance because extensive searches over wide areas failed to find any of the missing animals. Causes of the presumed mortality are unknown.

In summary, both cooperative and competitive elements occur in the social behavior of closely related yellow-bellied marmots. These results suggest that the recent controversey of whether black-tailed prairie dogs are cooperative breeders (Hoogland, 1983; Michener and Murie, 1983) was misdirected. Both yellow-bellied marmots and black-tailed prairie dogs are

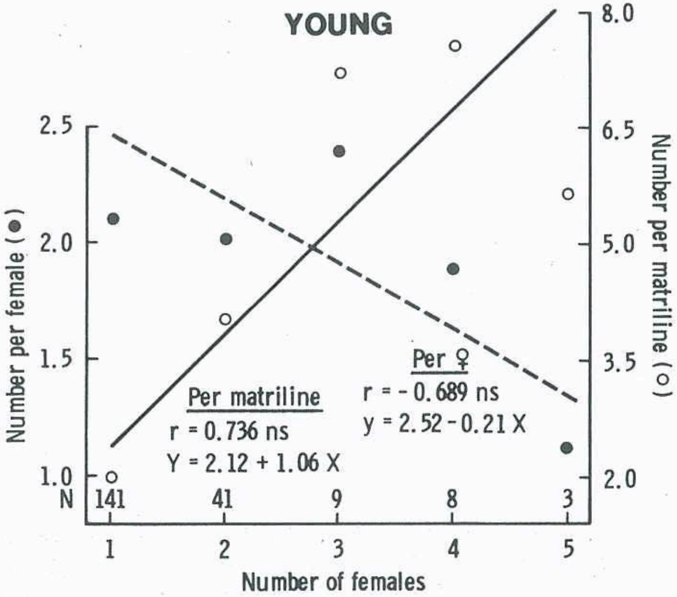

Fig. 14.3. The relationship between the production of young and the size of a matriline.

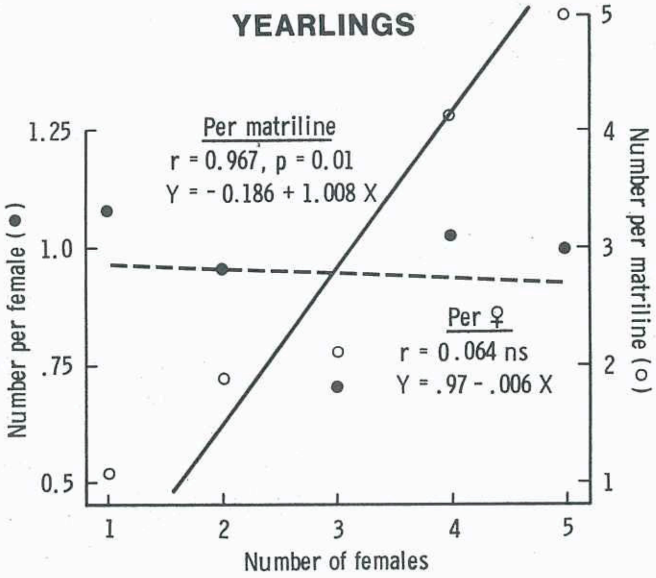

Fig. 14.4. The relationship between the production of yearlings and the size of a matriline.

social and both have cooperative and competitive components in their social systems (Hoogland, 1981, 1983; Armitage and Johns, 1982). What is important is not debating to what degree a species may be categorized as a communal breeder (e.g., Michener and Murie, 1983), but determining how animals try to maximize direct fitness. We expect that individuals should opt to maximize direct fitness because investing in the kin of other individuals may not be reciprocated (Rubenstein and Wrangham, 1980).

Reproductive Success

One possible consequence of living in groups is that direct fitness, measured as the per capita reproductive output of females, may decrease as group size increases. Such potential loss was reported for yellow-bellied marmots (Downhower and Armitage, 1971), black-tailed prairie dogs (Hoogland, 1981), and red deer (Clutton-Brock et al., 1982, p. 92).

The per capita production of young decreased and the total production of young increased with increased size of matrilines, but the relationships were not statistically significant (Fig. 14.3). There also is virtually no relationship between the per capita production of yearlings and size of matrilines (Fig. 14.4). Thus, for each additional adult female added to the matriline, one additional yearling is produced. If yearling output is used as an index of fitness, females lose no direct fitness (per capita production) by being members of matrilines and gain in indirect fitness (total output of matriline). However, inclusive fitness could decline if descendant kin do less well than collateral kin in subsequent years.

