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## Kinship, Demography, and Belding's Ground Squirrel Nepotism

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**Summary.** Social behavior and demography of a free-living population of individually marked Belding's ground squirrels (*Spermophilus beldingi*) were studied from 1974 through 1980 at Tioga Pass, California. Relative frequencies of fighting, chasing, cooperation in chasing conspecifics, and assisting conspecifics who were being chased were recorded for adult ( $\geq 1$ -year-old) female kin of nine different degrees of matrilineal relatedness. The animals' mortality and dispersal patterns were also analyzed.

Mothers and daughters, littermate sisters, and nonlittermate (half-) sisters were cooperative; their cooperation varied in proportion to relatedness. In contrast, grandmothers and granddaughters, aunts and nieces, great grandmothers and great granddaughters, aunts and half-nieces, first cousins, and first cousins once removed did not cooperate; their behavior was indistinguishable from that of nonrelatives.

While there were no consistent spatial differences among the burrows of the nine categories of female kin, only mothers and daughters, littermate sisters, and nonlittermate sisters were consistently alive simultaneously. The apparent correspondence between the relatives that received social favoritism and those that consistently co-occurred suggests that demography, particularly survivorship, may have determined the *extent* of ground squirrel favoritism, while kinship influenced its *pattern*.

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### Introduction

Hamilton (1964, 1972) hypothesized that two factors underlying variations in social cooperation are genetic relatedness and the ratio of benefit of an act to the recipient and its cost to the actor (also West Eberhard 1975). Since then, cooperation and kinship have been linked in a variety of insects (Greenberg 1979; Klahn 1979; Noonan 1981; Strassman 1981), birds (Wool-

fenden 1975; Reyer 1980; Ligon 1981; Emlen 1981; reviewed by Brown 1978; Emlen 1978), and mammals (Bertram 1976; Kurland 1977; Massey 1977, 1979; Kaplan 1978; Moehlman 1979; Hoogland 1981), including humans (Chagnon 1979; Chagnon and Bugos 1979).

An important implication of Hamilton's hypothesis is that cooperation should increase and competition decrease with increasing closeness of kinship, all other things being equal. I previously investigated whether the behavior of female Belding's ground squirrels (*Spermophilus beldingi*) was consistent with this corollary by recording the relative frequency of fighting, chasing, cooperative chasing, co-defending territories, and alarm calling among various matrilineal relatives (Sherman 1980a). My findings indicated that there was indeed a positive relationship between cooperation and kinship among pairs of adult ( $\geq 1$ -year-old) mothers and daughters, littermate sisters, and nonlittermate sisters (half-sib offspring of the same female, born in different years and sired by different males). Acts of social favoritism in *S. beldingi* are thus manifestations of nepotism (e.g., assisting kin: Sherman 1980b VS Shields 1980).

Interestingly, grandmothers and adult granddaughters, aunts and nieces, and first cousins did not cooperate; instead, they behaved like unrelated females. Furthermore, for all five behaviors studied, the limited extent of nepotism was the same. To understand the reason, I analyzed ground squirrel demography, including dispersal and mortality, and discovered that although closely and distantly related individuals lived in about equal proximity, close relatives were considerably more likely to be alive simultaneously than were distant kin. This led to my hypothesis that nepotism did not extend to distant relatives because of their historically infrequent interactions and a resulting lack of mechanisms for identifying them.

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This paper presents more complete information about how female Belding's ground squirrels treat variously related female conspecifics; the ontogeny and specificity of their kin recognition mechanism is discussed elsewhere (Holmes and Sherman 1981). My previous research (1974–1977) is augmented here by data gathered during 1978, 1979, and 1980, and by behavioral observations of three new pairs of distant relatives: great grandmothers and great granddaughters, aunts and half-nieces (females and adult offspring of their nonlittermate sisters), and first cousins once removed (females and adult offspring of their first cousins). Also presented here are the details of ground squirrel demography. This new information reaffirms that likelihood of survival and kinship probably influenced the extent and pattern of nepotism, respectively. My results thus suggest the importance of both 'extrinsic' and 'intrinsic' factors (Evans 1977) in the evolution of *S. beldingi* social behavior.

**Materials and Methods**

*Study Animals.* Belding's ground squirrels (Rodentia: Sciuridae) inhabit subalpine meadows in the western United States (Turner 1972). During the summers of 1974 through 1980, 22 assistants and I studied these animals in species-typical habitat in the central Sierra Nevada, at the 3,040 m summit of Tioga Pass, California. Ground squirrels (250–300 of them) are active diurnally from May through September at this site, hibernating the rest of the year (Morton 1975; Sherman and Morton 1979). A single litter of four or five young (range: 1–11) is born each summer. Juveniles first emerge aboveground at weaning in late July or early August. While females usually begin reproducing as yearlings, males are never sexually mature until 2 years of age (Morton and Gallup 1975).

