

## The function of kin discrimination

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Kin discrimination should be a tactic in the fitness strategy of individuals. Two postulates derived from inclusive fitness theory that fitness benefits toward kin are correlated with degree of relatedness and that social behavior of members of a kin group is always cooperative are refuted by analyses of the social dynamics of yellow-bellied marmots. Cooperative behavior occurs predominantly between mother/daughter and sister/sister pairs, but such pairs also compete. More distant kin are treated similarly to unrelated animals, social behavior is primarily agonistic. Patterns of space-use, matrilineal formation and organization, social dynamics, and reproductive suppression of close kin suggest that marmots attempt to maximize direct fitness.

KEY WORDS: yellow-bellied marmots, direct fitness, space-sharing, amicable behavior, agonistic behavior, relatedness.

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### KIN DISCRIMINATION AND LIFE HISTORY STRATEGY

Kin discrimination is a special case of individual discrimination. In general, the pattern of kin discrimination is expected to be appropriate to the life history strategy of the species (see BARNARD, this issue) and should be one of the tactics an individual may use in its attempts to maximize inclusive fitness. For example thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) pups reared together, whether foster or biological sibs, treat each other similarly; both related and unrelated pups reared apart also behave similarly, but all pups reared apart engage in significantly more exploratory encounters than all pups reared together (HOLMES 1984). Thirteen-lined ground squirrels live individually; juveniles disperse about 3 weeks after weaning (SCHWAGMEYER 1980, ARMITAGE 1981). There is virtually no intermingling of juveniles from different litters (SCHWAGMEYER 1980, RAYOR 1987); thus, familiarity serves as a proximal mechanism for kin (sibling) discrimination. Although home

ranges of adult female relatives (mother/daughter and sister/sister) overlap more than those of non-kin or other kin groups (e.g., brother/sister), individuals interact infrequently (VESTAL & MCCARLEY 1984).

By contrast, both relatedness and familiarity mediate discrimination among female Belding's (*S. beldingi*) and Arctic (*S. parryii*) ground squirrels (HOLMES & SHERMAN 1982, HOLMES 1986a). Relatedness does not affect male-male and male-female agonistic behavior. Furthermore, female Belding's ground squirrels reared apart discriminate paternal half-sisters, but not half-brothers nor do male Belding's discriminate half-brothers reared apart (HOLMES 1986b).

All three species form female kin clusters (VESTAL & MCCARLEY 1984); however, *S. beldingi* and *S. parryii* live at population densities up to 4 times greater than those of *S. tridecemlineatus*. Thirteen-lined ground squirrels interact infrequently and nepotistic behavior has never been reported whereas Belding's ground squirrels (SHERMAN 1981) and the Arctic ground squirrel (MCLEAN 1982) interact frequently and nepotistically. Thus, the likelihood that thirteen-lined ground squirrels could affect the reproductive success of kin is unlikely whereas both Belding's ground squirrel and the Arctic ground squirrel could differentially affect the reproductive success of kin and non-kin. Belding's ground squirrels are more cooperative with daughters than with any other kin group or than with non-kin and chase daughters less frequently than littermate sisters who are chased less frequently than non-littermate sisters (SHERMAN 1981).

The lack of male/male or male/female discrimination in these species is consistent with the pattern of dispersal; natal dispersal is male biased (HOLEKAMP 1984). The probability of close-kin mating is highly unlikely (ARMITAGE 1974, RALLS et al. 1986); therefore, male/male or male/female discrimination is not part of the life history strategy. In effect, for males, all females are potential mates and all males are potential competitors.

