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Title of Thesis — Titre de la thèse
DEMOGRAPHY, DISPERSION AND BEHAVIOUR OF FEMALE KIN IN COLUMBIAN GROUND SQUIRRELS

University — Université
UNIVERSITY OF ALBERTA

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée
MASTER OF SCIENCE

Year this degree conferred — Année d'obtention de ce grade 1984	Name of Supervisor — Nom du directeur de thèse DR. J. O. MURIE

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DEMOGRAPHY, DISPERSION AND BEHAVIOUR OF FEMALE KIN IN COLUMBIAN GROUND SQUIRRELS

by

WENDY JANE KING

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
FALL 1984

THE UNIVERSITY OF ALBERTA

RELEASE FORM

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Jan O. Murie
Supervisor

L.M. Fedigan

Date..10...OCTOBER...1984......

For Marco

Without whose pioneering work at Dyson Creek
this study would not have been possible
and without whose antagonism
this study would have been far less stimulating

Abstract

I investigated the role of matrilineal kinship in the social organization of female Columbian ground squirrels (*Spermophilus columbianus*). I examined the temporal overlap of female kin, the dispersion of relatives within a high density population and the nature of their behavioural relationships.

Columbian ground squirrels were live-trapped from five to seven years at three sites in southwestern Alberta, Canada. The two most common adult matrilineal relatives for two-year-old females were the mother and a one year older non-littermate sister. Co-occurrence of female kin depended firstly on size and sexual composition of litters and secondly on age-specific survival and recruitment rates. As breeding females, adult matrilineal kin frequently coexisted in the natal population, resulting in a social system potentially strongly influenced by nepotism. The life history traits of *S. columbianus* produce an adult female kin cluster unlike that found for other species of *Spermophilus* in which littermate sisters are common.

Females of all ages were active near their place of birth and adults tended to nest near their natal site when no other female occupied it. Adult females spaced themselves evenly so that relatives formed aggregations but not dense clusters. The only measurable indication of spatial attraction for close kin over distant kin was in the late post juvenile emergence period. The kin group was typically composed of a mother with one or two daughters that were non-littermate sisters. Although there was a lack of close spatial proximity between mothers and daughters of all ages, littermate sisters tended to associate closely as juveniles and yearlings. There was also some spatial attraction to an older or younger non-littermate sister. Adult females appeared to be attracted to natal areas and the resources they contained, perhaps burrows, rather than to matrilineal relatives.

Behavioural associations were not simply correlated with spatial associations. Although encounters were mostly agonistic, adult females had fewer agonistic encounters with mothers and daughters than with other females. Nonagonistic encounters between mothers and daughters consisted mostly of passive tolerance rather than active cohesion or cooperation, such as allogrooming or cooperative defense of areas. Tolerance between mothers and daughters had no discernable effect on time budgets, survival rates or reproductive success. However, female kin groups may have monopolized burrow systems, excluding distant kin from resources available to close kin. Analysis of the ontogeny of behavioural relationships among female kin revealed the influence of familiarity gained in early relationships. Cohesive relationships, typified by play, occurred among immature littermate sisters. Less familiar non-littermate sisters had agonistic but somewhat tolerant relationships.

Female *S. columbianus* may be less social than previously supposed because adult females have agonistic relationships, close adult kin do not cooperate, and immature littermate sisters form cohesive groups as opposed to associating with neighbouring litters.

Acknowledgements

This study could not have been completed in its present state without the advise, humour and encouragement of J.O. Murie, whom I thank. D.A. Boag and L.M. Fedigan served as instructive supervisory committee members. I am also grateful to many colleages and teachers for valuable discussions and lessons, especially J.L. Craig, L.S. Davis, M. Festa-Bianchet, M.A. Harris, S.B. Hrdy, I.G. Jamieson, I.G. McLean and G.E. Woolfenden.

J.O. Murie painstakingly provided geneologies and demographic data for female ground squirrels at Gorge Creek and Highwood Pass. M.A. Harris assisted with the projects at those areas. M. Festa-Bianchet, S.C. Lee and L.S. Rayor provided data from Dyson Creek in years 1979 and 1980, 1984 and 1983 respectively. Co-workers at the R.B. Miller Biological Station offered companionship and motorcycle maintenance ability. T.J. Ruck and D. Richardson of the Alberta Forest Service facilitated fieldwork at Dyson Creek. W. Klenner provided APL software for the analysis of use of space and M.A. Ramsay assisted with production of the tables.

Financial support was receieved from N.S.E.R.C. of Canada (as an operating grant to J.O. Murie and as a post-graduate scholarship to myself) and from the Department of Zoology.

Special thanks go to my parents, H.W. and V.A. King, for always having promoted my education and (more recently) to F. Festa for her altruistic behaviour above and beyond the call of kin selection.

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1. General Introduction

Many animals live in groups as a response to ecological circumstances, and cooperative behaviours within groups are often adaptive through natural selection. Individuals in group-living species experience on average greater fitness in groups than when solitary. Twenty years ago, Hamilton (1964) described how cooperative behaviours among related individuals could be adaptive through "kin selection" (Maynard Smith 1964). Individuals behaving in a way to promote the fitness of relatives at a personal cost in fitness could gain in "inclusive fitness". Hamilton's model of kin selection was examined and supportive evidence came from mammals (*e.g.*, Kurland 1977), birds (*e.g.*, Woolfenden 1975) and insects (*e.g.*, West Eberhard 1975). Eventually, wherever close kin interacted, researchers came to expect kin-differential behaviour without considering what costs and benefits might be involved. More recently, studies have suggested that when cooperation among animals occurs, kin-differential behaviour should occur if cooperation imposes costs on other group members but not if cooperation entails no costs for others (Wrangham 1982). Thus, kin-differential behaviour occurs for some social species (*e.g.*, lions, Bertram 1976) but not others (*e.g.*, bats, Vehrencamp 1979).

Ground-dwelling sciurids (Marmotini) usually live in groups, most likely an adaptive response to predator pressures (Michener 1983). Sex-differential dispersal results in most females remaining on their natal areas (Holekamp 1984). Female ground squirrels are thus likely to live near close kin and the resulting groups have been termed female kin clusters (Michener 1983). Kin-differential behaviour has been documented for adult females of several species of *Spermophilus* (*S. richardsonii*, Yeaton 1972, Davis 1982; *S. tereticaudus*, Dunford 1977; *S. beldingi*, Sherman 1981; and *S. parryii*, McLean 1982). Sherman (1981) suggested that differential behaviour may be limited by the historical likelihood of co-occurrence of kin in time and space. However, benefits and costs of differential behaviour have received little attention (but see Davis 1982).

Columbian ground squirrels (*Spermophilus columbianus*) have female kin clusters according to Michener (1983) and their social system is suspected to be based on matrilineal kin groups (Michener 1983). The co-occurrence of adult female kin has not been documented nor has their dispersion and behaviour.

The purpose of this study was to investigate the role of matrilineal kinship in the social organization of female Columbian ground squirrels. First I examine the temporal overlap of female kin in three populations. In so doing, I determine the availability of female relatives and delineate the demographic factors promoting co-occurrence of female kin (Chapter 2). Then I assess the spatial overlap of female kin in one population, making note of the extent of philopatry (Chapter 3). Finally, I describe the behaviour of close and distant kin for the same population and assess the potential advantages and disadvantages of kin-differential behaviour to female Columbian ground squirrels (Chapter 4).

2. Temporal Overlap of Female Kin in Columbian Ground Squirrels

2.1 Introduction

A basic feature of sociality in ground-dwelling sciurids is the retention of daughters in the natal area (Dunford 1977, Armitage 1981, Michener 1983). With the resulting development of female kin clusters, closely related individuals overlap in space and time and, as a result of kin selection, may interact more cohesively with one another than with less related neighbours (Hamilton 1964). Indeed, this type of matrilineal kin selection has been invoked in many studies of the social organization of *Spermophilus* (*e.g.*, *S. richardsonii*, Yeaton 1972, Davis 1982; *S. tereticaudus*, Dunford 1977; *S. beldingi*, Sherman 1981; and *S. parryii*, McLean 1982). Sherman (1981) stressed the importance of survivorship of females in determining the extent of favouritism based on kinship in *S. beldingi*. He postulated that favouritism would exist only among classes of kin that frequently co-occurred in time and space. Co-occurrence of different classes of kin has not been assessed in other species of ground squirrels.

Columbian ground squirrels (*Spermophilus columbianus*) have female kin clusters with male territoriality according to Michener (1983). Although they mature later and have smaller litters than other species of *Spermophilus* characterized by female kin clusters (Murie *et al.* 1980), females remain near their natal areas as adults (Murie and Harris 1984, see Chapter 3).

Here I examine the temporal overlap of matrilineally-related females in three populations of *S. columbianus* in southwestern Alberta, Canada, in order to determine the availability of female kin and also to examine the effects differences in demography may have on temporal overlap of those kin.

2.2 Materials and Methods

2.2.1 Study Areas

Gorge Creek (50°39'N, 114°39'W, elevation 1470 m) consists of 8 ha of grassy benchland. Highwood Pass (elevation 2170 m) is located 27 km west of Gorge Creek and encompasses an 8 ha subalpine shrub meadow. Dyson Creek (elevation 1570 m), which lies 3 km south of Gorge Creek, is a 0.76 ha grassy meadow surrounded by aspen and pine woodland. Descriptions of the study areas may be found in Murie and Harris (1982, for Gorge Creek and Highwood Pass) and Festa-Bianchet (1981, for Dyson Creek). Squirrels were live-trapped at Gorge Creek from 1976 to 1982, at Highwood Pass from 1974 to 1980, and at Dyson Creek from 1979 to 1983. All squirrels were permanently marked in both ears with individually-numbered fingerling fish tags (Monel No. 1). Juveniles were captured as they emerged from nest burrows and thus could be associated with the mother and littermates. The age of a squirrel was known if it had been trapped as a juvenile or early in the season as a yearling (see Boag and Murie 1981*a*). Members of all age classes were trapped each year except that only adults were trapped at Dyson Creek in the spring of 1983 and only adults and yearlings were trapped at Highwood Pass in 1975 and 1980.

Total numbers of individuals captured in the three areas (Gorge Creek, Highwood Pass and Dyson Creek) were 438, 466 and 225 respectively, of which 214, 233 and 104 were females. Numbers of litters (and juveniles) ascribed to known females were 84 (236), 61 (138) and 52 (191) respectively. J.O. Murie provided geneologies and demographic data from Gorge Creek and Highwood Pass and M. Festa-Bianchet provided information on reproduction and demography at Dyson Creek, 1979-1980.

2.2.2 Analysis

To calculate the probability that a female squirrel coexisted with various [illegible]s of female kin, I first made a graphical representation of the matrilineal history of ea[illegible]rrel.

For each kinship category, I noted the presence or absence of female relatives for each year that a particular female was present in the study population. Thus, for example, a female born in the first year of study and remaining for three more years could be checked for the presence of her mother and a littermate sister four times from juvenile to three years of age; however, the presence of an older non-littermate sister or grandmother could not be assessed. I took the proportion of each age class of females having relatives present as the probability of co-occurrence with that class of relative. Female Columbian ground squirrels usually mature at two years of age in these study areas (Festa-Bianchet 1981), so I used that age class to depict probability of co-occurrence of first breeders with adult (≥ 2 years old) female kin. I tested for significance of statistical tests using a P value of 0.05.

I define temporal overlap of female kin as the simultaneous presence during the summer active season of two matrilineally related females within a population. Survival refers to persistence within a study population; recruitment refers to persistence from yearling to two-year-old (and thus breeding) age. I do not distinguish between death and emigration because both result in the absence of a squirrel from the population in question.

2.3 Results

Overall, I found two-year-old female Columbian ground squirrels to have unequal probabilities for coexisting with different levels of adult female kin (Fig. 2.1, likelihood ratio test $G = 33.6$, $P = 0.001$). For a female first entering the breeding population at this age there was a 68% likelihood that her mother would be present but only a 24% likelihood that a littermate sister would be present. In contrast, there was a 50% probability of co-occurring with a non-littermate sister born one year earlier.