The analysis of matrilineal size and reproductive success lumped data from all colonies and years. Data are insufficient to do a similar analysis within years or within colonies. Different habitat quality might affect the matrilineal size:per capita production relationship. Large matrilines would be expected in better-quality habitat. The possible effects of habitat (= colony) differences were examined by testing for variation in the reproductive output of individual females per year and in the reproductive output per female per matriline per year. The first analysis examines the lifetime reproductive output of individual females, expressed as the average production per year, in order to account for differences in length of residency. A nested ANOVA tested for differences among matrilines. The second analysis ignores individual females and examines the yearly per capita production of matrilines. For both analyses, one objective is to partition the variance among groups (colonies), subgroups (matrilines), and within groups (individuals within matrilines or between years).

The production of young per female per year differed significantly among colonies ($F_{5,44} = 5.3, p < 0.001$), but not among matrilines ($F_{44,250} = 0.6, p > 0.75$). However, the differences among colonies explain only 5.3 percent of the variance; 94.7 percent of the variance occurs among individual females. When only those females that produced young are considered, the production of yearlings differed significantly among colonies ($F_{5,30} = 168.8$, $p < 0.001$), but not among matrilines ($F_{30,105} = 0.1$, $p > 0.75$). Again, all the variance is explained by variation among colonies (39.5%) or among individual females (60.5%). There is no relationship between the rank order of the size of the area the colony inhabits and the mean number of yearlings per female ($r_s = 0.03, n = 6, p >> 0.05$). Because our studies have not detected differences in habitat quality (Svendsen, 1974; Kilgore and Armitage, 1978), the differences among colonies may reflect sampling differences and differences in female residents. For example, Cliff Colony, with a mean significantly higher than all other means, was sampled only from 1976 to 1982 (Fig. 14.1). Unusually good success during that period could have biased the mean upward.

The yearly per capita production of young by matrilines does not differ among colonies ($F_{5,30} = 1.9, p > 0.1$) nor among matrilines ($F_{30,146} = 0.7$, $p > 0.75$). Only 1.4 percent of the variance is explained by differences among colonies; 98.6 percent of the variance is attributable to differences among years. The yearly per capita production of yearlings by matrilines does differ among colonies ($F_{5,30} = 3.8, p < 0.01$), but not among matrilines ($F_{30,145} = 0.8, p > 0.75$). Only 6.6 percent of the variance is explained by differences among colonies; 93.4 percent of the variance, by differences among years. In this analysis, the differences among years is best interpreted as differences among females. There are no significant differences in mean litter size associated with size of matrilines ($F_{4,140} = 1.8, p > 0.1$) or with colonies ($F_{5,139} = 2.2, p > 0.05$). However, the mean number of litters per female is 0.48. This value is not affected by the size of a matriline ($F_{4,199} = 0.2, p > 0.75$). Thus, on average, any female has a likelihood of producing a litter every other year. If she produces a litter, it is likely to consist of 4.2 juveniles. Some females produce a litter nearly every year of residency; others may skip several years in succession (e.g., Fig. 14.1). The variation in reproduction from year to year by individual females accounts for the variation among years in the reproductive output of matrilines. I conclude that the major source of variation in reproductive output is unequal reproductive success among females within matrilines. The lack of a significant effect of matrilineal size on the production of young and yearlings cannot be attributed to differences among colonies.

MALE REPRODUCTIVE STRATEGY

The production of young per female decreases significantly but the number of young per male increases significantly as harem size (= number of females two years old or older) increases (Fig. 14.5). Similarly, the number of yearlings per female decreases but the number of yearlings per male increases with increased harem size (Fig. 14.6). This disadvantage to females in large harems arises because the number of litters per female decreases (Fig. 14.7). Harem size does not affect litter size ($F_{5,136} = 0.6, p > 0.5$). However, the number of litters per male increases significantly as harem size increases. Therefore, a male increases his direct fitness by mating with as many females as possible. A male should never choose to be monogamous, but monogamy is better than not breeding. On average, an adult, territorial male has a harem for 2.24 years. If monogamous, he would produce (2.24 years × 2.54 young/year) 5.7 young. However, if bigamous, he would produce (2.24 × 4.34) 9.7 young. The average harem size is 2.27 adult females. Thus, the average male can expect a lifetime production of (2.24 × 2.27 × 2.19) 11.1 young. Monogamy cannot be a male evolutionarily stable strategy (Maynard Smith and Price, 1973) provided that resources, and thus females, are clumped and that either the resources, the females, or both can be defended (Emlen and Oring, 1977).