The failure to detect kin discrimination in the social behavior of natural populations may occur if at a particular life history stage discrimination is unnecessary. For example, female yellow-bellied marmots (*Marmota flaviventris*) usually bear their litters solitarily in a burrow that is distant from other lactating females. Thus, young yellow-bellied marmots typically associate only with littermates during lactation and for the first week or two above ground. When a population of eight young female yellow-bellied marmots from four litters from four colonies was established in a locality from which all adults were removed, the young interacted with each other amicably. Kinship was not the major determinant of the observed social behavior (ARMITAGE 1982). Nine of 115 litters were born in a burrow system with one or two other litters and with two or three adult females occupying the same burrow system. There was sufficient behavioral data for five adult females to determine if they interacted preferentially with any of the young from the mixed litters. For four females, no preference could be detected ( $P > 0.2$ ), for one female preferential behavior occurred ( $P < 0.01$ ). This preference represented one young male that interacted many times with one adult female, no other young/adult female preference was evident. These results indicate either that kin discrimination at this stage was not necessary or that discrimination was not possible. The typical pattern of young developing in isolation with their mother suggests that familiarity is the typical mechanism for kin discrimination. Learning kin through familiarity is open to cheating. We do not know to what degree litters mix below ground and whether communal nursing occurs. Because in

two instances we observed a female move her litter into a burrow system occupied by two related females and their litters, it seems unlikely that the mixing of litters is a rare accident. Possibly one female combines her litter with that of another adult female as part of a strategy to increase the likelihood that her young will be accepted by the other female and not treated agonistically. Interestingly, in all instances in which two or more female marmots produced litters in the same burrow system, the females were sister or mother:daughter associations and one of the females was clearly subordinate to the other.

#### KIN DISCRIMINATION AND FITNESS STRATEGIES

Two misconceptions of the meaning of inclusive fitness theory bear directly on kin recognition. First, it is generally assumed that fitness benefits toward kin are correlated with degree of relatedness. This correlation apparently is derived from the inclusive fitness model that states that benefits to kin are devalued by the degree of relatedness. Thus, an individual should direct progressively fewer benefits to kin as relatedness decreases (Fig. 7). Alternatively, an individual could direct progressively more benefits to kin as relatedness decreases in order to accrue the same degree of

#### RELATEDNESS AND FITNESS STRATEGIES

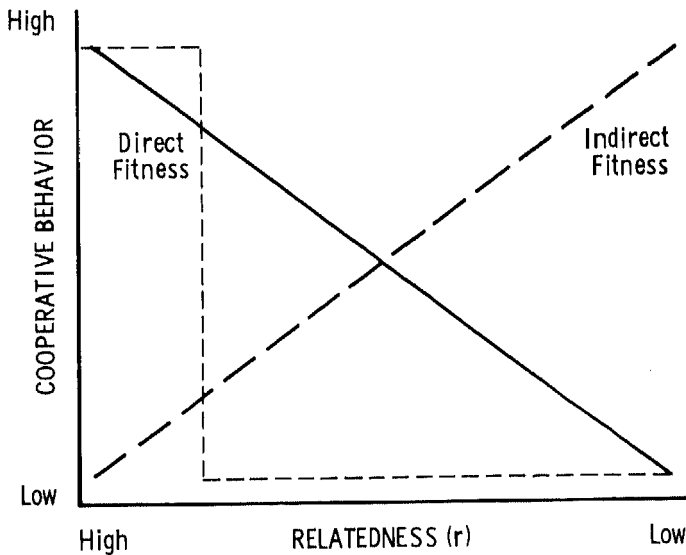


Fig. 7. — Graphical representation of the relationship between benefits and relatedness. Benefits are expressed as cooperative behavior. The diagonal lines represent indirect fitness relationships. The heavy dashed line sloping upward illustrates that cooperation may have to increase as relatedness decreases in order to achieve sufficient gain in indirect fitness to compensate for the loss of direct fitness. The solid line sloping downward illustrates the possible decrease in cooperation as relatedness decreases because payoffs decrease with decreasing  $r$ . The light dashed line illustrates the distribution of benefits if animals attempt to maximize direct fitness.

inclusive fitness (Fig. 7). Because it takes enormous gains in indirect fitness to compensate for losses in direct fitness, I predict that most animals attempt to maximize direct fitness. Thus, the relationship between benefits and relatedness should be a step function with benefits being directed to closely-related kin and more distant kin and non-kin treated alike. Only under extraordinary conditions should one expect to find individuals foregoing direct fitness in favor of indirect fitness. A common feature of such conditions would be the virtual zero probability that the individual could reproduce.