There is a marked sexual asymmetry in dispersal from the natal burrow. While females are sedentary from birth, males permanently disperse soon after they are weaned (Sherman 1977, 1980a). Following mating, adult males emigrate again, with the most polygynous moving farthest. Thus males seldom, if ever, interact with their matrilineal kin or with mates or mates' offspring; they do not behave parentally. Females, in contrast, spend their lives surrounded by and interacting with near and distant female relatives.

*Kinship.* Exact age and kinship through common female ancestors are known for most animals in the Tioga Pass population. Since 1969, 3,051 ground squirrels have been permanently marked with eartags, toeclips, or both; this total includes all 1,154 young that emerged from 237 litters. Because lactating females always nested alone, and because juveniles were captured before litters mixed, the assignment of young to sibling groups was unambiguous.

In this study, female kin of nine different degrees of uterine relatedness and 'nonkin' were observed (Fig. 1). Nonkin were females who shared no known ancestors; therefore, they were more distantly related than second cousins, if related at all. While estimating kinship among matrilineal descendants is straightforward (Hamilton 1972), I have recently discovered that collateral relationships are less certain in *S. beldingi*. This is because most females mate repeatedly with different males on their single afternoon of sexual receptivity per year. Paternity exclusion studies, using electrophoretically detectable allozyme products of six polymorphic blood loci as phenotypic markers, revealed that the majority of litters (78%) were multiply sired (Hanken and Sherman 1981). While multiple paternity does not affect relatedness among matrilineal descendants, relatedness among collateral kin is affected:

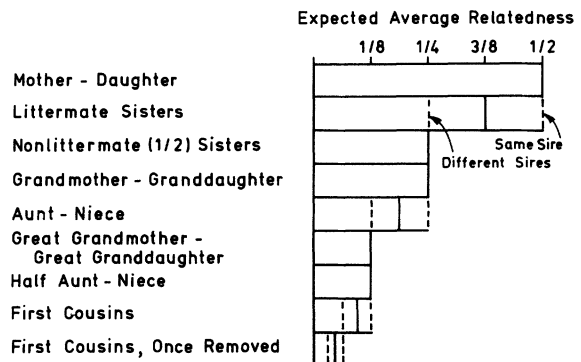
collateral kin are less closely related on average than in strictly monogamous species (Alexander 1979, pp. 169–191; Kurland and Gaulin 1979). For example, littermates could be either full-siblings or maternal half-sibs; therefore, aunt-niece and cousin pairs could also be either full- or half-kin. In the absence of paternity information about all pairs of collateral kin observed, I have depicted them (Fig. 1) as being, on average,  $\frac{3}{4}$  as related as collateral relatives in monogamous families.

*Demography.* The spatial dispersion of related females was assessed in the field by measuring distances between nest burrows. For reproductive females, this meant distances between burrows from which pups emerged at weaning; for nonreproductives, distances between burrows used on the mean date of juvenile emergence. Nest tunnels at Tioga Pass typically collapse overwinter so ground squirrels must re-burrow each Spring. Thus, inter-burrow distances were re-measured yearly.

Survivorship was determined directly from mark-recapture data. Every year from 1977 through 1980, I recorded the frequency of all nine kin pairs (Fig. 1) in the population. I also tallied the percentage of 1-year-old females with relatives of each sort alive; only for the yearling age class were distant relatives alive often enough to permit such complete quantification. I took two precautions to ensure that my analyses included only individuals whose distant relatives would have been identifiable if they had been alive. First, I began my analysis in 1977, the fourth consecutive year that I had intensively trapped and marked family groups. Second, I included only females whose matrilineal lines had been marked for at least the three preceding generations.

*Behavioral Observations.* Study animals were live-trapped, using peanut butter as bait, and handled with gloves. Each was marked with black hair dye for individual identification; such marks did not seem to affect the bearers' behavior (Sherman 1976). Animals were then released at their capture location. All trapping and marking took place during non-observation hours.

Behavioral data were gathered during 4,529 man-hours of unobtrusive observations over seven summers: 16 May–25 August 1974 (4 observers); 17 May–23 September 1975 (6 observers); 1 May–18 July 1976 (6 observers); 22 April–1 August 1977 (7 observers); 2 June–17 August 1978 (3 observers); 21 May–19 July 1979 (3 observers); 13 June–28 July 1980 (2 observers). Observers sat in trees or atop 2–3-m-tall tripods and recorded data in notebooks. Ground squirrels did not seem bothered by their presence. In most cases, observers were not aware of the genetic relationships among animals they watched.