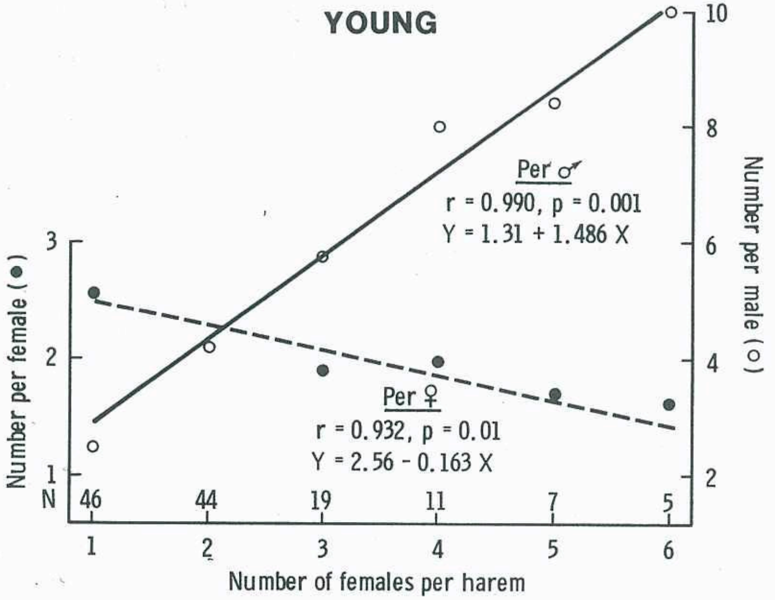

Fig. 14.5. The relationship between the production of young and the size of a harem.

The loss in annual reproductive output of females living in large harems could be compensated by increased survival. Additional years of reproduction may enable longer-lived females to have a lifetime reproductive output equal to or greater than those females living in small harems (P. F. Elliott,

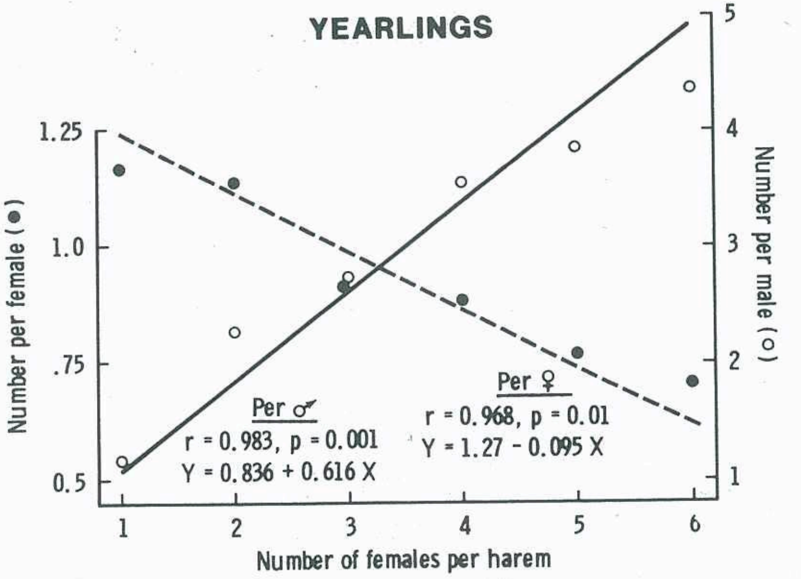

Fig. 14.6. The relationship between the production of yearlings and harem size.

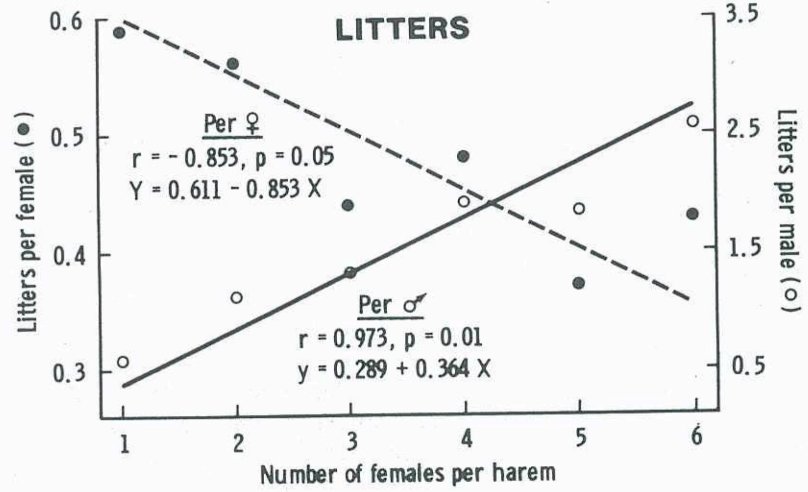

Fig. 14.7. The relationship between the number of litters per resident female and harem size.

1975; Wittenberger, 1979, p. 288). The survivorship of fifty-two known-aged females was compared to the mean harem size in which each female lived. There was no relationship ($r = -0.18, p > 0.1; Y = 4.7 - 0.34X$, where Y = survivorship and X = mean harem size in which each female lived). Similarly, lifetime production of young and yearlings was unrelated to the mean harem size in which each female lived (young: $r = -0.21, p > 0.1$; $Y = 11.2 - 1.16X$, where Y = number of young; yearlings: $r = -0.19, p > 0.1$; $Y = 5.6 - 0.61X$, where Y = the number of yearlings). These results are consistent with the previous analysis of lifetime reproductive output in matrilines in which most of the variation occurred among individual females.