A second misconception is that the social behavior of members of a kin group is always amicable or cooperative. What is more likely is that individuals adopt strategies to maximize their direct fitness. Individuals should compete or cooperate with kin to whatever degree such behavior increases their own fitness. Thus, among ground-dwelling squirrels, kin often cooperate to defend resources from incursions by conspecifics (ARMITAGE 1987). In black-tailed prairie dogs (*Cynomys ludovicianus*) the same individuals that cooperate in group defense attempt to commit infanticide on their nieces and nephews (HOOGLAND 1985). The interplay of cooperation and competition will be examined in more detail in the yellow-bellied marmot.

#### COOPERATION AND COMPETITION: DIRECT FITNESS STRATEGIES IN MARMOTS

The first question to be explored is are fitness benefits correlated with degree of relatedness? Resource acquisition and sharing should be related to social behaviors. Social behaviors can be generalized into two categories, amicable and agonistic (ARMITAGE & JOHNS 1982). Amicable behaviors are cohesive and can be treated as a benefit; agonistic behaviors are dispersive and can be treated as a cost, especially to the recipient. In yellow-bellied marmots, amicable and agonistic behaviors are non-randomly distributed (Table 2). Close kin receive more amicable and less agonistic behavior than expected whereas animals related by 0.25 or less receive more agonistic and less amicable than expected.

There is some variation depending on the pattern of relatedness. In addition to social behaviors, the sharing of space is a measure of the degree to which resources are shared with conspecifics. In yellow-bellied marmots, the space used by an animal includes two critical resources, burrows and foraging areas. The amount of space-sharing is an indirect measure of resource sharing. In 1972 at a Picnic Colony, four

Table 2.

Social behavior and relatedness among adult yellow-bellied marmots. The null hypothesis that there is no difference in the distribution of amicable and agonistic behavior is rejected ( $\chi^2 = 90.4$ ,  $P < 0.001$ ).

Average relatedness	Number of behavioral interactions	
	Amicable	Agonistic
0.5	162	21
<0.5	52	85

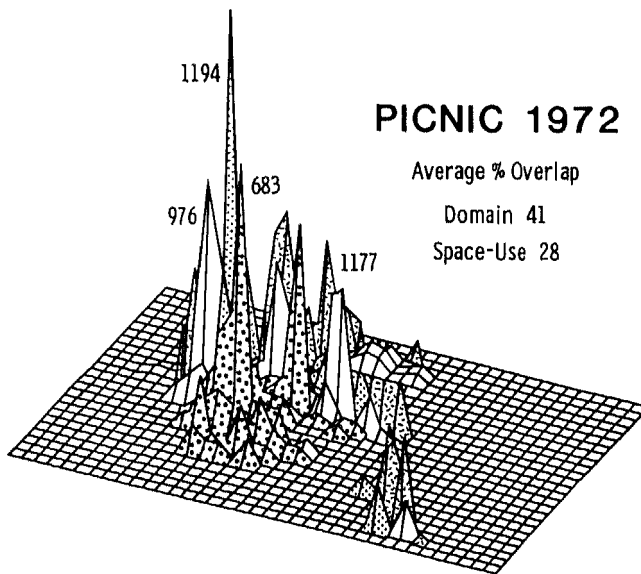


Fig. 8. — Patterns of space-use at Picnic Colony in 1972. Each grid square is  $45 \text{ m}^2$ . Domain is the surface area and space-use is the amount of use in any grid square. The height of the peaks represents the frequency with which an individual was censused in that location. Therefore, domain overlap represents the area a kin group (or set of individuals) used in common and space-use overlap represents the frequency with which an area was used in common. Each pattern represents an individual female who is identified by her left ear-tag number. Average overlap is calculated as the average of all values of the overlap of each animal with all other animals.

females shared a habitat patch. Female 683 was the mother of female 976 and the grandmother of yearling females 1177 and 1194, who were sisters and nieces of female 976. A group of females sharing space is called a matriline. Domain overlap and space-use overlap among all the females was 41% and 28%, respectively (Fig. 8). However, space overlap varied with relatedness and was lowest among aunts and nieces (Table 3). Although the same females were present in 1974, average overlap

Table 3.