To examine demographic influences on the coexistence of certain categories of kin, I compared patterns between the study areas. I present detailed data only for mothers and for littermate sisters because sample sizes for other categories are small. Mothers were always present when the daughters first emerged as juveniles and often remained until the daughter was four years old in two of the areas (Fig. 2.2a). However, at Gorge Creek significantly fewer females co-occurred with their mothers at the ages of one to four years old (*e.g.* for two-year-olds, Yates' $X^2 = 6.09$, $P = 0.01$ for Dyson Creek and Yates' $X^2 = 5.34$, $P = 0.02$ for Highwood Pass). The survival rate of adult females, reflected by the curves in Fig. 2.2a, was lowest at Gorge Creek where co-occurrence of mothers and daughters was least (Table 2.1).

However, survival rate did not appear to be the only factor involved in determining the pattern of co-occurrence of female kin. Littermate sisters were sometimes present in all three populations as juveniles, but a juvenile female at Gorge Creek or Dyson Creek was more likely to have a sister than one at Highwood Pass (Fig. 2.2b, Yates' $X^2 = 15.13$, $P = 0.001$ for Gorge Creek; Yates' $X^2 = 8.51$, $P = 0.004$ for Dyson Creek). The presence of a sister initially depended not simply on production of female offspring which was highest at Dyson Creek, but on production of more than one female offspring within a litter which occurred most often at Gorge Creek (Table 2.2). Once the juvenile probability of coexistence was thus set, subsequent probabilities depended on age-specific survival and recruitment rates (Table 2.1). Co-occurrence of sisters at Gorge Creek rapidly declined from juvenile to yearling age as a result of low juvenile survival (37%). At Dyson Creek, coexistence of sisters declined a year later as a result of low recruitment (51%) of yearlings. Low production of sisters at Highwood Pass (Table 2.2) was compensated by high juvenile survival (61%) and yearling recruitment (68%) so that no difference existed between areas in prevalence of littermate sisters at two years of age (Fig. 2.2b).

For two-year-olds, co-occurrence with a non-littermate sister one year older was similar at Gorge Creek (43%) and Dyson Creek (38%) but higher at Highwood Pass (80%). Overlap with the grandmother and with a non-littermate sister two years older at Gorge Creek (0% for both) and at Dyson Creek (0% and 50% respectively) was less than at Highwood Pass (33% and 100% respectively). Although all sample sizes are small, the greater overlap with these categories of female kin at Highwood Pass is a further indication of the influence of high survival rates.

2.4 Discussion

Few studies documenting differential behaviour toward close adult kin have analyzed the likelihood of co-occurrence of those kin. Nepotistic behaviour is unlikely to have marked effects on the social organization of a species unless adult kin are frequently available and thus may frequently benefit in terms of reproductive success. In a population in which a consistently low proportion of the adults coexist with close kin, nepotistic behaviour may occur, but it could not play a significant role in the evolution of the social system. For Columbian ground squirrels, I found that 77% of 43 females of two to four years of age had at least one adult female relative (mother, daughter, littermate or non-littermate sister) present in the breeding population. This prevalence of kin could be a short term result of population expansion. Altmann and Altmann (1979) proposed that primates are likely to grow up surrounded by numerous close kin in rapidly expanding populations where births greatly exceed deaths and dispersal from natal groups is low. The populations of *S. columbianus* did not appear to be rapidly expanding. Densities of adult females increased 1.7- fold over 5 years at Dyson Creek and decreased 0.95- fold and 0.74- fold over 7 years at Highwood Pass and Gorge Creek respectively. I believe that the populations were relatively stable in comparison to other species of ground squirrels (see Boag and Murie 1981*b*). Thus, any nepotistic behaviour found for this species could be a prominent force in determining the pattern of social organization.

The only ground squirrel, or indeed rodent, for which comparable data on co-occurrence of kin are available is the Belding's ground squirrel (*Spermophilus beldingi*, Sherman 1981). Sherman also looked at age of first reproduction, presenting availability of female kin as means over a four year period. For *S. beldingi*, the frequency of co-occurrence of adult female kin decreased from mother/ daughter pairs to littermate sisters to non-littermate sisters (see Fig. 2.1) in conjunction with decreasing average relatedness (assuming some multiple paternity of litters (Hanken and Sherman 1981)). Production of female offspring was not considered an important factor, probably because litter size is high (4-5) and females usually first reproduce as yearlings (Sherman 1981). For Columbian ground squirrels, age-specific survival rates influenced patterns of temporal overlap of adult female kin only after initial probabilities of coexistence were established by size and sexual composition of litters. Littermate sisters appear to be less common in the Columbian ground squirrel than in the Belding's ground squirrel (Fig. 2.1) because of the smaller litter size (Murie *et al.* 1980) or because the former values are computed for two-year-olds rather than yearlings. However, mother/ daughter pairs and non-littermate sisters appear to be more common as a result of higher survival rates (see Sherman 1981 and Table 2.1). Additional factors promoting temporal overlap of female kin include regularity of iteroparity and success of females born into extensive family groups (unpubl. data). In the populations of *S. columbianus*, these demographic factors influencing co-occurrence of kin are complex and act synergistically.

The demographic characteristics of other species of ground squirrels that are postulated to form female kin clusters are similar to those for *S. beldingi*; *S. richardsonii*, *S. tereticaudus* and *S. parryii* all tend to be characterized by relatively high litter size, low survival and reproductive maturity of yearling females (see Armitage 1981 for review). Those life history traits lead to a relatively high turnover of individuals, and researchers have documented kin-differential behaviour between adult mother/ daughter pairs and between adult littermate sisters (*S. richardsonii*, Yeaton 1972, Davis 1982; *S. tereticaudus*, Dunford 1977; *S. parryii*, McLean 1982). In *S. columbianus*, litter size is smaller, survival rates are higher and females usually do not reproduce until two years of age. Thus one might expect to find not a kin cluster of a mother and her adult sibling daughters, as for the above four species, but rather a kin cluster of a mother with a series of adult daughters of differing ages. If likelihood of co-occurrence dictates the limits of nepotism, kin-differential behaviour should occur between mother-daughter pairs and also between non-littermate sisters.

Table 2.1. Survival rates for three age classes of female Columbian ground squirrels in three different populations. All disappearances of squirrels were considered mortalities for this table. Significant differences for pairwise comparisons of areas according to Yates' X^2 tests for independence are indicated by superscripts.

	Gorge Creek		Highwood Pass[1]		Dyson Creek	
Age	n	% recaptured	n	% recaptured	n	% recaptured
Juvenile	98	37^{ab}	87	61^{a}	56	61^{b}
Yearling	36	75^{c}	56	68	41	51^{c}
Adult	114	65^{d}	303	73	59	83^{d}

[1] these data from Murie (in press); $^{a}P = 0.002$; $^{b}P = 0.007$; $^{c}P = 0.05$; $^{d}P = 0.02$

Table 2.2. Reproductive parameters for Columbian ground squirrels in three different populations. Sample sizes are given in parentheses. Significant differences for pairwise tests between populations are indicated by superscripts for Mann-Whitney U tests (MW), Pearson (P) or Yates' (Y) X^2 tests for independence.

	Gorge Creek		Highwood Pass[1]		Dyson Creek[2]		Test
Litter size at emergence (n litters)	2.8[ab]	(84)	2.3[ac]	(61)	3.7[bc]	(52)	MW
Sex ratio among juveniles ♂:♀ (n juveniles)	0.9:1.0	(236)	1.2:1.0	(138)	1.2:1.0	(191)	PX^2
% adult females lactating (n females)	83[d]	(162)	65[de]	(298)	91[e]	(54)	PX^2
No. juvenile females per litter containing at least one female (n litters)	1.9[f]	(65)	1.3[fg]	(49)	1.8[g]	(49)	MW
% female litters containing at least two females (n litters)	63[h]	(65)	29[hi]	(49)	55[i]	(49)	YX^2

[1] these data from Murie (in press) for litter size and % adult females lactating; [2]includes litters from seven yearling mothers for litter size and sex ratio among juveniles; [a] $P = 0.001$; [b] $P = 0.001$; [c] $P = 0.001$; [d] $P = 0.001$; [e] $P = 0.001$; [f] $P = 0.001$; [g] $P = 0.003$; [h] $P = 0.001$; [i] $P = 0.01$

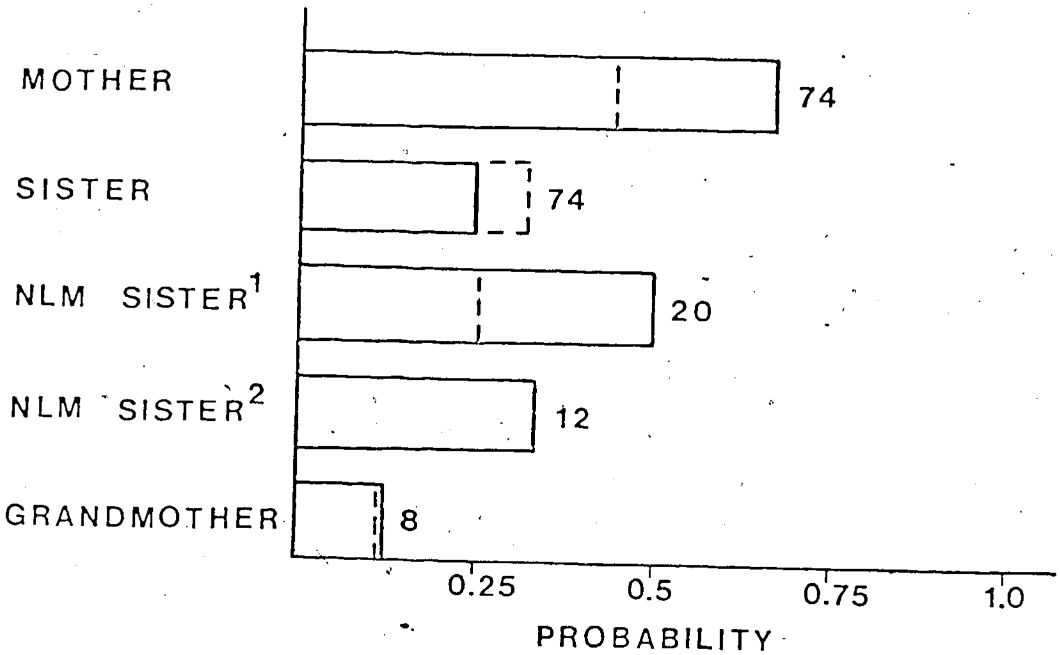

Figure 2.1. The likelihood of two-year-old female Columbian ground squirrels having a member of the five most common adult kinship classes present in the breeding population. Numbers on bars represent sample sizes of two-year-olds. Dotted lines indicate data for yearling female Belding's ground squirrels from Sherman (1981, Fig. 5c; no data for nlm sister[2]).