**Fig. 1.** Expected mean relatednesses (in genes identical by descent) among the nine categories of female Belding's ground squirrel kin observed in this study. Because of multiple paternity in *S. beldingi* litters, collateral kin pairs could be either fully or half-related, depending on whether or not they shared the same sire (see text)

During gestation and lactation, female Belding's ground squirrels protect the area surrounding their nest burrows, probably to thwart infanticide, a major source of juvenile mortality (Sherman 1980a, 1981). Reported here are observations of social cooperation and competition as manifested by variations in four behaviors associated with burrow establishment and maintenance of defense perimeters: chases, fights, cooperation in chasing conspecifics, and assisting conspecifics who were being chased. I defined a 'chase' as pursuit of one animal by a conspecific for at least one meter; chases involving the same two participants but interrupted by brief pauses ( $\leq 5$  s) were counted as one event. A 'trespass' was the intrusion of one animal into the territory of another, when the owning female was present and aboveground. An 'encounter' between two animals occurred if they came within 50 cm of each other. A 'fight' was an aggressive interaction involving physical contact, usually kicking, scratching, and biting; fights involving the same two participants but interrupted by brief breaks in contact ( $\leq 5$  s) were counted as one. If more than one type of interaction occurred between two participants in the same bout (e.g., a fight and a chase), only the interaction that occurred first was analyzed. A 'cooperative chase' occurred when a female joined an ongoing chase, which was not occurring on or obviously headed into her territory, on the side of the chaser; this usually resulted in the rapid expulsion of the intruder. Finally, 'assistance while being chased' occurred when a female joined an ongoing chase, which was not occurring on or obviously headed into her territory, on the side of the chasee; this typically resulted in either a quick termination of the chase or a reversal of the original chaser-chasee roles.

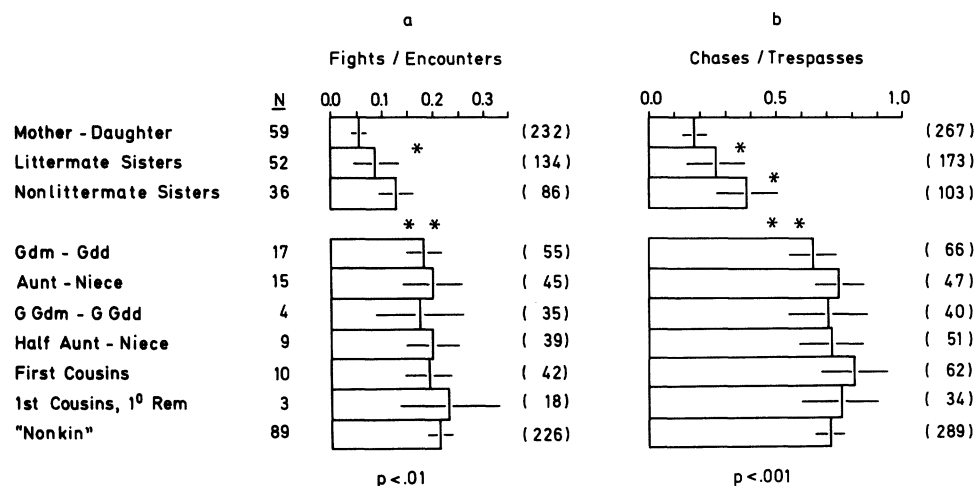
**Statistical Analyses.** One-way analysis of variance (ANOVA), Student-Newman-Keuls a posteriori tests (Sokal and Rohlf 1969), Pearson product-moment correlations, and *t*-tests were used to evaluate differences in behavior and demography; Mann-Whitney *U*-tests were used in two sample comparisons when the assumptions of *t*-tests were violated.

Data from pairs of relatives differing in age were combined because significant differences were not detected between the behavior of younger relatives toward elders versus elders toward younger kin (Sherman 1980a). For example, in terms of frequency of chases/trespasses and cooperative chasing, adult daughters treated their mothers the way mothers treated their daughters regardless of their age difference ( $P \geq 0.07$ , all ANOVAs and yearly pairwise tests for age differentials of 1 to 4 years). Similarly, regardless of age differential (1 to 3 years), aunts treated adult nieces the way nieces treated aunts ( $P \geq 0.08$ , all ANOVAs and yearly pairwise tests).