Average percent overlap in domain and space-use for kin-groups at Picnic Colony in 1972 and 1974.

	1972		1974	
	Domain	Space-use	Domain	Space-use
Sisters	46	45	43	41
Mother:daughter	45	24	28	45
Grandmother:granddaughters	43	28	23	16
Aunt:nieces	33	21	25	16

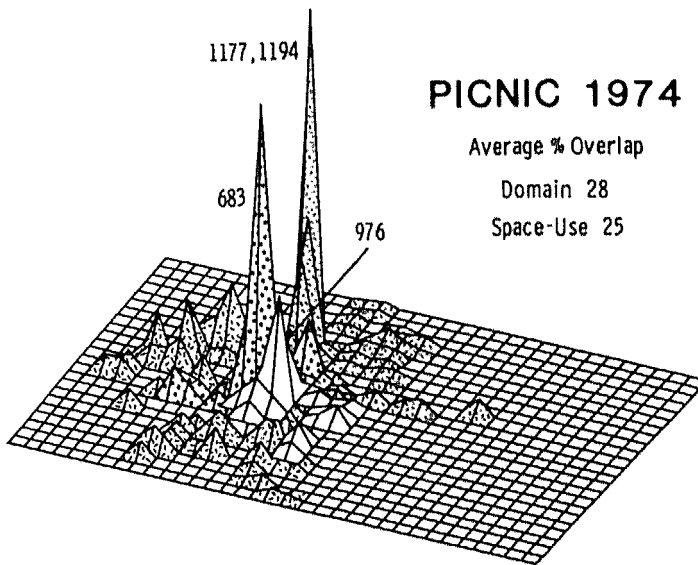


Fig. 9. — Patterns of space-use of Picnic Colony in 1974. The mother (683), her daughter (976) and two granddaughters (1177, 1194), who are sisters, are represented by different patterns.

declined (Fig. 9). Overlap of the two sisters remained high, but overlap between grandmother:granddaughters and aunt:nieces markedly decreased (Table 3).

The pattern of space-sharing with relatedness is reflected in social behaviors. Sisters were far more amicable and less agonistic than expected; whereas aunt:nieces were less amicable and much more agonistic than expected (Table 4). Surprisingly, the behavior of mother:daughter was less amicable than expected from inclusive fitness theory but was less agonistic than expected, as predicted from theory. Grandmother:granddaughter social behavior, somewhat more agonistic than predicted, is consistent

Table 4.

Amicable and agonistic behavior by relatedness for female yellow-bellied marmots at Picnic Colony in 1972 and 1974 combined. The expected values are adjusted for the frequency of each kin grouping in the population and for the amount of overlap in space-use; e.g., kin groups with a higher space-use overlap would be expected to interact more frequently. The null hypothesis that there is no difference in the expected and observed distributions was rejected for amicable behavior ( $\chi^2 = 16.2$ ,  $P < 0.001$ ) and for agonistic behavior ( $\chi^2 = 6.4$ ,  $0.1 > P > 0.05$ ). Although there is no test for individual comparisons, those kin groups that contributed in a major way to the total  $\chi^2$  are marked with an asterisk.

Kin group	r	Amicable behavior		Agonistic behavior	
		Expected	Observed	Expected	Observed
Sisters	0.5	12.6	24*	4.1	1*
Mother:daughter	0.5	8.4	2*	2.7	1
Grandmother:granddaughters	0.25	11.4	10	3.7	6*
Aunt:nieces	0.25	13.5	10	4.4	7*

Table 5.

Average domain and space-use overlap for kin-groups at Picnic Colony in 1978. The mother:daughter pair were the half-niece and half-grand-niece, respectively, of the pair of sisters.