[1] non-littermate sister born one year before; [2] non-littermate sister born two years before

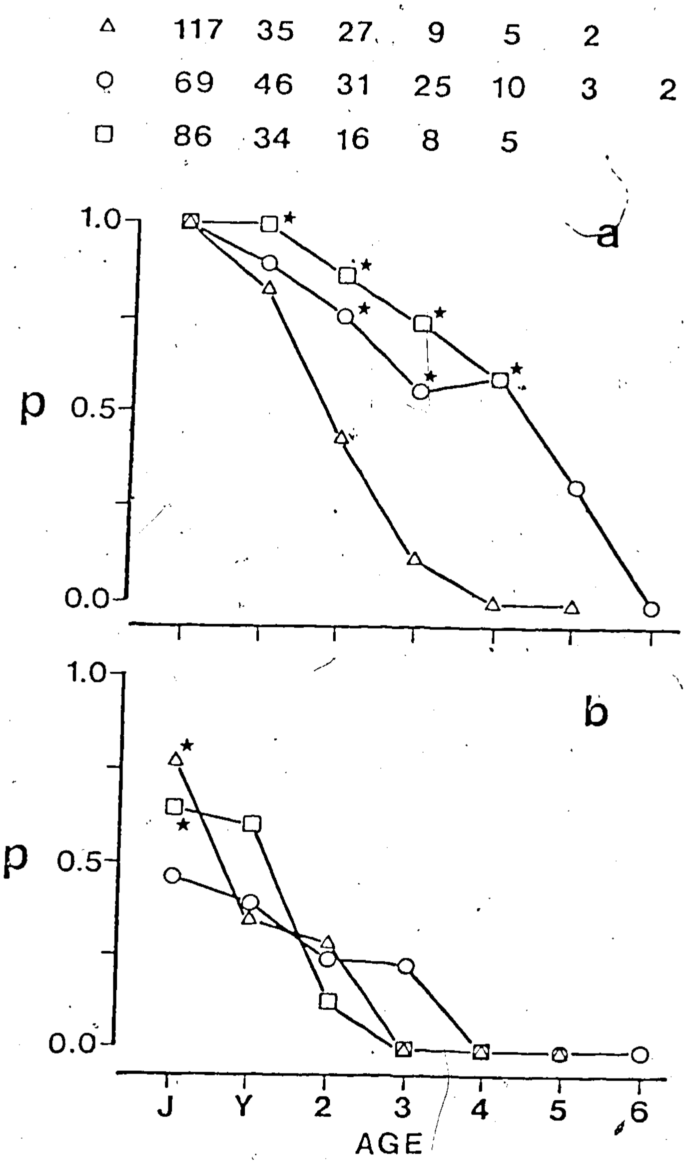

Figure 2.2a. The probability of seven age classes of female Columbian ground squirrels having the mother present for three different populations. Sample sizes are shown above respective ages. Stars indicate points significantly different from those for Gorge Creek (Yates' X^2 and Fisher exact tests); no other significant differences between populations were found.

b. The probability of seven age classes of female Columbian ground squirrels having a littermate sister present for three different populations. Stars indicate points significantly different from those for Highwood Pass (Yates' X^2); no other significant differences between populations were found. △ = Gorge Creek; ○ = Highwood Pass; □ = Dyson Creek; J = juvenile; Y = yearling

3. Spatial Overlap of Female Kin in Columbian Ground Squirrels

3.1 Introduction

A primary force shaping the social organization of many species of ground-dwelling sciurids appears to be the retention of daughters within the mother's home range (Dunford 1977, Armitage 1981, Michener 1983). Closely related females overlapping in both space and time may then exhibit mutual favouritism and enhance each others reproductive success through kin selection (Hamilton 1964).

In several species of the genus *Spermophilus*, related females have been found to live in close proximity as a result of male-biased dispersal and female philopatry (Michener 1983). The Columbian ground squirrel (*Spermophilus columbianus*) has been suggested by Michener to have female kin clusters with male territoriality. Males typically disperse as yearlings in this species (Boag and Murie 1981*b*, Festa-Bianchet and King 1984) and the demographic characteristics of *S. columbianus* promote temporal overlap of adult female kin (see Chapter 2). Thus the potential exists for adult females to form kin clusters and exhibit nepotism. However, the pattern of spatial overlap of females has not been investigated in detail with respect to kinship.

The term kin cluster or group has been poorly defined in the literature and may vary from a complete matriline (Armitage 1984) to any two neighbouring females that are related as mother and daughter or littermate sisters (Davis 1982). Michener (1983) briefly described female kin clusters in terms of home range overlap and dispersion of related females. Her graphical representation of kin clusters (1983, Fig. 1) depicted four situations along a continuum from no association to complete range overlap. However, she did not incorporate locations of unrelated or distantly related females. In a population of Columbian ground squirrels, where home range overlap of adult females can be extensive and where each female has from one to seven contiguous neighbours (Festa-Bianchet and Boag 1982, Figs. 4 and 5), some females most likely share part of their range with distantly related neighbours. To determine whether closely related females are clustering or preferentially associating in space, one must compare use of space between closely related females to that between distantly related or unrelated females.

Here I assess the pattern of spatial overlap of adult females with respect to matrilineal kinship for a population of Columbian ground squirrels in southwestern Alberta. I also describe the extent of female philopatry and the ontogeny of spatial overlap between matrilineally related juvenile and yearling females.

3.2 Materials and Methods

3.2.1 Study Area and Field Methods

Columbian ground squirrels were studied at an elevation of 1570 m on the north side of Dyson Creek in the Rocky Mountain foothills (50° 37' N, 114° 39' W), approximately 32 km due west of Turner Valley, Alberta. The study area consists of a 0.76 ha grassy meadow which is surrounded by boreal mixedwood forest (full details in Festa-Bianchet 1981). A small meadow to the south of the creek was occasionally used by the squirrels but was not observed intensively. Cattle graze the area from July to September.

Daily obervations were made, weather permitting, from a 2 m high wooden stand using 10 X 50 mm binoculars from 22 April to 16 August, 1981 and from 25 April to 18 August, 1982. A total of 377 hrs on 176 days was spent observing, primarily between 0800 and 1130 hrs MDT. In regular scans of approximately 30 min interval, I noted squirrels' identification, activity and location to the nearest meter on a 10 X 10 m grid. Brightly coloured plastic flags marked the intersection of grid lines at 10 m intervals. Additional notes, including location and nature of any encounters seen, were taken during and between scans. An encounter was considered to occur when two (or more) squirrels approached within 0.5 m. Detailed descriptions of social activities observed are given by Steiner (1970).

Squirrels were trapped using 30 National live traps baited with peanut butter, and were individually marked with Monel metal fingerling eartags together with hair dye on the pelage or coloured plastic flags attached to the eartags. Trapping took place in the afternoon approximately every two to three days throughout the active season as needed to mark newly-emerged squirrels or those whose individual dye mark or earflag combination was fading or incomplete. Juveniles were assigned to mothers and littermates when they were trapped as they first emerged from nest burrows. Age, sex, weight and reproductive condition were recorded for each animal trapped. A total of 221 hrs was spent trapping on the north side and 77 hrs on the south side of Dyson Creek over the two years. M. Festa-Bianchet had live-trapped and marked all squirrels on the area in 1979 and 1980 (see Festa-Bianchet 1982 for further details on trapping procedures).

3.2.2 Analyses

The active period was divided into five biologically-relevant periods. Breeding was the 16-day period encompassing all the days on which females bred and commenced within a few days of emergence of the first overwintering squirrel each year. Gestation was the 16-day period following Breeding, extending five or six days past the birth of the first litter. Lactation was the 24-day period following Gestation, extending one or two days after the first litter emerged. The time period following Lactation was arbitrarily divided into Early Post Juvenile Emergence, the 24-day period following Lactation during which the last squirrels emigrated from or immigrated to the study area, and Late Post Juvenile Emergence, the 35- or 36-day period extending to the last day of observation. These five periods correspond to those used by Festa-Bianchet and Boag (1982) on the same area as follows: Breeding = Periods 1-2; Gestation = Periods 3-4; Lactation = Periods 5-7; Early Post Juvenile Emergence = Periods 8-10; and Late Post Juvenile Emergence = Periods 11-12.

Centres of activity for each period were calculated as the mean X and Y coordinate of all sightings for each squirrel, based on a minimum of nine sightings for each period. Distances between any locations, *e.g.*, locations within scans, centres of activity or nest burrows, were measured as straight line distances. Nest burrows are the typically small holes (McLean 1978) from which litters first emerge. Locations of nest burrows in 1979 and 1980 were provided by M. Festa-Bianchet. "Natal site" refers to the nest burrow from which a squirrel first emerged as a juvenile.

Home ranges were drawn as minimum convex polygons (Mohr 1947) for those individuals with at least 20 sightings per period. The outermost 50% of the locations from the geometric centre of activity was dropped using a computer algorithm leaving core areas of 50% usage. Core areas were used since adult ground squirrels, being sedentary, tend to use areas of their home range disproportionately (Michener 1979, Davis 1982).

Yearling females that bred in 1982 were included in the analysis of use of space among breeding females only.

All values presented for distance or overlap measures are means plus or minus one standard error. Data sets were compared using Wilcoxon signed-rank tests and differences were considered significant when $P<0.05$.

3.2.3 Kin Relationships

All kin relationships were determined matrilineally. Squirrels having shared a natal burrow, *i.e.*, mothers and their offspring or full siblings, are referred to as uterine kin. Those squirrels known not to be uterine kin were those known not to have shared a natal burrow, and are referred to as non-uterine kin. Uterine kin plus non-littermate siblings are referred to as specified kin (= close kin). Those squirrels known not to be specified kin are referred to as non-specified kin (= distant kin). Non-uterine kin and non-specified kin include more distantly related kin as well as some individuals of unknown relationship. Use of space between uterine kin was compared to that between non-uterine kin to determine whether mothers and their offspring or full siblings were preferentially associating with each other over all animals that were not uterine kin. Further comparisons between specified kin and non-specifed kin were made to assess the influence that non-littermate sisters had on use of space. The content of uterine kin and specified kin categories differed between certain comparisons as noted in the table headings.

3.3 Results

3.3.1 Demography

In 1981, 16 adult females, 10 yearling females and 17 juvenile females emerged on the north side of Dyson Creek. One non-lactating adult female subsequently took up residence on the south side of the creek. In 1982, 14 adult females, 9 yearling females and 24 juvenile females emerged, of which 3 yearling females raised young. In total, seven matrilines of 17 breeding females were investigated; however, the relationship between the founding females was unknown. Numbers of known female kin pairs used in analyses are given in Table 3.1. Nest burrows were known for successful females; 9 adults in 1979, 10 adults and 4 yearlings in 1980, 8 adults in 1981 and 12 adults and 3 yearlings in 1982. Natal sites were known for the four breeding yearling females in 1980 and for seven adult females and all yearlings and juveniles in both 1981 and 1982.

3.3.2 Site Attachment

Females of all ages had centres of activity that averaged 12 to 27 m from their natal site (Table 3.2). At reproductive maturity, females either nested within 10 m (54% of 13 cases) or further than 20 m (46%) from their natal site. I thus used a 10 m radius from the natal site to define a natal area. This area was considered used if a female had her nest burrow within it. When the daughter nested near the natal site, in 6 of 7 cases the mother was nesting further than 10 m away from the site or had disappeared (presumed dead) and in 1 case the daughter shared the area with her mother. When the daughter did not nest near the natal site, the mother remained at the natal area (2 cases), another (older) female occupied the area (2 cases) or the mother had moved 10 m but the area was not used (2 cases). There were three cases that did not fit the pattern, *i.e.*, two daughters not using a natal area that no other female used and one daughter not using another area when her mother remained at the natal area. Special circumstances surround the case of one unused natal area in 1982. The mother originally used the natal area and was observed to move her juveniles 17.5 m five days prior to emergence. Thus the daughter's natal area was occupied by her mother during late gestation/ early lactation. Similar circumstances may have accompanied the other unused natal area in 1980. The daughter that shared the area with her mother was one of seven breeding yearling daughters. Although these 13 cases involving eight individuals lack independence, it does appear that females nested near their natal site (*i.e.* within 10 m) when it was left unoccupied.

During lactation, 50% usage areas of adult females accounted for an average of 14% of the total range in 1981 and 20% of the total range in 1982. Mean core area size ranged from 68 m^2 during gestation 1981 to 364 m^2 during the early post juvenile emergence period in 1982 and increased both years from gestation to lactation (Fig. 3.1). Eleven adult females were present in both years and the location of their core areas shifted little. The overlap of core areas between years accounted for an average of 76% of the core in 1981 and 68% of the core in 1982.

3.3.3 Breeding Females

Between 1980 and 1982, females did not locate their nest burrows closer to their nearest uterine kin (20.6 ± 2.5 m) than to their nearest non-uterine kin (15.3 ± 1.7 m, $P = 0.09$, n = 14 pairs). When specified kin were considered, the trend to nest closer to distant kin was less apparent (17.6 ± 2.8 m to nearest non-specified kin versus 21.7 ± 4.1 m to nearest specified kin, $P = 0.25$, n = 6 pairs). In any case, the nest burrows of closely related females were not randomly distributed through the population. The distance between burrows of nearest uterine kin when females were randomly assigned nest sites and each individual tested once was 60.0 ± 11.4 m as opposed to the observed 18.2 ± 2.3 m, $P = 0.01$, n = 11 pairs (see also Fig. 3.2).