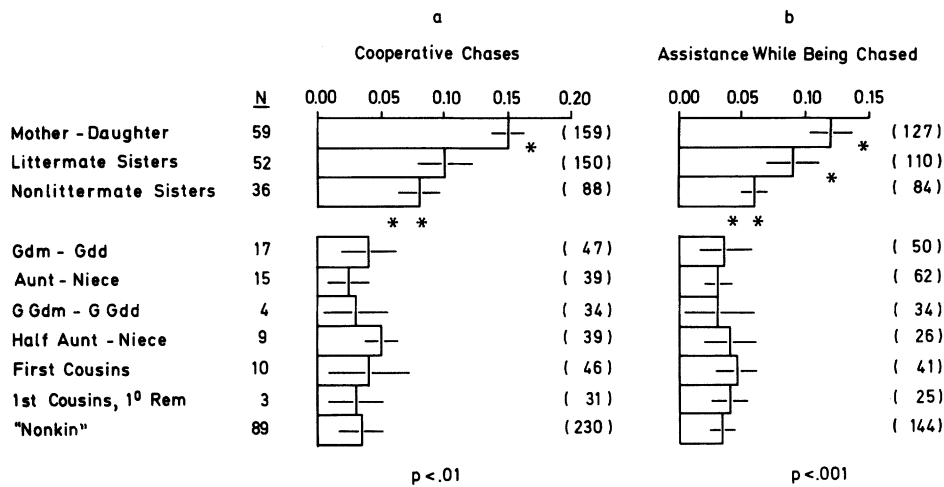
## Results

### Behavior

Female Belding's ground squirrels always nested and nursed their young alone. However, cooperation in nest burrow establishment and territorial defense occurred. Mother-daughter, littermate sister, and nonlittermate sister pairs rarely fought when they encountered each other (Fig. 2a) and seldom chased each other from territories (Fig. 2b). Such kin also joined together to chase conspecific trespassers (Fig. 3a) and came to each other's assistance when one of the pair was being chased (Fig. 3b). Among such close female kin, cooperation usually increased with increasing relationship. Mothers and their adult daughters were always significantly more cooperative than other pairs. Littermate sisters (full- and half-sibs of the same age) were always more cooperative than nonlittermates (half-sisters of different ages), but the differences



**Fig. 2a, b.** Aggression among adult ( $\geq 1$  year) female Belding's ground squirrels at Tioga Pass, California, from 1974 through 1980. **a** Proportion of times pregnant females fought with various relatives and 'nonkin' (see text) when they came within 0.5 m of each other (i.e., an 'encounter') on the territory of one of them. Numbers in parentheses are the total number of encounters for each category. **b** Proportion of times pregnant and lactating females chased various relatives and 'nonkin' from their territories; only trespasses that occurred when territory owners were present and aboveground are graphed. Numbers in parentheses are the total number of trespasses for each category. For both **a** and **b**, means and standard deviations are shown; *n* is the number of different dyads observed. Probability that each data set is homogeneous (i.e., no difference among means) is shown (ANOVA). Stars indicate sequential means that differ significantly, tested with the Mann-Whitney *U* statistic (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ). Student-Newman-Keuls a posteriori tests confirmed homogeneity of behavior among the seven lower categories of animals, in both **a** and **b** ( $P > 0.20$ ).



**Fig. 3a, b.** Cooperation among adult female Belding's ground squirrels at Tioga Pass, California, from 1974 through 1980. **a** Proportion of chases in which territory owning females were joined by various relatives and 'nonkin' to evict trespassers (see text). **b** Proportion of chases in which the chasee was joined by various relatives and 'nonkin'. The usual effect of such intervention was termination of the chase. For both **a** and **b**, means and standard deviations are shown; *n* is the number of different dyads observed. Numbers in parentheses are the numbers of chases that occurred when both members of a focal pair of animals were present and aboveground. Statistical analyses are the same as in Fig. 2. Student-Newman-Keuls a posteriori tests confirmed homogeneity of behavior among the seven lower categories of animals, in both **a** and **b** ( $P > 0.09$ )

were significant only for 'chases/trespasses' (Fig. 2b) and 'assistance while being chased' (Fig. 3b) behaviors. Taken together, these results imply that neonatal ground squirrels were protected from potentially predatory conspecifics not only by their mothers, but also by their mother's closest female relatives (see also Sherman 1981).

More distant female kin behaved differently: Competition rather than cooperation characterized the interactions of grandmothers and granddaughters, aunts and nieces, great grandmothers and great granddaughters, aunts and half-nieces, first cousins, and first cousins once removed. Such relatives fought (Fig. 2a) and chased each other from territories (Fig. 2b) as frequently as they fought and chased nonkin. They also failed to cooperate in ejecting trespassers (Fig. 3a) or to assist each other when one of the pair was being chased (Fig. 3b). There were no consistent or statistically significant differences in behavior among the six categories of distant kin, or between them and nonkin. Therefore, for every behavior studied, conspecifics other than daughters, littermate sisters, and nonlittermate sisters were treated similarly.