COMPARISON OF MATRILINES AND HAREMS

The different effects of increased size of matrilines and harems on per capita female reproductive success suggest that reproductive costs are not a function of groups per se but of the kind of group. Harems may consist of one or more matrilines. Therefore, the reduced per capita reproductive success of females in harems > 1.0 may result from competition between matrilines. In a given location, the density of females in a matriline may be reduced to one for one or more years. Although the mechanism by which competition acts is unknown, evidence for a competitive effect is apparent from an analysis of reproductive success of females living alone in matrilines when harems of different sizes consist of more than one matriline.

Harem size affects the mean number of young produced by females ($F_{3,172} = 2.4, 0.1 > p > 0.05$). A female living singly in a harem > 2.0 produced fewer young than females living singly in a harem consisting of one or two females or than two females associating in a matriline (Table 14.6). The production of yearlings is affected similarly ($F_{3,172} = 2.7, p < 0.05$, Table 14.6). The lower reproductive success of females who are the sole members of matrilines in harems > 2.0 occurs because they produce fewer litters ($F_{3,172} = 2.2, 0.1 > p > 0.05$). The number of young ($F_{3,87} = 1.3, p > 0.25$) or yearlings ($F_{3,87} = 1.5, p > 0.25$) per litter does not differ among the four groups of females. These data suggest that the presence of two or more females in a matriline adjoining a female living singly inhibits her ability to reproduce; but if she reproduces, she is as successful in rearing young to one year of age as females living in more favorable social situations. Although these group effects are biologically significant, they account for only about 3 percent of the variance in the reproductive success of females living singly. Thus 97 percent of the variance is attributable to variation among females.

Harem size affects the number of recruits retained in the natal area ($F_{3,172} = 3.9, p < 0.025$). Significantly more yearling females are recruited into

TABLE 14.6
Reproductive success of females of matrilines in harems of different sizes

	Social groups			
	Only 1 female present, both matriline and harem = 1.0	2 females present, each is a matriline of 1.0; harem = 2.0	1 female in a matriline of 1.0; other matriline(s) total 2 or more females; harem > 2.0	2 females in a matriline; other matriline of 1 or more females; harem ≧ 3.0
Young	2.54	2.38	1.48	2.71
Yearlings	1.17	1.36	0.56*	0.71
Litters	0.54	0.61	0.37	0.57
Recruits	0.13	0.58*	0.14	0.29
Young/litter	4.20	3.91	4.00	4.75
Yearlings/litter	2.3	2.20	1.50	1.30

NOTE: All values are means per female. Means that differ statistically from other means in each row are marked with an asterisk. Means whose values are of probable biological significance are underlined.

matrilines when harem size is 2.0 (Table 14.6). This group effect explains 10 percent of the variance; the remaining 90 percent of the variance stems from individual variation among females. Two females associating in a matriline when harem size ≧ 3.0 produce more young, more young per litter, and as many litters as females living alone, and produce more recruits than females living in harems of 1.0 or harems > 2.0. Apparently there are reproductive benefits in matrilineal living beyond those obtained from suppressing reproduction in nonmatrilineal competitors. However, recruitment is lower than in harems of 2.0; why recruitment is more successful when harem size is two requires further analysis.

The causes of variation in reproductive success are largely unknown, but at least some variation is associated with differences in behavioral phenotypes (Armitage, 1983). Two lines of evidence suggest that social repression of reproduction occurs. Although two-year-old females may reproduce, only 32 percent of seventy-four did so. Because half of the adult females produce a litter, on average, I assumed that two-year-old females should have a 50 percent chance of reproducing. The presence or absence of adults significantly affected the reproductive success of two-year-olds. When adult females were present, reproduction was significantly reduced (fourteen of forty-eight two-year-olds produced litters; $\chi^2 = 8.3, p < 0.01$). If the two-year-old's mother was present, only eleven of thirty-six two-year-olds reproduced ($\chi^2 = 13.3, p < 0.001$). None of the seven two-year-olds reproduced when more distant kin were present ($\chi^2 = 7.0, p < 0.001$) but three of five reproduced when only unrelated adults in different matrilines were present. When no adults were present, ten of twenty-six two-year-olds reproduced. This proportion does not differ significantly from the expected 50 percent reproductive ($\chi^2 = 1.38, p > 0.1$). I identified from trapping records fifty-six females three-years-old or older who were recorded as pregnant or lactating. Whether females lived solitarily or in proximity to other adult females significantly affected their success at weaning a litter of juveniles (Table 14.7).