Mature females in 1981 and 1982 had centres of activity approximately equidistant from their closest uterine kin and their closest non-uterine kin for all periods except late post juvenile emergence when they tended to be closer to uterine kin (Table 3.3a). This tendency remained when each individual was tested once to avoid violating assumptions of independence (n = 7, *P* = 0.09). A similar situation was apparent for possible attraction to or lack of repulsion from specified kin more than non-specified kin neighbours during this last period only (Table 3.3b).

However, centres of activity are not necessarily locations where individuals concentrate activities. Comparisons using core areas based on the innermost 50% of a squirrel's sightings should more clearly indicate spatial associations. Great variability in amount of overlap within all groups was evident. There was no significant difference in amount of overlap of core areas between uterine kin and non-uterine kin nor between specified kin and non-specified kin for any time period (Table 3.4a and b). Thus, females did not appear to preferentially share core areas with close kin. In addition, time spent within overlapping portions of core areas did not differ between uterine kin and non-uterine kin nor between specified kin and non-specified kin (Table 3.5a and b).

Although core areas of individuals typically overlapped core areas of one to five others, distantly related squirrels may have been avoiding each other while close relatives may not have been and hence were more likely to be found in proximity to each other. This, however, was not the case. The mean distance between nearest uterine kin when simultaneously active was 22.4 ± 1.3 m while that between nearest non-uterine kin was 21.9 ± 1.5 m (*P* = 0.55, n = 13 pairs). Nor were nearest specified kin closer when simultaneously active (20.1 ± 2.3 m) than nearest non-specified kin (22.0 ± 1.3 m, *P* = 0.31, n = 7 pairs).

In summary, although there was little indication of attraction among close kin over distant kin, the dispersion of the nest burrows with respect to close kin was non-random. The spatial distribution of centres of activity of related females resembled that of nest burrows (Figs. 3.2 and 3.3). Lines drawn between uterine (or specified) kin nest burrows or centres of activity produced discrete groups each year. Those groups often neighboured on other groups, but were never intermixed with them.

3.3.4 Juvenile Females

In the early post juvenile emergence period, the centres of activity of juvenile females were located equidistant from their mothers and their closest adult female neighbour, but were closer to the non-uterine kin neighbour in the late post juvenile emergence period (Table 3.6a). When adult non-littermate sisters were included as specified adult kin, juvenile females were not closer to non-specified kin in either period (Table 3.6b). Juvenile females were no closer to a yearling non-littermate sister than to any other yearling female during the early period but showed some closer association with the non-littermate sister in the late period (Table 3.6c). However, juvenile females were much closer to a juvenile sister than to any other juvenile female, a non-littermate yearling sister or their mother in the early post juvenile emergence period (Table 3.7a, b and c). The trend to be closer to a sister than another juvenile female or the mother persisted into the late post juvenile emergence period (Table 3.7a and c). Thus juvenile females showed strong spatial attraction to littermate sisters over all classes of female kin, except yearling non-littermate sisters in the late post juvenile emergence period.

3.3.5 Non-breeding Yearling Females

Non-breeding yearling females had little close association with adult female kin. In fact, yearling females were closer to a non-uterine kin female than their mother during lactation and the early post juvenile emergence period (Table 3.8a). The non-uterine kin neighbour may have been an older non-littermate sister since yearlings were not significantly closer to non-specified adult kin in any period (Table 3.8b). However, yearling females appeared to maintain close association with their littermate sisters from gestation through the early post juvenile emergence period when one or both members of the pair disappeared and presumably dispersed (see Festa-Bianchet and King 1984). Sample sizes are low, but yearling sisters tended to be closer to each other than to their nearest yearling female neighbour (Table 3.9a) or their mother (Table 3.9b). In addition, yearling females tended to be closer to a younger non-littermate sister than to another juvenile female during the late post juvenile emergence period (Table 3.10).

Discussion

The distribution of females within this high density population of Columbian ground squirrels is best explained by philopatry. Individual females of all ages were active near their place of birth. Yearling females showed attachment to their natal site just prior to recruitment in this population (Festa-Bianchet and King 1984). Females also tended to nest near their natal site when no other female nested within 10 m. Females of all species of *Spermophilus* are likely to reside near their natal site (see Holekamp 1984 for review). Also, for those species for which the extent of sedentariness has been measured, adult females tend to remain in the same area from one year to the next (*S. columbianus*, Murie and Harris 1984; *S. tereticaudus*, Dunford 1977; *S. beldingi*, Sherman 1976; *S. richardsonii*, Michener 1979).

Michener (1983) proposed that social systems of ground-dwelling sciurids developed from the "fundamental unit" of the mother-daughter bond. However, at reproductive maturity, female *S. columbianus* did not show particular spatial proximity to their mothers or daughters. Among juvenile and yearling females, there was also a noticeable lack of association with the mother. In contrast, immature females tended to associate with a littermate sister when present.

There also was some spatial attraction to an older or younger non-littermate sister during the late post juvenile emergence period. Since adult females rarely have a littermate sister present, whereas an adult non-littermate sister is more often present (Chapter 2), it is reasonable to expect that adult non-littermate sisters would maintain spatial proximity. The presence of a non-littermate sister did appear to somewhat lessen the trend of breeding females nesting closer to non-uterine kin than to uterine kin. In terms of spatial proximity, littermate sisters were closest followed by non-littermate sisters and then mother/daughter pairs. This pattern contrasts with the relative frequency of kin pairs found in Chapter 2, where mother/daughter pairs were most prevalent followed by non-littermate sisters and then littermate sisters. It is important to note that spatial proximity does not necessarily lead to nonagonistic associations (see Chapter 4).

There is, however, potential for variation in the closeness of the association between non-littermate sisters. Mothers that nested at the same site in two consecutive years could produce non-littermate sisters who would be both attracted to the same natal site. Mothers that moved their nest site in consecutive years (see Harris and Murie 1984) could produce non-littermate sisters who would be attracted to different, although likely neighbouring, natal sites. Since dominance in female *S. columbianus* appears to be age-related (Festa-Bianchet 1982), mothers that do not move or previously established daughters probably limit a younger daughter's choice of site of residency, especially under high density conditions. At Dyson Creek, nest sites appear to be individually defended (Festa-Bianchet and Boag 1982). Females that were unable to nest within 10 m of their natal site may have been forced to nest further than 20 m away.

Nevertheless, breeding females formed loose but stable aggregations of matrilineal kin as exemplified by the non-random distribution of nest burrows of closely related females. Typically, the kin group was composed of a mother with one or two daughters that were themselves non-littermate sisters. In time, additional daughters should remain near their natal site to increase the size of the kin group. Also the group might extend with the recruitment of granddaughters or shrink in years of poor survival.

In this study, the only measurable indication of spatial attraction of breeding females for close kin over distant kin was in locations of centres of activity in the late post-juvenile emergence period. Females did not nest nearer close kin at Dyson Creek where densities have been relatively high (Festa-Bianchet and King 1984).

Related adult females of some other species within the genus *Spermophilus* share more of their home range with uterine kin than with non-uterine kin (*S. parryii*, McLean 1982; *S.*

tridecemlineatus, Vestal and McCarley 1984), are likely to have matrilineal kin as neighbours and preferentially share sleeping burrows with them (*S. tereticaudus*, Dunford 1977), and are more likely to be found simultaneously closer to uterine kin than non-uterine kin (*S. richardsonii*, Michener 1979, Davis 1982). Adult females also may preferentially associate with matrilineal kin in terms of home range overlap, core area overlap or distance between centres of activity (*S. columbianus*, Harris and Murie 1984; *S. richardsonii*, Michener 1981, Davis 1982). Davis (1982) suggested that association in terms of home range and core area overlap between adult uterine kin *S. richardsonii* was greatest after juvenile emergence. Adult female kin in *S. parryii* frequently move their litters upon emergence to one major burrow system (McLean 1982) and thus may also show greater association at that time. In *S. richardsonii*, *S. tridecemlineatus* and possibly *S. tereticaudus*, juveniles preferentially associated with siblings rather than non-siblings (Davis 1982, Michener 1981; Vestal and McCarley 1984; Dunford 1977). In the former two species, juvenile females also showed more spatial attraction to the mother than to another adult female (Michener 1981, Vestal and McCarley 1984) but the strength of the attraction to a sister was not directly compared to that to the mother.

Some studies have shown that females nest closer to uterine kin than to non-uterine kin (Harris and Murie 1984, McLean 1982) while others indicate that females use nest burrows equidistant from all levels of adult female kin (*S. beldingi*, Sherman 1981). However, where females are nesting nearer close kin, densities are relatively low and females appear to evenly space their nests. At higher densities, any advantages to evenly distributed nests (*e.g.*, in avoiding predation, Krebs 1971) may be lost if females attempt to nest near close kin.

There was an indication that all adult females in my study (including close kin) were spacing themselves over the meadow, rather than clustering, because pairs of centres of activity were closer together than were the individuals during simultaneous scans. This same result was obtained in two different studies of *S. richardsonii* (Michener 1979, Davis 1982). Females thus avoided being in close proximity to their neighbours.

Definitions of "clusters" tend to be subjective (Kendall 1975) but statisticians agree that in two dimensions humans can pick out clusters by eye (Carmichael *et al.* 1968). Apparently, we compare the relative distance between points and search for continuous relatively densely populated regions of space surrounded by continuous relatively empty regions. Using this criterion and the lack of greater proximity to close than distant kin, related female *S. columbianus* did not form clusters (see Figs. 3.2 and 3.3). The grouping of breeding relatives does have internal homogeneity, which is the only criterion sometimes used by Everitt (1980) to describe a cluster. However, I prefer to describe the distribution of breeding female kin as an aggregation rather than a cluster.

Although I found no strong spatial attraction toward close kin rather than distant kin, breeding female Columbian ground squirrels were highly philopatric and tended to nest near their natal site. No other study of use of space by females within the genus *Spermophilus* has attempted to compare the attraction of matrilineal relatives to the attraction of the natal area. The difficulty lies in the fact that matrilineal relatives also reside near the natal burrow so the basis for association between relatives is difficult to discern. At intermediate densities, female ground squirrels can recruit near their place of birth and preferentially share space with kin. Such occurs in *S. columbianus* where densities were less than 10 adult females/ ha (Harris and Murie 1984). At high densities, space should become limited and females will not always be able to recruit near their natal site. The outcome would be related females not preferentially sharing space. This occurred in my study where densities were 18-21 adult females/ ha. Thus the attraction of females to natal areas, which occurs across the genus, may lie in essential resources they contain rather than the presence of matrilineal relatives. Thus, the use of aggregation, a term not implying elements of social cohesion, is more apprrpriate than the term cluster to describe the dispersion of female relatives.

Although ground squirrels have been named for their habit of burrowing, the relation of burrow systems to their social organization has received little attention (J.A. King 1984). Burrows have prime importance to all ground squirrels for raising altricial young, protection from predators, refuge from adverse weather, and in most cases, for hibernation. Also, even in the most social of ground-dwelling sciurids (*Cynomys ludovicianus*, Michener 1983), females raise their young in separate burrows that are defended from all conspecifics (J.A. King 1955). Burrow systems are likely valuable resources worth maintaining, protecting and inheriting (J.A. King 1984).

Among some primate societies, which tend to be more free-ranging than spermophiles, related females form cooperative groups (*e.g.*, Kurland 1977). Food is considered to be the resource controlling the distibution of females (Wrangham 1982). When preferred food sources are defensible and patchily distributed, as in fruit groves, females band together to defend feeding grounds from competing groups. Wrangham argued that the disadvantage to remaining near relatives who directly compete for resources is offset by the advantage gained in defense of the family's feeding grounds against other matrilineages. Groups of related females occur in red deer (*Cervus elaphus*) and females also appear to compete primarily for food (Clutton-Brock *et al.* 1982). These authors hypothesized that females associate with relatives to reduce direct interference while feeding. Again, residents appeared to exclude members of other matrilineal groups from certain resources within their range.