Is it possible that social favoritism among close female kin is a manifestation of reciprocity as well as nepotism? I investigated this question in three slightly different ways; each test was based on the premise that reciprocity should be most evident among pairs of animals that had had frequent, long-term social contacts. I thus first asked whether the proportion of fights/encounters and chases/trespasses

varied with the number of years particular pairs of females had defended contiguous territories. There were no significant correlations between behavior and length of association in any of the kinship categories with sufficient sample sizes to enable testing: mothers and daughters (1–4 years of association;  $P \geq 0.07$  for both tests,  $n = 33$  pairs), littermate sisters (1–3 years,  $P \geq 0.10$  for both tests,  $n = 26$ ), nonlittermate sisters (1–3 years,  $P \geq 0.08$  for both tests,  $n = 16$ ), and nonkin (1 to 5 years,  $P \geq 0.07$  for both tests,  $n = 54$ ). Second, I tested to see if kin pairs that defended contiguous territories were more cooperative than similarly related, same aged pairs of animals not defending contiguous territories. I found that close female relatives behaved the same regardless of contiguity (Table 1). Finally, I investigated whether a year of spatial separation affected the behavior of littermate sisters. Six 3-year-old littermate sister pairs defended contiguous territories in years '1' and '3', but not in year '2'; 11 other same-aged littermate sister pairs defended contiguous territories in all 3 years. Using data from year '3', I tested for differences in the behavior of these two sets of animals and found that they behaved similarly in terms of proportion of fights/encounters ( $P \geq 0.10$ ) and chases/trespasses ( $P \geq 0.20$ ). Taken together, these three sorts of observations offer no obvious support for the reciprocity hypothesis.

### Demography

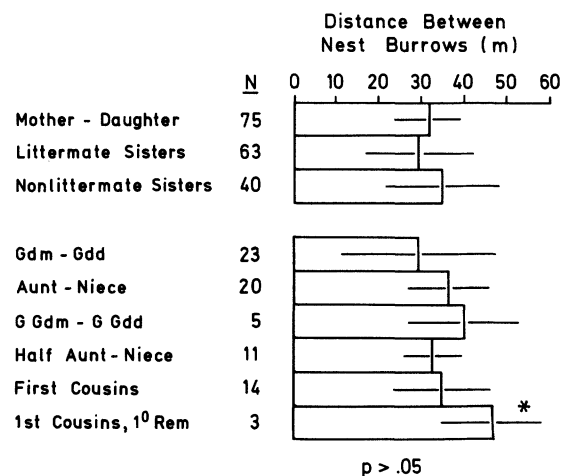
In addition to observing the animals' behavior, I investigated the demography of the Tioga Pass popula-

**Table 1.** Social behavior of pairs of female Belding's ground squirrels depending on whether or not they had defended contiguous territories over the indicated time period*P* level of significance of difference; *n.s.* not significant; *n* is the number of pairs observed

Category of relatives	Fights/encounters			Chases/trespasses		
	Contiguous	Noncontiguous	<i>P</i>	Contiguous	Noncontiguous	<i>P</i>
Mother-daughter (1 year apart in age)	0.06 ± 0.01 ( <i>n</i> = 23)	0.06 ± 0.02 ( <i>n</i> = 12)	<i>n.s.</i>	0.18 ± 0.05	0.19 ± 0.07	<i>n.s.</i>
Littermate sisters						
One-year-old pairs	0.08 ± 0.04 ( <i>n</i> = 21)	0.08 ± 0.04 ( <i>n</i> = 10)	<i>n.s.</i>	0.24 ± 0.07	0.26 ± 0.06	<i>n.s.</i>
Two-year-old pairs	0.07 ± 0.03 ( <i>n</i> = 13)	0.08 ± 0.05 ( <i>n</i> = 4)	<i>n.s.</i>	0.27 ± 0.05	0.24 ± 0.04	<i>P</i> < 0.05
Nonlittermate sisters (1 year apart in age)	0.13 ± 0.04 ( <i>n</i> = 10)	0.16 ± 0.03 ( <i>n</i> = 7)	<i>P</i> < 0.05	0.38 ± 0.09	0.40 ± 0.08	<i>n.s.</i>
Nonkin (same age pairs)						
One-year-old pairs	0.21 ± 0.03 ( <i>n</i> = 28)	0.20 ± 0.02 ( <i>n</i> = 21)	<i>n.s.</i>	0.73 ± 0.05	0.78 ± 0.04	<i>P</i> < 0.05
Two-year-old pairs	0.22 ± 0.04 ( <i>n</i> = 19)	0.27 ± 0.03 ( <i>n</i> = 15)	<i>P</i> < 0.05	0.74 ± 0.06	0.73 ± 0.05	<i>n.s.</i>

tion. Demography has a temporal component – mortality – and a spatial component – dispersal. I gathered data on both to see how frequently various kin pairs co-occurred in time and space. By measuring inter-burrow distances every year, I found that living close and distant female relatives nested in about equal proximity (Fig. 4; Sherman 1980a). In other words, distance between nest burrows was not an accurate predictor of relationships among either descendant or collateral kin.