Kin group	Average $r$	Domain	Space-use
Sisters	0.5	60	61
Mother:daughter	0.5	39	50
Aunts:half-nieces	0.09	4	3

with the prediction that females may attempt to maximize their own direct fitness. Therefore, one would expect competition to develop between kin related by 0.25. Some of the unexpected values likely reflect small sample size and the high degree of individual differences in marmot behavior (SVENDSEN & ARMITAGE 1973, ARMITAGE 1986a).

Another source of variation in behavior among kin is whether kin belong to the same or different matriline. In 1978, the habitat patch at Picnic Colony contained two matriline, one consisting of two sisters (female 301 and 349) and the other, a mother (female 1194) and her daughter (female 920). Average overlap among the four marmots was relatively low and the two sisters occupied the area with the best burrows and foraging areas (Fig. 10). Similarly to the 1972-1974 overlap patterns, the

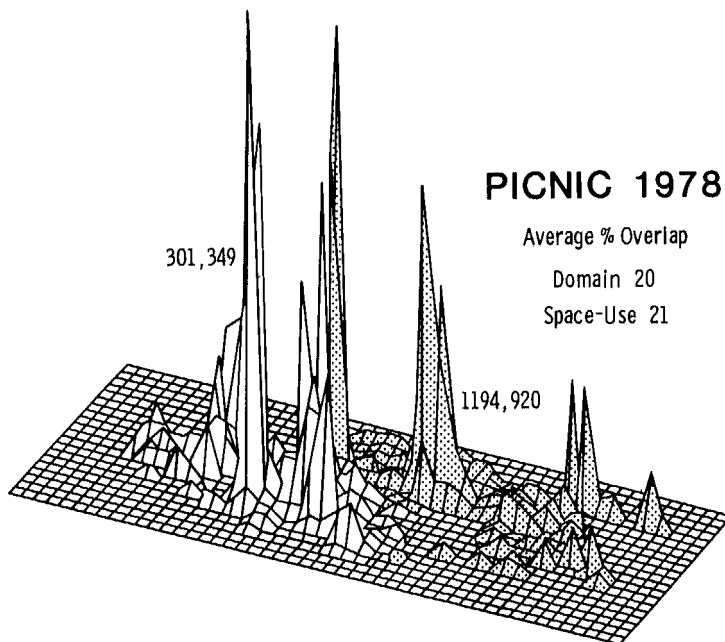


Fig. 10. — Patterns of space-use at Picnic Colony in 1978. The two matriline are represented by different patterns. Females 301 and 349 are sisters and female 1194 is the mother of female 920. The two matriline bear aunt:half-niece relatedness.

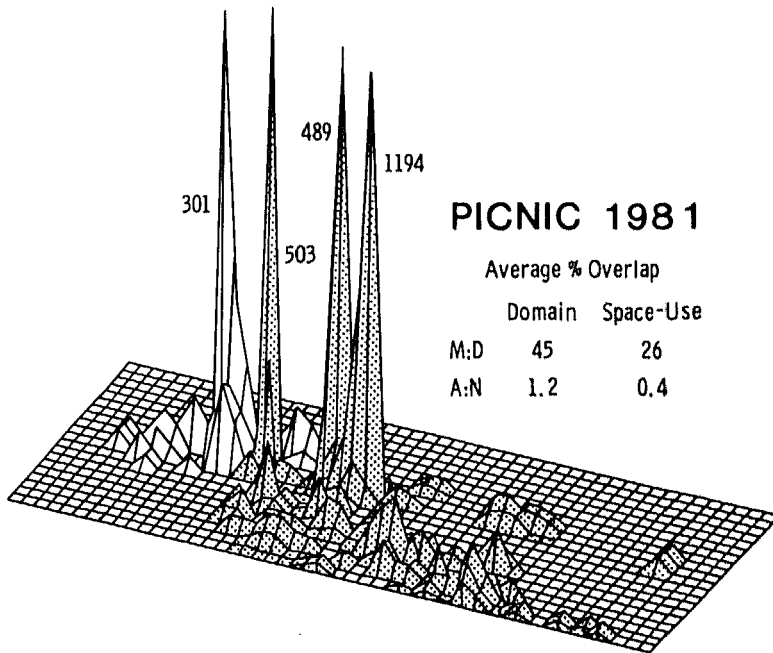


Fig. 11. — Patterns of space-use at Picnic Colony in 1981. The patterns represent the same matriline as in Fig. 10. Females 489 and 503 are daughters of female 1194.