Applied to ground squirrels, then, I suggest that although females are competing individually for resources such as burrows and perhaps food (Dobson 1984), they should tolerate relatives in close proximity if relatives thereby gain access to certain resources unavailable to non-relatives. Perhaps females with close relatives as neighbours can spend more time feeding and less time alert. That appears likely in *S. richardsonii* (Davis 1982). Perhaps females cooperatively defend burrow systems from other family groups. Such may occur in *S. beldingi* (Sherman 1981). Or perhaps females recruit into the population near their place of birth simply because their mothers and sisters (if present) tolerate them whereas distant relatives would be more aggressive. In both the primate and the red deer situations, there appeared to be a cost, albeit minor, to associating with relatives in terms of local competition. This aspect of nepotism in *Spermophilus spp.* has been neglected but one would expect the same to hold true for ground squirrels. Further study is warranted on the behaviour of female *S. columbianus* to determine the advantages and disadvantages in terms of reproductive success to females living in loose aggregations of matrilineal kin.

Table 3.1. Known pairs of mothers and daughters, littermate sisters and non-littermate sisters for Columbian ground squirrels at Dyson Creek, 1981 and 1982.

Type of relative	Age-class combination	n pairs 1981	n pairs 1982
Mother/ daughter	Adult/ adult	5	4(3)[1]
	Adult/ non-breeding yearling	10	6
	Adult/ juvenile	17	21
Littermate sister	Adult	0	0(1)
	Non-breeding yearling	2	1
	Juvenile	14	15
Non-littermate sister	Adult/ adult	0	1(2)
	Adult/ non-breeding yearling	5	3
	Adult/ juvenile	8	6
	Non-breeding yearling/ juvenile	14	13

[1] additional pairs of breeding relatives resulting from breeding yearlings in parentheses

Table 3.2. Mean distances (m) from natal site to centres of activity of females, 1981 and 1982 combined. Range given is for all periods combined. PJE1 = Early Post Juvenile Emergence; PJE2 = Late Post Juvenile Emergence.

		Time Period				
Age	Range	Breeding	Gestation	Lactation	PJE1	PJE2
Juvenile	2-66				17.1 (25)[1]	25.6 (22)
Yearling[2]	3-57	23.4 (12)	20.8 (13)	21.0 (13)	26.8 (13)	22.3 (7)
Two	3-45	16.0 (6)	11.6 (7)	23.9 (7)	23.8 (7)	24.0 (5)
Three	9-33	18.5 (4)	20.6 (4)	23.4 (4)	15.5 (4)	18.5 (4)

[1] mean (n); [2] non-breeding yearling females only

Table 3.3. Mean distances (m) between centres of activity of mature females by time period, 1981 and 1982 combined. Analysis includes three breeding yearlings from the breeding period through the early post juvenile emergence period and only one yearling for the late post juvenile emergence period. UK = uterine kin, in this case, mother, daughter, or littermate sister; SK = specified kin, in this case, mother, daughter, littermate or non-littermate sister; NUK = non-uterine kin; NSK = non-specified kin; PJE1 = Early Post Juvenile Emergence; PJE2 = Late Post Juvenile Emergence.

a.

Period	n pairs	Nearest UK	Nearest NUK	*P* Value
Breeding	15	10.2 ± 1.1	10.8 ± 2.3	0.91
Gestation	13	15.5 ± 1.8	15.0 ± 2.1	0.60
Lactation	16	16.2 ± 1.7	13.3 ± 1.8	0.22
PJE1	12	13.3 ± 2.7	14.4 ± 1.6	0.58
PJE2	9	9.7 ± 3.2	14.7 ± 1.4	0.07

b.

Period	n pairs	Nearest SK	Nearest NSK	*P* Value
Breeding	6	7.7 ± 1.9	6.6 ± 1.4	0.92
Gestation	6	16.0 ± 2.6	15.4 ± 3.1	0.75
Lactation	4	15.0 ± 3.5	15.8 ± 5.5	--
PJE1	8	15.0 ± 3.0	13.9 ± 1.8	0.78
PJE2	3	5.0 ± 3.4	11.6 ± 0.9	--

Table 3.4. Percent area overlap of 50% usage core area of mature females, 1981 and 1982 combined. Symbols and number of breeding yearlings as in Table 3.2.

a.

Period	n pairs	Nearest UK	Nearest NUK	*P* Value
Breeding	14	41.2 ± 7.3	45.4 ± 10.0	0.92
Gestation	12	24.0 ± 9.0	21.7 ± 10.0	0.68
Lactation	15	26.2 ± 8.3	24.1 ± 7.9	0.83
PJE1	12	30.3 ± 8.1	15.4 ± 5.9	0.21
PJE2	9	36.9 ± 12.2	29.4 ± 10.4	0.40

b.

Period	n pairs	Nearest SK	Nearest NSK	*P* Value
Breeding	9	58.7 ± 9.5	39.2 ± 12.8	0.11
Gestation	10	32.2 ± 12.5	13.9 ± 8.5	0.18
Lactation	8	26.6 ± 9.9	12.9 ± 12.4	0.24
PJE1	7	27.7 ± 10.5	11.6 ± 7.5	0.31
PJE2	5	36.8 ± 17.8	10.4 ± 6.6	--

Table 3.5. Percent of points within overlap area of 50% usage core areas of mature females, 1981 and 1982 combined. Symbols and numbers of yearlings as in Table 3.2.

a.

Period	n pairs	Nearest UK	Nearest NUK	*P* Value
Breeding	14	47.7 ± 6.8	49.8 ± 9.1	0.98
Gestation	12	27.4 ± 8.8	26.8 ± 10.2	0.89
Lactation	16	20.8 ± 6.8	23.9 ± 7.1	0.71
PJE1	12	38.8 ± 9.0	20.4 ± 7.0	0.18
PJE2	9	33.5 ± 10.1	24.3 ± 9.0	0.16

b.

Period	n pairs	Nearest SK	Nearest NSK	*P* Value
Breeding	8	59.9 ± 9.8	36.8 ± 12.8	0.16
Gestation	10	35.5 ± 12.3	16.1 ± 8.9	0.25
Lactation	8	20.3 ± 6.8	12.5 ± 12.2	0.24
PJE1	7	40.0 ± 10.4	13.2 ± 10.3	0.18
PJE2	5	29.3 ± 15.4	7.7 ± 5.3	--

Table 3.6. Mean distances (m) between centres of activity of juvenile females and

a. their mother (UK) compared to another adult female (NUK)

b. their mother or adult non-littermate sister (SK) compared to another adult female (NSK)

c. a non-breeding yearling female non-littermate sister (SK) compared to another non-breeding yearling female (NSK).

Time period symbols as in Table 3.2. UK = uterine kin; NUK = non-uterine kin; SK = specified kin; NSK = non-specified kin.

a.

		Adult female		
Period	n pairs	Nearest UK	Nearest NUK	*P* Value
PJE1	24	12.8 ± 1.7	13.0 ± 1.0	0.91
PJE2	20	12.0 ± 1.8	8.5 ± 1.1	0.04

b.

		Adult female		
Period	n pairs	Nearest SK	Nearest NSK	*P* Value
PJE1	15	11.6 ± 2.2	14.8 ± 1.1	0.28
PJE2	7	10.9 ± 4.3	10.8 ± 1.6	1.00

c.

		Non-breeding yearling female		
Period	n pairs	Nearest SK	Nearest NSK	*P* Value
PJE1	15	16.9 ± 2.0	20.2 ± 2.6	0.21
PJE2	10	10.7 ± 2.4	14.5 ± 2.0	0.07

Table 3.7. Mean distances (m) between centres of activity of juvenile females and
a. a littermate sister (UK) compared to another juvenile female (NUK)
b. a littermate sister (UK) compared to a non-breeding yearling non-littermate sister (SK)
c. a littermate sister (juvenile UK) compared to their mother (adult UK).
Time period symbols as in Table 3.2. UK = uterine kin; NUK = non-uterine kin; SK = specified kin; NSK = non-specified kin.

a.

Period	n pairs	Juvenile female		*P* Value
		Nearest UK	Nearest NUK	
PJE1	21	3.9 ± 0.4	17.4 ± 3.3	0.001
PJE2	13	9.1 ± 1.7	11.4 ± 1.9	0.05

b.

Period	n pairs	Juvenile female Nearest UK	Non-breeding yearling female Nearest SK	*P* Value
PJE1	13	4.3 ± 0.7	16.8 ± 1.9	0.002
PJE2	8	9.1 ± 2.0	12.8 ± 2.4	0.21

c.

Period	n pairs	Juvenile female Nearest UK	Adult female Nearest UK	*P* Value
PJE1	21	3.9 ± 0.4	13.6 ± 1.8	0.001
PJE2	13	9.1 ± 1.7	14.5 ± 2.4	0.05

Table 3.8. Mean distances (m) between centres of activity of non-breeding yearling females and

a. their mother (UK) compared to another adult female (NUK)

b. their mother or adult non-littermate sister (SK) compared to another adult female (NSK).

Time period symbols as in Table 3.2. UK = uterine kin; NUK = non-uterine kin; SK = specified kin; NSK = non-specified kin.

a.

Period	n pairs	Adult female		*P* Value
		Nearest UK	Nearest NUK	
Breeding	11	13.0 ± 2.4	8.2 ± 1.4	0.09
Gestation	13	16.4 ± 2.8	12.4 ± 1.4	0.42
Lactation	13	14.8 ± 1.8	7.1 ± 0.8	0.009
PJE1	12	17.2 ± 2.7	9.9 ± 1.0	0.03
PJE2	6	6.9 ± 1.4	5.9 ± 1.2	0.60

b.

Period	n pairs	Adult female		*P* Value
		Nearest SK	Nearest NSK	
Breeding	7	15.0 ± 3.5	10.0 ± 1.1	0.40
Gestation	7	17.5 ± 4.5	11.2 ± 2.2	0.50
Lactation	7	13.5 ± 2.7	9.7 ± 2.0	0.31
PJE1	9	17.1 ± 3.2	13.6 ± 2.2	0.37
PJE2	4	7.9 ± 1.9	10.0 ± 2.9	--

Table 3.9. Mean distances (m) between centres of activity of non-breeding yearling females and

a. a non-breeding littermate sister (UK) compared to another non-breeding yearling female (NUK)

b. a non-breeding littermate sister (non-breeding yearling UK) compared to their mother (adult UK).

Time period symbols as in Table 3.2. UK = uterine kin; NUK = non-uterine kin; SK = specified kin; NSK = non-specified kin.

a.

		Non-breeding yearling	
Period	n pairs	Nearest UK	Nearest NUK
Breeding	4	7.0 ± 2.8	7.6 ± 1.1
Gestation	4	4.2 ± 0.4	22.3 ± 0.4
Lactation	4	3.9 ± 0.6	18.6 ± 4.2
PJE1	4	3.2 ± 0.2	10.6 ± 0.8
PJE2	0	--	--

b.

Period	n pairs	Non-breeding yearling female Nearest UK	Adult female Nearest UK
Breeding	4	7.0 ± 2.8	12.1 ± 3.6
Gestation	4	4.2 ± 0.4	13.6 ± 2.8
Lactation	4	3.9 ± 0.6	17.9 ± 2.1
PJE1	4	3.2 ± 0.2	16.3 ± 5.1
PJE2	0	--	--

Table 3.10. Mean distances (m) between centres of activity of non-breeding yearling females and a juvenile non-littermate sister (SK) compared to another juvenile female (NSK). Time period symbols as in Table 3.2. SK = specified kin; NSK = non-specified kin.