TABLE 14.7
Contingency table analysis of the effects of living solitarily or in proximity to other adult females on weaning success of female yellow-bellied marmots

	Solitary	In proximity to others
Litter weaned	14	20
No litter weaned	2	20

NOTE: Subjects were females aged three or older who were recorded as pregnant. The "proximity" group included females of the same matriline or of adjacent matrilines when the home ranges of the females were contiguous. $\chi^2 = 6.7, p < 0.01$

Females may reduce the reproductive success of other females if they can prevent their access to resources, especially food. Competition for resources would be most effective during early pregnancy when much of the area may be snow-covered, food resources are scarce, and females may be forced to utilize fat reserves for maintenance rather than for reproduction. Snow cover varies from year to year (Armitage and Downhower, 1974); perhaps only in those years of late snow cover does competition for food affect reproductive success. At our high altitude study site in North Pole Basin, females with inadequate foraging areas during gestation and lactation either failed to produce young or produced litters of lower than average size (D. C. Andersen et al., 1976). These females did not encroach on foraging areas of other females, which suggests that female competition, either active or potential, affects reproductive success of nearby females who are likely members of the same harem and may be kin. In ten of the twenty instances in which females failed to wean litters when they were presumed to be pregnant and living in proximity to other females, the other females were kin. In seven of the ten, all females were members of the same matriline.

DISCUSSION

Mate Choice

There is no evidence that females choose among males. Females are far more philopatric than males; sixty-three of ninety-one resident females were born in their colony of residency; only two of fifty-two males became resident in their colony of birth. The mean lengths of residency of males (2.24 years), females (3.26 years), and matrilines (4.35 years) differ significantly from one another ($F_{2,15} = 16.1, p < 0.001$). Therefore, most females during their residency can expect to mate with two males. Males disperse and settle, when possible, with resident females. Males may live peripherally to a population of females, but are prevented from residing with the females by the territorial defense of the resident male (Armitage, 1974). The strategy of living peripherally and waiting for an opportunity to become colonial is often successful; thirty of fifty-two colonial males were known to live peripherally for one or more years before becoming colonial. Social interactions between resident females and a strange male initially occur at a high level and then decrease (Armitage, 1974). Males always establish dominance; we have no evidence that females can exclude a potential colonial male. A female could refuse to mate, but she would pay a high direct fitness cost in that, on average, she would lose nearly one-third of her breeding potential. It is not practical for a female to travel to find a different male because she would be forced to travel across snow and be highly vulnerable to predation and exposure. In those instances when no male was present with a group of females, females did not emigrate and failed to breed. Thus, the lengths of residency, pattern of philopatry, and social behavior all support the interpretation that males seek out and attempt to associate with already resident females.

The Yellow-Bellied Marmot and the Polygyny Threshold Model

The polygyny threshold model does not apply to marmots. The fundamental assumption underlying the model is stated in the following quotation (Wittenberger, 1979, p. 288): ''In territorial systems, polygyny can evolve only when already mated males attract additional females to their territories, so its evolution is clearly dependent on the choices made by unmated females.'' Marmots do not meet that requirement. Rather than females being attracted to males, males are attracted to females. Whether a male is monogamous or polygynous depends on the number of females residing in a habitat patch, not on the ability of the male to attract females. Furthermore, the organization of female yellow-bellied marmots into matrilines does not meet the implicit assumption that females act independently. The density of females on a habitat patch is determined by females (Armitage, 1975); I have no evidence that colonial males affect the density of resident females. In effect, females, by regulating the number of resident females in a habitat patch, determine the reproductive success of colonial males. The strategy available to a resident male is to increase his territory size to include additional females. In some habitats, males do expand territories when the opportunity arises (Armitage, 1974).

The question then arises, should a male remain in a habitat patch with only one female? We have little direct evidence that bears on this question, but several lines of evidence suggest moving is risky. First, a male must be able to add sufficient fat and locate a hibernaculum in order to survive until the next breeding season. If he emigrates, he is leaving a habitat already proven successful and with no assurance that he will find the necessary resources. Second, if he finds the resources, he may also find a resident male. More importantly, he needs to locate females. If he finds females, most likely a resident male will be present. Then our questing male must risk conflict in order to drive out the resident, or live as a peripheral and forgo reproduction until he can replace the resident. We have never observed a resident male lose an encounter with a potential usurper. Therefore, our male most likely will forgo reproduction and would likely be less fit than if he had remained in his original habitat. We do not know to what degree males move about seeking females. We currently are investigating this problem by radio-tagging males and tracking their movements.

Marmots were considered a mammalian example of resource defense polygyny (Emlen and Oring, 1977). However, Greenwood (1980) suggested that because of male-biased dispersal in mammals, males defend mates. This mate defense is similar to the harem-defense polygyny of Emlen and Oring. One source of confusion is whether females congregate to resources which males defend or whether males attach themselves to females. Clearly males attach themselves to females. I conclude that male territoriality in yellow-bellied marmots evolved its present form in response to the patchy distribution of females and the need to maintain residency with the females as the mechanism with the highest probability of producing future matings.