sisters and mother/daughter kin groups had high overlap within their groups whereas the aunt/half-niece group had a very little overlap (Table 5). By 1981 the pattern changed (Fig. 11). Only one of the sisters (female 301) remained and she was forced to live at the edge of the habitat patch by the numerically dominant matriline consisting of female 1194 and two new littermate daughters, 489 and 503. The members of the mother/daughter matriline shared space whereas there was little overlap between the two matriline. The mother/daughter matriline now occupied the area with the best burrows and foraging patches. This shift in occupancy between 1978 and 1981 represents an advantage of the cooperative sharing of space by closely-related kin. The numerically/behaviorally dominant group is able to obtain the best resources.

The patterns of social behavior reflect both kinship and matrilineal organization (Table 6). Clearly, kin groups related by 0.5 were more amicable and less agonistic whereas the aunt/half-niece kin group was much less amicable and much more agonistic than expected. The possible effects of matrilineal organization can be observed by comparing aunt/niece relationships (Table 7). The higher agonistic and lower amicable behaviors in the between-matriline group than in the within-matriline group could reflect the lower average relatedness in the between-matriline group. However, the presence of female 683, the direct ancestor and matriarch of all-members of the within-matriline group, may have reduced conflict in the aunt/niece group. Among Belding's ground squirrels, the rate of agonistic behavior between 2-year-old females and their 1-year-old nonlittermate sisters was significantly lower



Table 6.

Amicable and agonistic behavior by relatedness for female yellow-bellied marmots combined for the years 1977-1981 inclusive. The expected values are adjusted for the frequency of each kin grouping in the population and for the amount of overlap in space-use. The null hypothesis that there is no difference in the expected and observed distributions of social interactions is rejected for both amicable ( $\chi^2 = 10$ ,  $P < 0.01$ ) and agonistic ( $\chi^2 = 134$ ,  $P < 0.001$ ) behaviors. Those kin groups that contributed importantly to the total  $\chi^2$  are marked with an asterisk.

Kin group	Average $r$	Amicable behavior		Agonistic behavior	
		Expected	Observed	Expected	Observed
Sisters	0.5	21.9	22	7.3	3*
Mother:daughter	0.5	55.0	63	18.7	4
Aunt(s):half-nieces	0.09	8.8	0*	3.0	22*

Table 7.

Social dynamics of aunt/niece kin groups occupying the same colony site. The 1972-1974 population formed one matriline whereas the 1977-1981 population was organized into two matriline.

	1972-1974 Within matriline		1977-1981 Between matriline	
	Expected	Observed	Expected	Observed
Amicable behavior	13.5	10	8.8	0
Agonistic behavior	4.4	7	3.0	22
Space-use overlap		24%		3%
Average relatedness		0.25		0.09

when their mothers were alive (SHERMAN 1980). In 1975, the first year in which female 683 was absent, average overlap decreased between 1974 and 1975 from 28% to 19% (domain) and from 25% to 11% (space-use). Although the effects of relatedness and the cross-generation effects of a matriarch cannot be disentangled, the data suggest that both effects contributed to the patterns of social dynamics.

Several lines of evidence demonstrate that competition also characterizes the social dynamics of close kin. Such competition is to be expected if individuals attempt to maximize the direct component of inclusive fitness. Matrilineal composition varies from mother/daughter, sister/sister groups to more complex associations that include aunt/niece and/or cousin assemblages. Of 55 matriline, 30 were initiated as mother: daughter associations and 20 began as sister:sister groups. Eight of the 20 sister:sister groups clearly were derived from mother:daughter associations (ARMITAGE 1988). Only 27% of the matriline were formed in the absence of the mother, but she usually was present the previous year and died before her daughters were categorized as residents. (A daughter was considered a resident if she remained on her natal habitat throughout her yearling year). As the number of females increases on a habitat patch, the number but not the size of matriline increases (ARMITAGE 1988). The number of

Table 8.