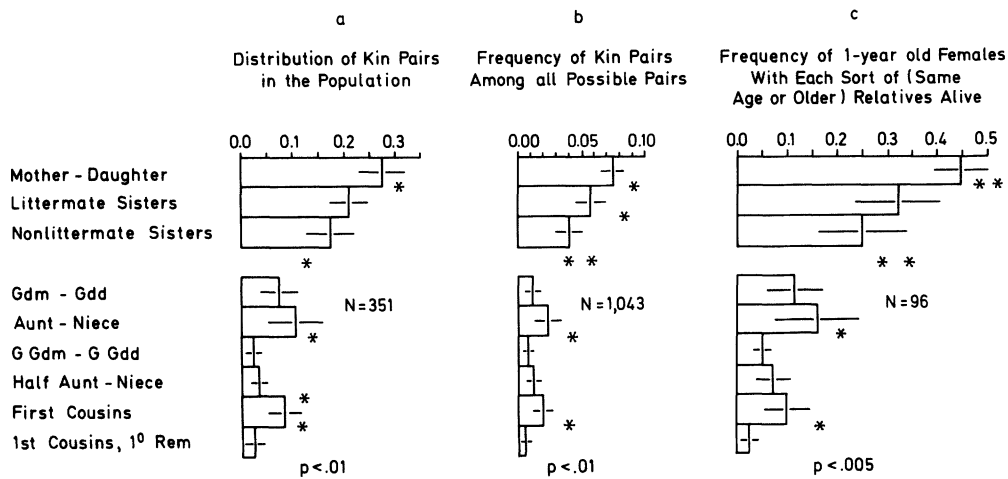
Using 4 years of mark-recapture data (1977–1980), I investigated kin co-occurrence in time. I analyzed these survivorship data in three slightly different, complimentary ways. First, for every year, I totaled the number of living kin pairs in each kinship category (Fig. 1); by adding these totals, I determined the number of kin pairs alive in the population each year. These data allowed me to construct a histogram of the average relative frequency of each of the nine kin pairs among all living pairs of relatives (Fig. 5a). Next, I examined the likelihood that any two randomly chosen females were related in each of the nine different ways. For this analysis, I considered only animals living on the most intensively marked and studied sub-area of Tioga Pass Meadow (ca. 200 m × 150 m), where the relationships of all females were known. The resulting histogram (Fig. 5b) shows the average frequency of various kin pairs as a fraction of all possible pairs of living females. Finally, for all 4 years, I determined the percent of 1-year-old



**Fig. 4.** Inter-burrow distances among adult female Belding's ground squirrel kin that were alive simultaneously. All distances were measured in the field. Means and standard deviations are shown; *n* is the sample size. Statistical analyses are the same as in Fig. 2. Student-Newman-Keuls a posteriori tests confirmed homogeneity in this sample (*P* = 0.07)

females in the entire population with at least one female relative in each kinship category (Fig. 5c).

By each of my three measures of kin co-occurrence, mothers and daughters, littermate sisters, and nonlittermate sisters were significantly more likely to be alive simultaneously than other kin pairs (Fig. 5). Among these three categories of kin, mother-daughter pairs were always significantly most likely to co-exist in time.



**Fig. 5a-c.** The matrilineal kin universe for female Belding's ground squirrels at Tioga Pass, California, for 1977 through 1980. **a** Relative frequency of the nine kinship categories in the population (means total 1.00).  $n$  is the total number of kin pairs that co-occurred during the 4 years of study considered in this analysis (see text). **b** Proportion of the nine kinship categories among all possible pairs of ground squirrels living on an intensively marked and studied sub-area of Tioga Pass (Meadow (see text)).  $n$  is the total number of animal pairs alive during 1977 through 1980 (i.e., each living animal paired once with every other one each year). **c** Proportion of 1-year-old females with at least one living relative in each kinship category.  $n$  is the total number of yearling females during 1977 through 1980 for which complete data were available. For this ANOVA, variances were stabilized with the arcsine square root transformation. For **a**, **b**, and **c**, between-year means and standard deviations are shown. Statistical tests are the same as in Fig. 2. Student-Newman-Keuls a posteriori tests confirmed heterogeneity among the lower six kinship categories in **a** and **c** ( $P < 0.05$ ); significant between-category differences are indicated