THE MATING SYSTEM OF GROUND SQUIRRELS

Mating systems may be viewed as attributes of grades of sociality (Michener, 1983). This proximate description of social structure has an underlying assumption that the various grades of sociality represent an evolutionary sequence; sociality is an end-point of evolutionary mechanisms rather than a means for increasing fitness. By classifying some societies as egalitarian, the intense female competition and the conflict between the reproductive interests of males and females is devalued. Finally, grades of sociality imply that males and females form a single social unit whereas it is more likely that social systems should be treated as two separate units; a male system, focusing on mate acquisition, and a female system, focusing on kinship (Armitage, 1984). Mating systems should be viewed as one of the life-history tactics comprising a species' reproductive strategy (Armitage, 1981). In this view, sociality is a consequence of the convergence of individual life-history strategies, which leads to the formation of a social unit characterized

TABLE 14.8
Selected characteristics of the mating systems of the Marmotini

	Breeding sex ratio as no. ♀♀/♂	% of adult ♀♀ breeding	Dispersing sex	Type of kin group	Infanticide committed by	Sex expressing territoriality, or IA	Kin-biased behavior	References
Spermophilus tridecemlineatus	2.9–3.3	>95	♂	C	—	Breeding adults IA	Alarm-calling	McCarley, 1966, 1970; Rongstad, 1965; Schwagmeyer, 1980; Schwagmeyer and Brown, 1983; Wistrand, 1974
beldingi	1.3–3.0	>95	♂	C	Unrelated ♂♂ or ♀♀	Parous ♀ Breeding ♂ IA, "resource-based lek"	Avoid fighting with close kin, close relative codefended, alarm-calling	Hanken and Sherman, 1981; Morton and Parmer, 1975; Sherman, 1977, 1980, 1981; Sherman and Morton, 1984
tereticaudus	2.6	>90	♂	C	—	Parous ♀	Reduced aggressiveness toward ♀ kin, alarm-calling	Dunford, 1977a, b, c
richardsonii	2.6	>95	♂	C	—	Parous ♀ Breeding ♂	Mother: Young, fewer chase-flee and more appeasement behaviors among uterine kin, alarm-calling	L. S. Davis, 1983, 1984; Michener, 1973, 1979a, b, 1980; Michener and Michener, 1977; Yeaton, 1972
armatus	3.3	>90	♂	CP	—	Parous ♀		Balph and Stokes, 1963; Slade and Balph, 1974
beecheyi	1.2–1.9	>90	♂	CP	—	Parous ♀ IA Breeding ♂		F. C. Evans and Holdenreid, 1943; Dobson, 1979, 1983; Fitch, 1948; Owings et al., 1977
parryii	2.0	>95	♂	C	Adult ♂♂	Breeding and prehibernation ♂	More amicable among ♀♀	Carl, 1971; McLean, 1982, 1983

columbianus	1.27	65–84	♂	C	Adult ♀♀	Breeding ♂ Parous ♀	Behavior among ♀♀	Balfour. 1983; Boag and Murie, 1981; Festa-Bianchet, 1981; Festa-Bianchet and Boag, 1982; Festa-Bianchet and King, 1984; Murie and Harris, 1978, 1982
Cynomys								
leucurus	2.2	88	♂	CP	—	Parous ♀	Litters of "family groups" intermingle	Clark, 1977; Stockard, 1929
gunnisoni	1.6	52–80	♂	C, MP	—	Parous ♀ Harem ♂	Among yearlings	Fitzgerald and Lechleitner, 1974; Longhurst, 1944; Rayor, pers. comm.
ludovicianus	1.5	66	♂	M	Related ♀♀	Parous ♀ Harem ♂	Amicable behaviors, space sharing and defense	J. A. King, 1955; Hoogland, 1979, pers. comm.
Marmota								
monax	1.0–2.0	>95	♂?	CP	—	Parous ♂?	Alarm-calling Mother: Young, possible with ♀ yearling	Grizzell, 1955; Snyder, 1962; Svendsen, pers. comm.
flaviventris	3.1	45–50	♂	M	Adult ♀♀	Parous ♀ IA Harem ♂	Amicable behaviors, defense of shared space	Armitage, 1965, 1974, 1975, 1984; Armitage and Downhower, 1974; Armitage and Johns, 1982, Armitage et al., 1979; Brody and Melcher, pers. comm.; S. E. Thompson, 1979
caligata	1.0–1.8	40–50	♂?	MP	—	Parous ♀ Harem ♂	Probable	Barash, 1974, 1980, 1981; Holmes, 1984
olympus	1.6	40–50	♂	MP	—	Parous ♀ Harem ♂	Probable	Barash, 1973

KEY: C = kin clusters, M = matrilineal group, P = probable, IA = increased aggressiveness. Kin clusters occur when home ranges of closely related females are contiguous; M species form social groups.

by sharing resources (at least to some degree) and kin-biased social behavior. In effect, the life-history tactic model emphasizes looking at mating systems as the result of individuals' attempting to maximize inclusive fitness, especially direct fitness.