Period	n pairs	Juvenile female		*P* Value
		Nearest SK	Nearest NSK	
PJE1	8	14.6 ± 2.8	14.9 ± 2.4	0.78
PJE2	5	5.1 ± 1.4	10.3 ± 1.2	--

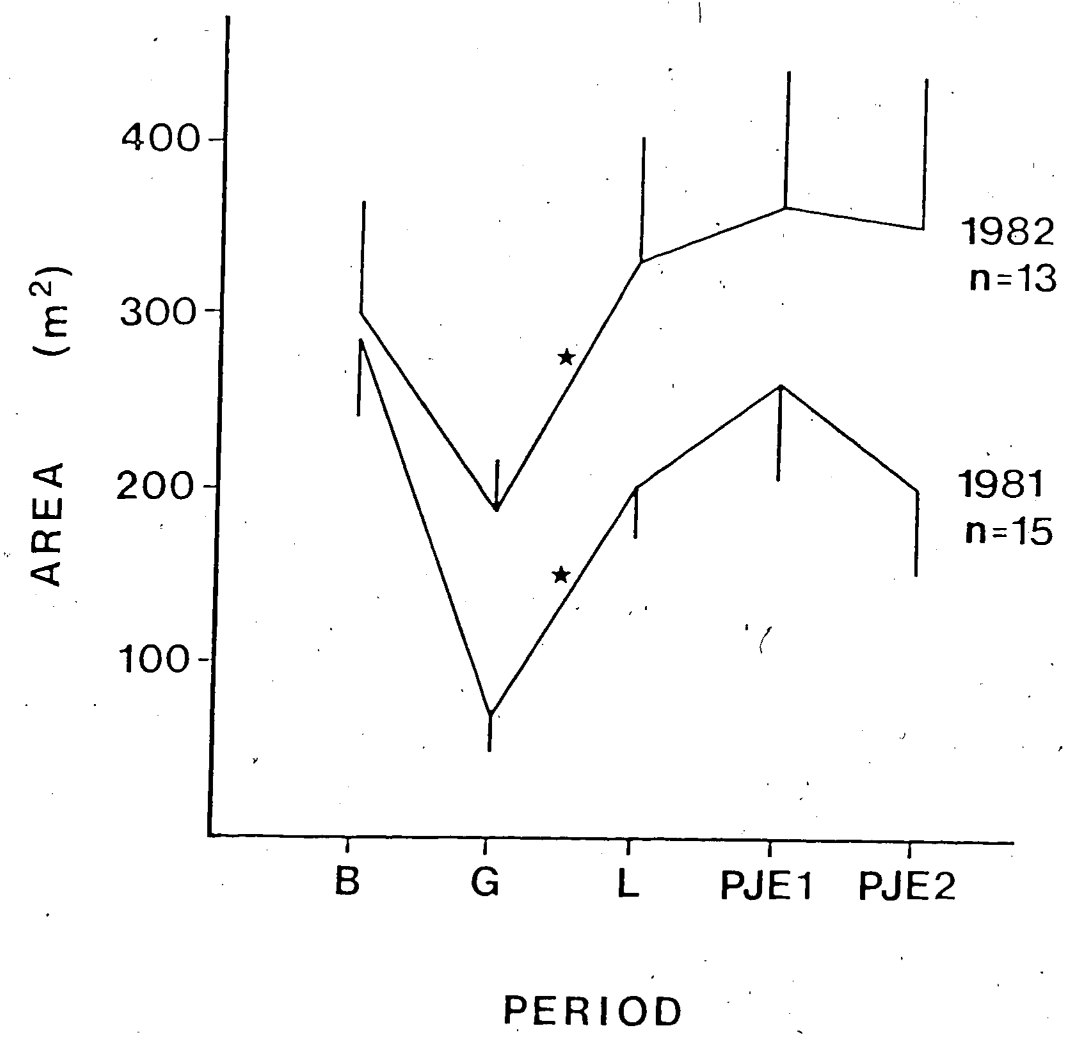

Figure 3.1. Mean size of 50% usage areas for adult females. Vertical lines indicate 1 S.E.. There were no significant differences between years in core area size for any period (Wilcoxon signed rank test for same individuals, $P > 0.1$). Stars indicate significant changes in core area size from one period to the next (Wilcoxon signed rank test for same individual, $P < 0.05$). B = Breeding; G = Gestation; L = Lactation; PJE1 = Early Post Juvenile Emergence; PJE2 = Late Post Juvenile Emergence

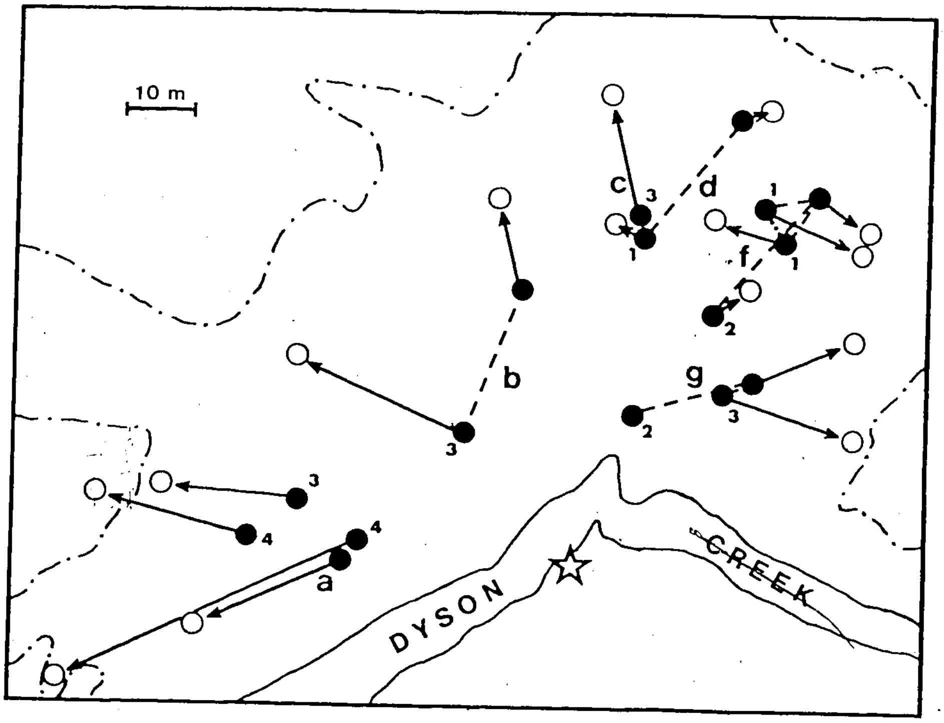

Figure 3.2. Map showing centres of activity (closed circles) and nest burrows (open circles) of breeding females at Dyson Creek during lactation, 1982. Arrows indicate ownership of burrows, dashed lines indicate known mother- daughter relationships and dotted line indicates known littermate sister pair. Dash dot line indicates approximate forest boundary. Star is at location of observation stand. Letters indicate known matrilines or a female resulting from a matriline of the previous year. Numbers indicate age of female if known; 1 = breeding yearling.

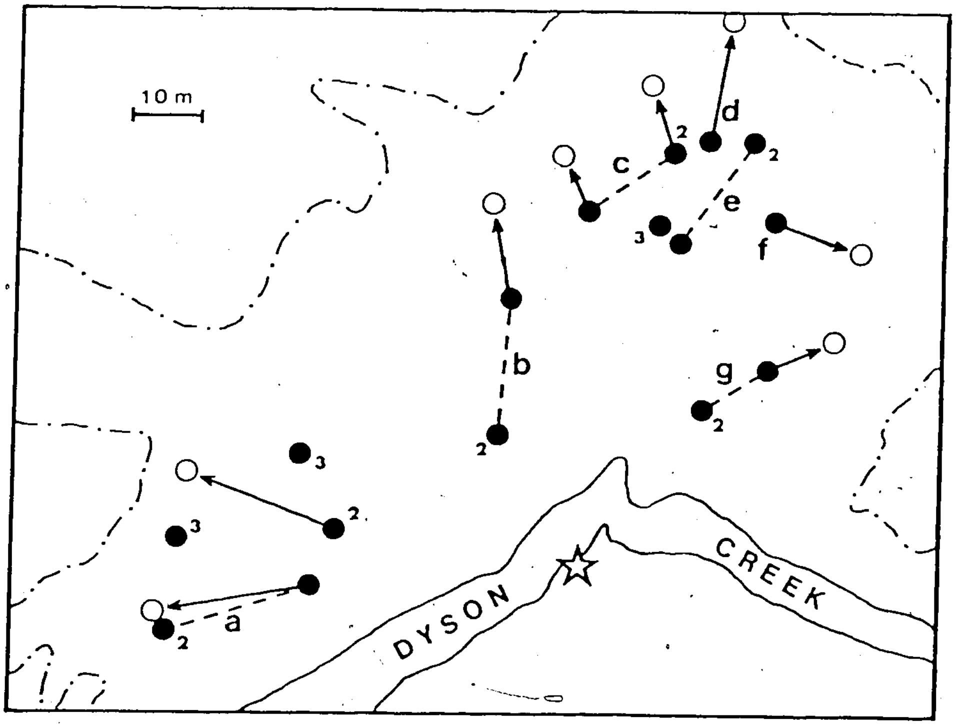

Figure 3.3. Map showing centres of activity and nest burrows of adult females at Dyson Creek during lactation, 1981. Symbols as in Figure 3.2. Letters indicate known matrilines or females that founded matrilines the following year.

4. Kin-differential Behaviour of Female Columbian Ground Squirrels

4.1 Introduction

A body of evidence is steadily accumulating that is consistent with Hamilton's (1964) hypothesis of "kin selection" (Maynard Smith 1964). According to this hypothesis, an individual in a social situation will behave in such a way as to "value his neighbour's fitness against his own according to the coefficients of relationship appropriate to that situation" (Hamilton 1964:19). Studies have indicated that individuals exhibit kin-differential behaviour when ecological circumstances favour sociality and cooperation (*e.g.*, Bertram 1976, Kurland 1977, Brown 1978). Thus patterns of asymmetrical favouritism based on closeness of genetic relationship (sometimes termed nepotism (Sherman 1980*a* and 1980*b*)) may be predicted from considerations of shared genes and "inclusive fitness" (West Eberhard 1975). Animals should be particularly inclined to favour relatives when cooperation is advantageous and imposes costs on other group members (Wrangham 1982).

Within the semi-fossorial sciurids, sociality ranges from solitary in the woodchuck (*Marmota monax*) to colonies of several "harems" in Olympic marmots (*Marmota olympus*) and black-tailed prairie dogs (*Cynomys ludovicianus*) (Armitage 1981, Michener 1983). In most social species, there is differential dispersal of the sexes and the sex ratio of the breeding population is biased in favour of females. The basic social unit thus consists of a group of females, often a mother and her adult female offspring, accompanied by one or more males (Michener 1983).

Kin-differential behaviour has been investigated in a variety of social ground squirrels and has been documented for adult females in Richardson's ground squirrels (*Spermophilus richardsonii*, Yeaton 1972, Davis 1982), round-tailed ground squirrels (*Spermophilus tereticaudus*, Dunford 1977), Belding's ground squirrels (*Spermophilus beldingi*, Sherman 1980*b* and 1981) and Arctic ground squirrels (*Spermophilus parryii*, McLean 1982). The social system of the Columbian ground squirrel (*Spermophilus columbianus*) has been likened to that of *S.*

parryii, since males are territorial and females usually outnumber males in the breeding population (Armitage 1981, Michener 1983). Adult female kin have been found to overlap in both time (Chapter 2) and space (Chapter 3) and thus have the opportunity to exhibit nepotism.

Here I present data on the effects of matrilineal kinship on the behaviour of female Columbian ground squirrels. The pattern of temporal overlap of adult female kin is such that I predict favouritism between mothers and daughters and between non-littermate sisters (see Chapter 2). The pattern of spatial distribution of adult female kin is such that females occur in kin groups with their mothers, daughters, non-littermate sisters and sometimes littermate sisters (see Chapter 3). I expect kin-differential behaviour to occur between mother/ daughter and littermate sister pairs involving immature squirrels as found for other ground squirrel species (*e.g., S. richardsonii*, Michener 1981). In addition, I investigate the effect that any kin-differential behaviour found may have on the participants by comparing activity budgets, survival rates and reproductive success of those individuals associated in kin aggregations to those individuals without close kin.

4.2 Materials and Methods

4.2.1 Study Area

Columbian ground squirrels were observed at Dyson Creek (50° 37' N, 114° 39' W, elevation 1570 m), approximately 32 km west of Turner Valley, Alberta. Most of the squirrels inhabited a 0.76 ha isolated meadow surrounded by mixedwood forest and bounded to the south by Dyson Creek. A smaller meadow to the south of the creek was frequented by a few squirrels and it was monitored but not observed intensively. Festa-Bianchet (1981) provides details of the study area. The procedures I used for collecting behavioural data are presented in Chapter 3.