## Discussion

To understand the extent and pattern of cooperation in Belding's ground squirrels or any other species, two questions about behavior must be considered: (1) what is socially possible? and (2) what is reproductively ideal? With his formulation of 'inclusive fitness', Hamilton (1964) proposed a mathematical way of answering question (2). I suggest that the answer to question (1) may depend on demography. The two components of demography – mortality and dispersal – determine, respectively, which relatives will consistently be available and accessible for social interactions. Together, these ecological or 'extrinsic' selective factors define the substrate of socially possible behaviors on which 'intrinsic' factors such as kin selection might operate (Evans 1977; Koenig and Pitelka 1981). Kin that are seldom alive simultaneously or that seldom live in proximity might behave as if unrelated on the rare occasions when they co-occur temporally and spatially because behavior appropriate to their relatedness (mathematically) may not have evolved.

Female Belding's ground squirrels favored their daughters, littermate sisters, and nonlittermate sisters. In accord with Hamilton's (1964) hypothesis, but in contrast to Altmann's (1979), among these kin cooperation increased and competition decreased with increasing relatedness (Figs. 2 and 3). As in several primates, females and their daughters were more cooper-

ative than other adult relatives (e.g., macaques: Yamada 1963; Sade 1965; Kurland 1977; Massey 1977, 1979; Kaplan 1978; baboons: Cheney 1977). My data thus reconfirm the influence of kinship on the pattern of *S. beldingi* social favoritism.

Interestingly, females treated all adult conspecifics other than daughters, littermate sisters, and nonlittermate sisters the same, regardless of their relatedness. Likewise, they did not distinguish among distant kin and nonkin. While there was no correlation between the spatial dispersion of various relatives (Fig. 4) and the extent of nepotism, there appeared to be a rough symmetry between cooperation and kin co-occurrence (Fig. 5). This survivorship-nepotism correlation suggests that the temporal component of demography may have influenced the extent of *S. beldingi* social favoritism, perhaps by restricting the relatives with whom females predictably interacted.

It seems puzzling that living pairs of distant collateral kin, such as cousins, were less instead of more numerous than pairs of closer relatives, like sisters. In most long-lived species, the frequency of co-occurrence of distant relatives is expected to increase as genetic relatedness decreases (Goodman et al. 1974). A key difference between such species and *S. beldingi* may be that in the ground squirrels mortality is not constant with age. During 1974 through 1977 at Tioga Pass, between 54% and 93% of juvenile ground squirrels perished before they were 1 year old. Most of these apparently froze or starved during their first

winter's hibernation. Adult mortality was lower, with between 23% and 68% of animals  $\geq 1$ -year-old disappearing between years (Morton and Sherman 1978).

The likelihood that adult kin pairs would co-exist seemed to depend on the number of high mortality 'episodes' that pair had jointly survived (i.e., number of juvenile hibernation periods). Consider, for example, yearling first cousins. In order for them to be alive simultaneously, two sisters born in year '0' both had to survive until year '1'; then each had to bear at least one daughter who survived until year '2'. Thus, four episodes of high mortality must have been survived for 1-year-old first cousins to co-occur. In contrast, for a mother-yearling daughter pair to co-exist, a daughter born in year '0' had to survive until year '1' along with her mother; co-occurrence here involves only one high and one lower mortality episode. By similar reasoning, co-occurrence of yearling littermate and nonlittermate sister pairs involves, respectively, survival of two high, and two high plus two lower mortality episodes. It appears that the consistently co-occurring kin pairs were those separated by the fewest juvenile hibernation periods (Fig. 5).

Is it possible to distinguish between demography and relatedness as factors influencing the extent of *S. beldingi* nepotism? I attempted to do so by examining the behavior of similarly-related kin pairs that differed in their likelihood of co-occurrence. I previously contrasted the behavior of nonlittermate sisters and aunts and nieces in this context (Sherman 1980a, p. 530) and found that the former pairs were significantly more cooperative. This difference notwithstanding, the recent discovery that most *S. beldingi* litters are multiply sired (Hanken and Sherman 1981) renders the comparison inappropriate: when litters comprise both full- and half-sibs, aunt-niece pairs may not be as closely related on average as nonlittermate sisters (Fig. 1). A more pertinent comparison is between nonlittermate sisters and grandmother-granddaughter pairs (Fig. 5). In this paper, I have shown that these relatives treated each other quite differently: nonlittermate sisters were consistently and significantly more cooperative (Figs. 2 and 3). While differences in age and thus 'reproductive value' (Hrды and Hrды 1976; Schulman and Chapais 1980) may have accounted for some of the behavioral differences (nonlittermate sisters are  $\geq 1$  year apart in age; grandmother-granddaughter pairs are  $\geq 2$  years apart), they were not due solely to these factors. For example, grandmothers chased trespassing granddaughters from their territories as frequently as granddaughters chased trespassing grandmothers; furthermore, grandmothers joined granddaughters to chase intruders and came to their assistance during