In the well-studied Marmotini, dispersal is male-biased (Holekamp, 1984); breeding sex-ratios are female-biased (Table 14.8). Philopatric females form kin clusters. In *M. flaviventris* and *C. ludovicianus*, the female kin-groups persist over time as closed matriarchal societies in the same area. In these species, and probably in *C. gunnisoni, M. olympus*, and *M. caligata*, the female group cooperates to exclude conspecifics and shares in kin-based behaviors, such as alarm-calling and amicable behavior (Table 14.8). However, kin-based behavior is not limited to matriarchal groups. Alarm-calling is kin-directed in *S. tridecemlineatus, S. beldingi, S. richardsonii*, and *S. tereticaudus*. Other kin-directed behavior may be characterized as reduced fighting and/or increased amicable behavior among closely related females (Table 14.8). Adult female *S. columbianus* may relinquish nest-sites to their yearling daughters (M. A. Harris and Murie, 1984).

Males and females of spermophiles are either territorial or are more aggressive during breeding (Dobson, 1983, 1984). Male territories or increased agonistic behavior by the spermophiles (Table 14.8) and *C. leucurus* usually are concentrated on a core area around their burrows. Male *S. beldingi* defend small mating territories on snow-free ridges near females' hibernacula (Sherman and Morton, 1984). Because these territories usually do not include the nest burrows of females, the function of territorial behavior is unclear, but probably assures the male of residency in the breeding population. Males unable to maintain territories are forced to live peripherally, usually in poorer habitat (e.g., Armitage, 1974; Carl, 1971; Morton and Parmer, 1975). Male *S. tridecemlineatus* wander widely during the breeding season and attempt to mate with estrous females in a scramblelike competition (Schwagmeyer and Brown, 1983). Males may guard females following copulations (e.g., *S. beecheyi*, Dobson, 1983). Male territories may overlap the core areas of several females with whom the males may have a higher probability of mating (e.g., *S. beecheyi*, Owings et al., 1977; *S. columbianus*, Murie and Harris, 1978). Where females are clumped on patchy habitat, territoriality is well developed, (e.g., *S. parryii*, Carl, 1971; McLean, 1983; *M. olympus*, Barash, 1973; *M. caligata*, Barash, 1981; and *M. flaviventris*, Armitage, 1974). In the prairie dogs *C. ludovicianus* and *C. gunnisoni*, clumped females apparently occur as kinship groups in an otherwise continuous population. The female groups form as a consequence of postweaning reproductive investment in which juveniles are provided space, food, and a social environment in which to mature (Armitage, 1981). These female groups are defended by adult males. In general, male territoriality prolonged beyond the breeding season occurs in those species in which the females are clumped and, hence, are defendable. Territoriality in these species is best interpreted as defense of females, i.e., mate guarding (Barash, 1981).

Female *S. beldingi* (Hanken and Sherman, 1981) and *S. tridecemlineatus* (Schwagmeyer and Brown, 1983), species in which males do not defend females, may mate with two or more males. In the territorial *M. flaviventris* (O. A. Schwartz and Armitage, 1980) and *C. ludovicianus* (Foltz and Hoogland, 1981), genetic analysis indicated that the territorial male most likely fathered all offspring of females in his harem. Thus, territoriality may also assure paternity and, in addition, may protect young from infanticide by other males (McLean, 1983).

Female defense of burrows or increased aggressiveness during pregnancy and lactation apparently is universal among the Marmotini (Table 14.8). Defense seems not to be related to resources, i.e., food or burrows, but to young (e.g., Festa-Bianchet and Boag, 1982). Although protection against predators likely is partially responsible for female defensiveness, the major selective factor may be defense against infanticide. Infanticide occurs in several species (Table 14.8) and indirect evidence suggests infanticide or the potential for infanticide may be widespread among the Marmotini (Sherman, 1981, 1982).

Mating systems of the Marmotini are consistent with the model that females are philopatric, that philopatry leads to the close association of female kin, and that males attach to female groups. Polygyny occurs when males achieve differential access to females either by scramble competition or by contest competition in which clumped females (harem polygyny) are defended. Although most marmot species are harem polygynous, polygyny is not obligate. Slightly more than one-third of yellow-bellied marmot mating associations were monogamous (Fig. 14.5). One of twelve woodchuck mating groups was monogamous (Svendsen, pers. comm.) and 19 percent of the social groups of the Olympic marmot were monogamous (Barash, 1973). In some populations, all hoary marmots are monogamous (Holmes, 1984). Holmes concluded that resources would not support more than one female at a site with a hibernaculum and that hibernacula were too far apart for a male to control more than one. Hoary marmots support the interpretation that harem polygyny occurs when resources permit the clumping of females.