4.2.2 Behavioural Analysis

For analysis of social behaviours, encounters were classified as agonistic or nonagonistic. Agonistic encounters include fights, chases and threats. I observed only the final stages of 4% of the 530 agonistic encounters among females; I was unable to classify them as above, but included them when comparing percentages of agonistic encounters. Fights involved squirrels scratching and biting each other, usually while tumbling over each other in one spot. Chases were less intense and involved one squirrel chasing and the other fleeing; brief contact between the squirrels may or may not have occurred. Threats began like chases but in a threat, the "chaser" did not run beyond the initial location of the "chasee". Thus a threat was a shorter and less intense interaction. Reverse chases were counted as two encounters, regardless of the number of consecutive reversals, and interactions involving both chasing and fighting were counted as both. Nonagonistic encounters include carrying on amicable activities within 0.5 m of another squirrel without contact (such as feeding or sitting) and also those involving contact (playing, naso-oral contact, and oro-genital contact) or at least some sort of response (approach, following and lateral displays with no further escalation) (for descriptions see Steiner 1970). Nonagonistic encounters involving contact or response are referred to as "other" nonagonistic encounters. Agonistic encounters resulted in the displacement of one or both of the participants whereas non-agonistic encounters did not. Yearling females that breed behave differently from both non-breeding yearling females and adult females (Festa-Bianchet 1981) and were therefore excluded from the analysis. Uterine kin (mothers, daughters and littermate sisters), non-uterine kin, specified kin (mothers, daughters, littermate and non-littermate sisters) and non-specified kin are defined as in Chapter 3. In neither year of observation were there known adult littermate sisters at Dyson Creek, so the results for adult uterine kin are for mother/daughter pairs only (see Figs. 3.2 and 3.3 for distribution of known adult kin pairs).

For calculation of activity budgets, only first observations made of an individual during scans were used. Activities were classified into the following categories: Feeding, Resting/ Maintenance, Moving, Alert, Interacting Agonistically, Interacting Nonagonistically, Nesting and Scentmarking. "Interacting" included encounters with all other squirrels. For each period, the proportion of time spent in each category was calculated for a group of individuals by summing the observations in each category and dividing by the total number of scans per individual per period. Individuals were observed in a minimum of 25 scans to be included in this analysis. Measures of reproductive success, such as production and survival of offspring, and survival rates of adults were calculated for squirrels on both the north and south sides of Dyson Creek. Production of juveniles was measured as the mean number of juveniles a female raised to litter emergence and differed from mean litter size which included only females that had emerging litters. M. Festa-Bianchet and S.C. Lee provided data on reproduction at Dyson Creek in 1980 and 1984 respectively. L.S. Rayor provided data on survival of juveniles to yearling age in 1983.

Nonparametric statistical tests are used throughout and results with a probability value of ≤ 0.05 are considered statistically significant.

4.3 Results

4.3.1 Adult Females

Among adult females, 210 encounters were observed in each of 1981 and 1982. In 1981, 64% of these encounters could be classified as occurring between uterine or non-uterine kin. In 1982, this figure rose to 78%. Other encounters were between squirrels of unknown relationship and were excluded from analyses. Although the majority of encounters were agonistic each year, the proportion of different types of encounters differed between uterine and non-uterine kin. The total proportion of agonistic encounters was less among uterine kin (61%, n = 82) than non-uterine kin (96%, n = 215, Pearson $X^2 = 51.94$, $P = 0.001$). Agonistic encounters with non-uterine kin contained a higher proportion of chases and a lower proportion of threats than with uterine kin (Table 4.1a).

More agonistic encounters between both uterine kin (33%) and non-uterine kin (50%) took place during lactation than during other periods (Table 4.2). The few nonagonistic encounters between non-uterine kin occurred in the breeding period while those between uterine kin were more evenly spread over the season. Uterine kin differed significantly from non-uterine kin in proportion of agonistic encounters during all three periods following birth of the juveniles (Table 4.2).

Amount of core area overlap did not differ between uterine kin and non-uterine kin (Chapter 3). However, reduced agonism between uterine kin suggests that females behaved differently in overlap areas with uterine kin. Encounters between non-uterine kin were much more likely to be agonistic than nonagonistic no matter where they took place with respect to the 50% core areas of the participants (Table 4.3). In contrast, encounters between uterine kin were equally likely to be agonistic or nonagonistic except in core overlap areas where agonistic interactions were more likely. Proportionally fewer agonistic encounters were initiated between uterine kin in all areas (Table 4.3).

4.3.2 Yearling Females

The pattern of interaction of non-breeding yearling females with their mother was similar to that with other females. Overall, encounters were predominantly agonistic, with 79% agonistic (n = 81) between mothers and daughters and 85% agonistic (n = 187) for yearlings and other adult females (Pearson $X^2 = 1.46$, $P = 0.23$). However, mothers and daughters tended to have proportionally more "other" nonagonistic encounters (Table 4.4). Among yearling females, littermate sisters had no agonistic encounters (n = 22) which differed (Yates' $X^2 = 16.12$, $P = 0.001$) from more distantly related yearlings for which 57% of the encounters were agonistic (n = 32). The non-agonistic encounters of uterine kin were more often of the "other" type, in particular, play encounters (Table 4.5b). The behaviour of yearling females with their littermate sisters was quite different from that with their mothers. The encounters between mothers and daughters were proportionally much more agonistic (79% compared to 0%, Yates' $X^2 = 42.61$, $P = 0.001$). Yearling females interacted with chases and threats with their mothers (Table 4.4) but with similar proportions of nonagonistic encounters as with littermate sisters, except possibly more play with sisters (Table 4.5).

4.3.3 Juvenile Females

Juvenile females had proportionally fewer agonistic encounters with their mother (12%, n = 33) than with another adult female (69%, n = 26, Yates' $X^2 = 17.91$, $P = 0.001$). However, among both agonistic and nonagonistic encounters, different behaviours occurred in similar proportions (Table 4.6). Among juvenile females, there was no significant difference in the proportion of agonistic encounters with sisters (0%, n = 24) compared to non-sisters (6%, n = 17, Fisher Exact Test, $P = 0.41$). Proportions of nonagonistic encounters did not differ (Table 4.7) except that littermate sisters tended to play more. Although the overall proportion of agonistic encounters between juveniles and their mothers (12%) was not different from with their littermate sisters (0%, Fisher Exact Test, $P = 0.13$), littermate sisters had proportionally more "other" nonagonistic encounters, in particular play (Table 4.7).

4.3.4 Non-littermate Sisters

Sample sizes for encounters involving non-littermate sisters were generally small (<10) and thus were not usually classified beyond agonistic and non-agonistic categories. "Non-specified kin" refers to females that are not mothers, daughters, littermate or non-littermate sisters (see Chapter 3). All four encounters observed among adult non-littermate sisters were agonistic. That result did not differ from 63% agonistic encounters for adult mothers and daughters (Fisher Exact Test, $P = 0.29$) or from 97% agonistic (n = 30) for adult non-specified kin (Fisher Exact Test, $P = 1.00$). Yearling females showed no more agonistic behaviour with an adult non-littermate sister (67% agonistic, n = 33) than with the mother (79% agonistic, Yates' $X^2 = 1.32$, $P = 0.25$) but had proportionally fewer agonistic encounters with an adult non-littermate sister (67%) than with adult non-specified kin (89%, n

= 154, Fisher Exact Test, $P = 0.003$). The proportions of different agonistic and nonagonistic encounters were similar for yearling and adult non-littermate sisters, for yearling females with their mothers and for yearling females with other adult females with the exception that there was no play observed for non-specified kin (Table 4.8). Juvenile females, however, had proportionally more agonistic encounters with an adult non-littermate sister (75% agonistic, n = 8) than with the mother (12% agonistic, Fisher Exact Test, $P = 0.001$). There was no difference in proportion of agonistic encounters of juveniles with an adult non-littermate sister (75%) and with adult non-specified kin (67%, n = 18, Fisher Exact Test, $P = 1.00$).

Neither yearling nor juvenile females had any agonistic encounters with littermate sisters which differed significantly from 67% agonistic encounters (n = 9) between yearling and juvenile non-littermate sisters (Fisher Exact Test, $P = 0.001$ for both). The 67% agonistic encounters between yearling and juvenile non-littermate sisters did not differ significantly from 100% agonistic encounters (n = 3) between other yearlings and juveniles (Fisher Exact Test, $P = 0.51$).

4.3.5 Effects of Kin-differential Behaviour

Adult females with their mother or daughter (*i.e.*, uterine kin) breeding on the same side of the creek apportioned their time like adult females without uterine kin (Table 4.9). Both groups spent the majority of time feeding in all periods. Those with uterine kin spent proportionally less time interacting agonistically (Fisher Exact Test, $P = 0.05$) and more time feeding (Pearson $X^2 = 7.06$, $P = 0.008$) in the late post juvenile emergence period. These two differences may not be meaningful, since among the 40 comparisons 5% (= 2) are expected to differ significantly due to random error.

The behaviour of females with and without kin including non-littermate sisters (*i.e.* specified kin) could not be compared because only one female without specified kin resided on the north side of Dyson Creek in either 1981 or 1982.

Survival rates of adult females at Dyson Creek (measured as persistence within the population) have been high (83%, see Chapter 2). The presence of breeding uterine kin neighbours did not affect survival rates measured over three years. Of nine adult females without uterine kin, 78% survived to the following season. Of 22 adult females with uterine kin, 77% survived (Fisher Exact Test, $P = 1.00$). However, only one of three females (33%) without specified kin survived.

Yearling females had smaller litters than did adult females over two seasons combined (2.71 juveniles, n = 7, compared to 3.74 juveniles, n = 27, Mann-Whitney $U = 39.00$, $P = 0.01$). For this reason, I calculated reproductive success for adult females only. The presence of breeding uterine kin did not significantly improve overall reproductive success (Table 4.10). Nor was there a difference in survival of juveniles to yearling age born to females with breeding uterine kin compared to those born to females without breeding uterine kin. However, litter size of females with specified kin was greater than that of females without specified kin (Table 4.10).

In conclusion, there were no measurable advantages or disadvantages to females having their mother or adult daughter present. However, females without their mother, adult daughter, adult littermate or non-littermate sister may have been at a disadvantage because of reduced survival and smaller litters.

4.4 Discussion

The effect of matrilineal kinship on the behaviour of female Columbian ground squirrels was to increase the proportion of nonagonistic encounters between mothers and daughters and among littermate sisters. There was some suggestion of differential treatment of non-littermate sisters compared to more distant relatives, but sample sizes were too small to be conclusive. Littermate sisters maintained the least agonistic associations although I was unable to determine their behaviour as adults owing to the absence of known pairs. Mothers were generally less agonistic towards their daughters than daughters of other females, although agonism towards yearling daughters was high. Juvenile and yearling littermate sisters had proportionally more nonagonistic encounters, such as play, with each other than with their mothers and proportionally fewer agonistic encounters than with non-littermate sisters. Only for juveniles were encounters with the mother proportionally less agonistic than with adult non-littermate sisters.

Among juvenile and yearling siblings, the high proportion of play encounters and lack of agonism probably functions to maintain amicable ties and spatial attraction among littermates. In the somewhat uncommon event of co-occurrence of adult littermate sisters (see Chapter 2), this close association may extend into adulthood. Close relationships between animals of similar ages that are formed early in life may persist (Hunter and Davies 1963). However, competition for nest burrows between littermate sisters is a distinct and interesting possibility and requires further research (see Chapter 3).