chases as (in)frequently as granddaughters helped grandmothers (2–5 years' age differential:  $P \geq 0.07$ , all ANOVAs and yearly pairwise tests). Likewise, elder females chased younger nonlittermate sisters as infrequently as the younger half-siblings chased such elder trespassers; elder females also joined younger nonlittermate sisters to chase intruders and came to their assistance during chases as often as they were helped by their younger half-siblings (1–3 years' age differential;  $P \geq 0.10$ , all ANOVAs and pairwise tests). I conclude that differences in the behavior of these similarly-related kin pairs were probably due to the disparity in their likelihood of co-occurrence (Fig. 5).

Is it possible to distinguish between demography and relatedness as factors influencing the pattern of *S. beldingi* nepotism? I attempted to do so by comparing the behavior of littermate sisters and nonlittermate sisters, kin pairs differing in average relatedness (Fig. 1), but not always likelihood of co-occurrence (Fig. 5a, 5c). Data presented in this paper indicate that such kin treated each other quite differently (Figs. 2 and 3). Again, age differential is potentially a confounding variable: littermate sisters are the same age, while nonlittermate sisters are not. However, the apparent behavioral symmetry between elder and younger nonlittermate sisters (above) implies that age was not the major factor leading to differences in cooperation between littermate and nonlittermate sisters. Such differences may have instead been due to their asymmetry in average relatedness.

It seems possible that cooperation in *S. beldingi* is a manifestation of reciprocal altruism (Trivers 1971) as well as nepotism. Reciprocity, according to Trivers's original formulation, refers to circumstances (p. 35) 'when the recipient is so distantly related to the organism performing the altruistic act that kin selection can be ruled out' (e.g., Packer 1977). Therefore, in my previous publication (Sherman 1980a), I examined reciprocity by searching for indications that among conspecifics more distantly related than nonlittermate sisters, cooperation increased or competition decreased with their spatial proximity or length of association. No evidence suggested that such variations in social favoritism occurred. The realization that reciprocity can also occur among relatives (Cheney 1977; Alexander 1979, pp. 52–58; Rothstein 1980), has led me to search for evidence of reciprocal altruism among close kin. Data presented in this paper (e.g., Table 1) suggest that among mothers and daughters, littermate sisters, and nonlittermate sisters, social favoritism is not correlated with proximity or length of association. In other words, close kin that consistently associated and thus had opportunities to develop reciprocal interactions, behaved the same as



similarly related female pairs that had not associated as closely or as long. The implication is that reciprocity is less important than kinship as a factor underlying variations in Belding's ground squirrel social behavior.

The abrupt limit of nepotism (Figs. 2 and 3) might conceivably be explained by an hypothesis alternative to the discontinuity in kin co-occurrence (Fig. 5). Perhaps the costs of social cooperation are great enough or the benefits small enough that assisting distantly related, often different aged conspecifics does not increase inclusive fitness. Because I did not gather data to quantify either phenotypic or genotypic (Alexander 1974) cost/benefit ratios, this possibility cannot be rejected. However, for every behavior I studied, fighting, chasing, cooperative chasing, assistance while being chased (Figs. 2 and 3), co-defense of territories, and alarm calling (Sherman 1980a), the limit of nepotism was the same. If similar costs and benefits accompanied each behavior, their ratio might underly this consistent limit. The apparent diversity of the behaviors, some involving one-on-one interactions (fights), others more generalized nepotism (alarm calling), implies that different costs and benefits may have been associated with each. If so, the unvarying limit of nepotism documented here is more consistent with my demographic explanation than the hypothetical cost/benefit ratio alternative.

## Conclusion

The behavior of female Belding's ground squirrels toward adult daughters, littermate sisters, and nonlittermate sisters – relatives that were most frequently alive simultaneously – supports Hamilton's (1964) inclusive fitness hypothesis. Kinship apparently underlies the *pattern* of cooperation and competition in these rodents. At the same time, the animals' behavior toward female relatives that did not consistently co-occur suggests that kinship may not be the sole factor determining the *extent* of cooperation. Instead, there seems to be a correlation between survivorship and the limit of nepotism. The general significance of this intriguing correlation, and the effects on social cooperation of 'extrinsic' selective factors (Evans 1977) like mortality and 'intrinsic' factors such as kinship, merit further investigation.

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#### Note Added in Proof

After this paper was submitted, F.S. Dobson sent me a manuscript in which the consequences of multiple paternity for genetic relatednesses in *S. beldingi* are discussed, in a manner similar to Fig. 1. I am grateful to him for his comments and for his careful reading of Sherman (1980a).