Problems and Perspectives

A major problem is to determine what limits the size of a matriline. Although resources doubtlessly are the ultimate limiting factor, they may not be the proximal factor determining reproductive strategies. In most of our study areas hibernacula and other burrows and food appear to be capable of supporting more females than are typically present. Females may share burrows; when only a few burrows are available, more females could be resident than usually are. Resources may be critical in years when spring begins later than usual. Reduced breeding occurs in years of late spring in *S. beldingi* (Morton and Sherman, 1978), *S. columbianus* (Murie and Harris, 1982), *S. lateralis* (Bronson, 1979), and *M. flaviventris* (Nee, 1969; Armitage and Downhower, 1974). Fat stores are inadequate to support pregnancy and lactation; tissue stores contributed only 31 percent of the calories required to produce a litter of *S. parryii* (Kiell and Millar, 1980). Thus, females must increase ingestion; if food is not available, reproduction fails (D. C. Andersen et al., 1976). Female *S. elegans* occupying certain burrow sites produced significantly more young than females in other sites (Pfeiffer, 1982). The more successful sites occurred in areas of early snowmelt, which suggests that access to green vegetation early in pregnancy may affect reproductive output. Yearling female *S. columbianus* normally do not breed; some yearling females living on a site apparently richer in food resources produced litters (Festa-Bianchet, 1981). Further studies on the nutritional ecology of ground squirrels are essential if the relative importance of food in shaping mating strategies is to be determined.

There is widespread evidence that social suppression of reproduction occurs. In those species in which individuals live by themselves within aggregations on favored habitat, more than 90 percent of the females breed each year (Table 14.8). In those species that form social groups, from 40 to 84 percent of the females breed annually. Although some decrease in the number of reproductive females may be attributed to late springs or biennial breeding (Barash, 1973, 1974), reproductive failure in *M. flaviventris* and the production of fewer young per female by subordinate *M. caligata* (Wasser and Barash, 1983) clearly implicate social suppression. Furthermore, when the population of *S. armatus* was reduced by removal of up to 60 percent of the residents, yearling males became scrotal and some bred, and a larger percentage of yearling females bred than prior to reduction (Slade and Balph, 1974). Although increased aggression and parasitism were suggested as costs of sociality (Hoogland, 1979), reproductive suppression may be the major cost.

If sociality imposes a high reproductive cost, why do these animals form social groups? All social species are those that mature reproductively at age two or later. They live in confined environments; either the habitat patch is limited (e.g., marmots), or the space available for settlement is restricted (e.g., black-tailed prairie dogs). Fitness is higher when the probability of leaving reproductive descendants is increased by retaining direct descendants in their natal area. Furthermore, the association of females provides for defense against acquisitive conspecifics. However, because females strive to maximize direct fitness, conflict increases as subsequent matings reduce average relatedness. Therefore, matrilines should remain small and divide into daughter matrilines. Females should stive to sequester resources for use by their direct descendants; hence they should react to the presence of other females as the proximal factor limiting matrilineal size. Therefore, agonistic behavior, matrilineal fission, and dispersal should be largely independent of resources. Females may not be successful in excluding conspecfics; therefore, they should prefer to share resources with closely related females. In summary, there should be an ongoing waxing and waning of cooperative and competitive behavior determined by the kin structure of the population, the abilities of individual females, the location and abundance of resources, and the prospects for reproductive success.

Better measures of fitness are required. Although reproductive output is useful, fitness requires that descendants reproduce. Because all males and many females disperse from their natal areas, we must determine the reproductive success of dispersers in order to understand the significance of life-history strategies. Dispersal may be a tactic for increasing the probability of future reproductive success when settlement in the natal area is unlikely to lead to reproduction. Dispersal could be imposed on juveniles by adults attempting to increase their reproductive success or could represent a decision by the dispersers who perceive little likelihood of reproducing in their natal area.

Finally, the reproductive success of males not associated with clumps of females needs to be determined. We know little about the reproductive success of isolated females. These animals could play an important role in continuing matrilines across space and time. Males who mate with isolated females may be as reproductively successful as those associated with clumped females. Are these males who mate with widely spaced females owners of exploded harems? Are they at greater risk of predation? Do these males follow a viable strategy or do they represent the losers who are making the best of a bad job?

Ground squirrel mating systems appear to be adaptable to prevailing conditions. They offer an excellent opportunity to test the relationship between environment and mating system plasticity (Emlen and Oring, 1977). Long-term studies should be planned so that lifetime reproductive success and measures of fitness may be obtained. The paucity of measures of lifetime reproductive success may be the most serious shortcoming in studies of mating systems.