Reproduction of 2-year-old female yellow-bellied marmots. Successful reproduction was measured as the weaning of a litter of one or more young. The expected number of reproductive females was calculated as 0.48 (the rate of reproduction of all adult females) times the number of 2-year-old females in the sample. The  $P$  values are for the  $\chi^2$  test for goodness of fit.

	Number reproductive	Number non-reproductive	$P$
Adult females present	14	34	<0.01
Mother present	11	25	<0.001
No other adult female present	10	16	>0.1

matrilines increases by the fission of larger matrilines (ARMITAGE 1984). As a consequence, the average relatedness of members of a matriline is usually 0.5 and average matrilineal size is 1.47. Although a large matriline may suppress reproduction in an adjoining smaller matriline, thus providing a benefit to the cooperating group (ARMITAGE 1986b), a cost may be assessed through reproductive inhibition within the group. Reproductive inhibition is most easily demonstrated by examining the reproductive success of 2-year-old females. No yellow-bellied marmot reproduces before the age of two and, on average, half of the adult females wean a litter averaging 4.2 young in any year. Two-year-old females reproduce less often than expected when adult females, including their mothers, are present (Table 8).

Competition also is evident in the behavior of adult females toward yearlings. At Marmot Meadow Colony in 1978, two adult sisters were highly agonistic to their nonlittermate full sibs; all yearlings dispersed (ARMITAGE 1986b). In the 1979, female 911 behaved cohesively toward the yearlings, who were her offspring, whereas her sister, female 918, behaved agonistically toward her nieces and nephews. Furthermore, the frequent agonistic behavior directed by female 918 toward her sister caused female 911 to move to a peripheral burrow site during 1979 when female 918 reproduced and female 911 did not (FRASE & ARMITAGE 1984).

This brief summary of 26 years of research on the yellow-bellied marmot demonstrates that both cooperation and competition characterize social dynamics. Competition may be directed toward close kin including sisters, daughters, and mother. Competition also occurs among black-tailed prairie dogs where it varies with the reproductive cycle, not with kinship (HOOGLAND 1986). When cooperation occurs, close kin participate. This pattern of cooperation suggests that individuals also gain in indirect fitness, but, overall, indirect fitness is best viewed as a fitness bonus derived from a strategy for maximizing direct fitness. In other words, individuals cooperate because they expect to benefit directly not because they are attempting to increase the fitness of collateral kin.

#### CONCLUSIONS

In yellow-bellied marmots, fitness benefits toward kin are not correlated with their degree of relatedness, but are limited to close kin, primarily direct descendants. Behavior toward kin may be either cooperative or competitive depending on the social

Table 9.

Summary of evidence that female yellow-bellied marmots attempt to maximize direct fitness.

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Preponderance of mother/daughter matriline
Small size of matriline
Subdivision of matriline when average relatedness decreases
Cooperative (amicable) behavior among close kin, especially mother/daughter groups
Competitive (agonistic) behavior among more distantly related kin and non-kin, including aunt/niece groups
Reproductive suppression, including daughters

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context and the tactics an animal adopts to implement its strategy for achieving evolutionary fitness. The overall pattern of social dynamics indicates that yellow-bellied marmots attempt to maximize the direct component of inclusive fitness (Table 9). Kin recognition is most likely to be important for distinguishing those individuals from the larger universe of individuals that will contribute to the protagonist's fitness. Clearly, habitat, mating system, demography and other factors affect the pattern of kin discrimination in particular species (see WILSON 1987, for further discussion). I predict that in most instances kin discrimination functions primarily to increase direct fitness, with indirect fitness a minor component of total fitness and important primarily where the association with other individuals is necessary in order to maximize direct fitness.

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