For mothers and daughters of all ages, the nonagonistic encounters in which they participated were rarely the active play of siblings. Their nonagonistic encounters consisted mostly of individuals feeding, sitting, carrying on nest activities or grooming within 50 cm without contact with or observable reaction to the other squirrel. Allogrooming made up only 2% of 201 nonagonistic encounters among female squirrels; one of 81 encounters between adult females and their yearling daughters, one of 33 between adult females and a yearling non-littermate sister and two of 22 among yearling littermate sisters. Thus the higher proportion of nonagonistic encounters between mothers and daughters probably does not function to maintain an amicable bond but rather indicates a passive tolerance within close proximity that could result in a loose spatial association. Mothers were not often observed within 50 cm of yearling daughters, but rather most nonagonistic encounters involved some sort of interaction with them. Adult females appear to influence the dispersion of yearlings through aggression (Festa-Bianchet and King 1984), and the high agonism toward yearling daughters indicates that adult females may also cause their own yearling daughters to avoid them. During lactation and the early post juvenile emergence period, yearling females used areas away from their mothers (Chapter 3).

Non-littermate sisters of all ages had mostly agonistic encounters. Encounters of yearling and adult non-littermate sisters were proportionally less agonistic than those of less closely related yearlings and adults. Adult non-littermate sisters co-occur frequently (Chapter 2) and perhaps their relationship is less agonistic than that of less closely related adult females as an extension of yearling/ adult relationships.

In general, juveniles in other species of ground squirrels have been found to treat siblings preferentially to non-siblings (*S. richardsonii*, Yeaton 1972, Michener 1981; *S. tereticaudus*, Dunford 1977) with more play and less chasing among siblings (Dunford 1977; Michener 1981). Encounters of mothers with their own juveniles were less agonistic than those with other juveniles (*S. richardsonii*, Yeaton 1972, Michener 1973, 1981; *S. tereticaudus*, Dunford 1977). Mothers and offspring were found to have more oral-nasal or oral-genital contact (Michener 1973; Dunford 1977), fewer chases (Dunford 1977; Michener 1981) and to terminate fewer encounters with displacement (Michener 1973; Dunford 1977). Among adult females, uterine kin had generally hostile relationships yet they were less agonistic than those between non-uterine kin (*S. richardsonii*, Yeaton 1972, Davis 1982; *S. tereticaudus*, Dunford 1977; *S. beldingi*, Sherman 1980*b* and 1981; *S. parryii*, McLean 1982). In particular, uterine kin had fewer fights (Yeaton 1972; Dunford 1977; Sherman 1981), more oral-nasal contact (Dunford 1977) fewer chases and more "cooperation" in territorial defense (Sherman 1981), possibly more allogrooming (McLean 1982) and fewer encounters resulting in displacement (Dunford 1977; Davis 1982).

Apart from a lack of "cooperation" in territorial defense and no difference in proportion of fights among adult uterine kin, my results for *S. columbianus* agree closely with those for other ground squirrels. Cohesive encounters among littermates and tolerance between mothers and daughters appear to be typical. Although Sherman (1981) contended that adult uterine kin "cooperate" in territorial defense, his analysis lacked specific information on locations of territories and all female relatives appeared to chase each other as or more often than they "cooperatively" chased a third squirrel (1981, comparing Fig. 2b to Figs. 3a and b).

Several patterns emerge when spatial relationships between related female Columbian ground squirrels (Chapter 3) are compared to their behavioural relationships. Certain relatives grouped together and showed amicable behaviour. Non-breeding littermate sisters showed a highly consistent close spatial association and absolutely no agonism. Other relatives less closely associated in space were frequently nonagonistic in their interactions. Daughters showed no spatial attraction to the mother and sometimes were closer to another female, possibly a non-littermate sister, yet mothers and daughters always showed differential behaviour. Still other relatives that appeared to associate in space showed no preferential behaviour. Although there may have been spatial attraction to an adult non-littermate sister over the mother, non-littermate sisters were not less agonistic, and in fact, juveniles had proportionally more agonistic encounters with an adult non-littermate sister than with the mother. Thus spatial associations were not simply correlated with behavioural associations.

I propose that the pattern of kin-differential behaviour in this species may be explained through the influence of familiarity gained in early relationships. Bekoff (1981) stressed the importance of familiarity in social relationships. Familiarity among littermates and between females and their mother is most likely established through early contact in the nest burrow (Holmes and Sherman 1982). Since adult females leave the nest burrow periodically to feed above ground, there is more opportunity for contact with littermates than with the mother. Juveniles remain in the nest burrow until weaning and thus have no opportunity to interact with non-littermate sisters until they emerge. Adult females appear to defend nest burrows from all other squirrels (Festa-Bianchet and Boag 1982) further reducing the frequency of contact with non-littermate sisters. I observed few encounters between juveniles and their yearling or adult non-littermate sisters, suggesting that juveniles have little opportunity to become familiar with these relatives. Yearling females did interact more extensively with adult non-littermate sisters and their encounters resembled those with mothers, being less agonistic than with other adult females. If relationships developed while females are immature extend into adulthood, then adult females should demonstrate cohesive relationships with littermate sisters and be tolerant to mothers, daughters and non-littermate sisters. My results indicate the tolerance between mothers and daughters but I have insufficient data to assess the other two relationships. Due to the demographic characteristics of *S. columbianus*, adult non-littermate sisters should be more prevalent than adult littermate sisters although that should not discount the possible cohesion developed through familiarity among littermates. Future research on the behaviour of adult littermate and non-littermate sisters should discriminate the relative importance of familiarity and likelihood of co-occurrence in determining the degree of nepotism.

At Dyson Creek, there was no measurable advantage apparent from analyses of activity budgets, survival rates or reproductive success for adult females to have uterine kin present. Time spent alert and defending a territory may be influenced more by the number and density of neighbours rather than their relationship. A female with five neighbours, two of which are uterine kin, would likely spend more time in territorial defense than a female with two distantly related neighbours. Therefore, at high density such as at Dyson Creek (Festa-Bianchet and King 1984), there was little difference in rates of agonistic interactions and time spent alert or feeding for females with and without uterine kin. In a study of *S. richardsonii*, Davis (1982) artificially reduced the density of adult females such that females did or did not have uterine kin neighbours. At the lowered density, females with kin as neighbours tended to spend less time alert and more time feeding during gestation and lactation than females without kin as neighbours. Females with uterine kin may experience greater reproductive success if followed throughout their lifetime. I found that adult females without specified kin appeared to experience poorer survival and have smaller litters.

Earlier, I suggested that female ground squirrels compete individually for resources, such as burrow systems, and that females should tolerate relatives in close proximity if relatives gain access to certain resources unavailable to non-relatives (Chapter 3). Adult female Columbian ground squirrels remain near their place of birth, associate in loose kin aggregations (Chapter 3) and maintain individual territories. Within these kin groups, females tolerate mothers and daughters, chasing each other less than other neighbouring adults and carrying on activities within proximity without observable interaction. There was no evidence of females cooperating in territorial defense against a third squirrel but females in kin groups appear to direct aggression more towards other females than each other. Female kin groups may thereby monopolize burrow systems.

Females without close adult kin may be at a particular disadvantage when trying to establish residency as a two-year old at Dyson Creek. Older females appear to dominate younger females (Festa-Bianchet 1982) and when a female's mother disappeared, another older female sometimes moved into the vacant area and the daughter moved away from her natal area (see Chapter 3). Thus females without close kin may be unable to attach themselves to an established kin group and presumably enjoy the benefits of previously successful burrows. This disadvantage would occur also for immigrants. At Dyson Creek, no female has successfully immigrated in six years (Festa-Bianchet and King 1984, L.S. Rayor and S.C. Lee pers. comm.). At lower densities, females appear to regularly relinquish nest sites to their recruiting daughters (Harris and Murie 1984) and successful female immigration occurs (Murie and Harris 1984).

If the advantage to female ground squirrels remaining near relatives is access to burrow systems, then the disadvantage would be local competition and sharing of those burrows. Such may be the case in *S. columbianus*. Although female kin did not share above ground space more than did non-kin, they may have shared burrow systems. Very little is known about use of burrow systems for any ground squirrels (J.A. King 1984), mainly because of difficulty of below ground observations. Yet related females in several species do share space (*S. richardsonii*, Michener 1979, Davis 1982; *S. tereticaudus*, Dunford 1977; *S. parryii*, McLean 1982; *S. tridecemlineatus*, Vestal and McCarley 1984). Perhaps at high densities the costs of associating with relatives increase so that large matrilineal groups have lower reproductive success than smaller ones. Such occurs in black-tailed prairie dogs, *Cynomys ludovicianus*, (Hoogland 1981) and red deer, *Cervus elaphus*, (Clutton-Brock *et al.* 1982).

In conclusion, nepotism in adult female Columbian ground squirrels appears to take the form of tolerance rather than cooperation. Cooperative groups of female kin are unlikely to form as they do in some species of primates (*e.g.*, Kurland 1977) because ground squirrels are sedentary and maintain individual territories. Banding together of female kin could only occur where female ground squirrels have mutually inclusive territories. Future research should be directed towards determining whether relatives gain access to certain resources, such as burrows, that are unavailable to non-relatives. Only then can the significance of tolerance toward close kin be fully evaluated.

Table 4.1. Percent of agonistic (a.) and nonagonistic (b.) encounters among adult female uterine and non-uterine kin, 1981 and 1982 combined. UK = uterine kin, in this case mothers and daughters; NUK = non-uterine kin.

a.

		Agonistic			
	n	% Fights	% Chases	% Threats	*P* Value[1]
UK	47	9	51	40	0.001
NUK	197	7	76	17	

[1] Pearson X^2

b.

		Nonagonistic		
	n	% within 50 cm	% other	*P* Value[1]
UK	30	53	47	0.28
NUK	10	30	70	

[1] Fisher Exact Test

Table 4.2. Percent of encounters that were agonistic among adult female uterine and non-uterine kin by time period, 1981 and 1982 combined. UK = uterine kin, in this case mothers and daughters; NUK = non-uterine kin; PJE1 = Early Post Juvenile Emergence; PJE2 = Late Post Juvenile Emergence.

	Time Period				
	Breeding	Gestation	Lactation	PJE1	PJE2
UK	53 (19)[1]	75 (12)	79 (34)	36 (14)	33 (3)
NUK	79 (39)	96 (28)	100 (107)	96 (28)	100 (13)
P Value[2]	0.07	0.07	0.001	0.001	0.02

[1] % agonistic (n); [2] Yates' X^2 or Fisher Exact Test

Table 4.3. Initial location of encounters among adult females that were agonistic within or outside 50% core areas, 1981 and 1982 combined. UK = uterine kin, in this case mothers and daughters; NUK = non-uterine kin.

	Within core area of:					
	One		Both		Neither	
	n	% Agonistic	n	% Agonistic	n	% Agonistic
UK	19	53	20	65	24	50
NUK	50	92	31	90	23	100
P Value[1]	0.001		0.04		0.001	

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[1] Yates X^2 or Fisher Exact Test

Table 4.4. Percent of agonistic (a.) and nonagonistic (b.) encounters between non-breeding yearling females and their mother (UK) compared to other adult females (NUK), 1981 and 1982 combined. UK = uterine kin; NUK = non-uterine kin.

a.

	n	Agonistic			P Value[1]
		% Fights	% Chases	% Threats	
UK	64	5	59	36	0.32
NUK	157	7	67	26	

[1] Pearson X^2

b.

	n	Nonagonistic		P Value[2]
		% within 50 cm	% other[1]	
UK	17	24	76 (6)	0.06
NUK	28	57	43 (11)	

[1] % of total nonagonistic encounters that were play given in parentheses; [2] Yates' X^2

Table 4.5. Percent of agonistic (a.) and nonagonistic (b.) encounters among non-breeding yearling females and littermate sisters (UK) and with other non-breeding yearling females (NUK), 1981 and 1982 combined. UK = uterine kin; NUK = non-uterine kin.

a.

		Agonistic	
	n	% Chases	% Threats
UK	0	--	--
NUK	14	71	29

b.

		Nonagonistic			
	n	% within 50 cm	% other[1]	*P* Value[2]	*P* Value[3]
UK	22	27	73 (55)	0.06	1.00
NUK	14	64	36 (29)		

[1] % of total nonagonistic encounters that were play given in parentheses; [2] Yates' X^2 comparing UK to NUK; [3] Fisher Exact Test comparing UK to UK Table 4.4b.

Table 4.6. Percent of agonistic (a.) and nonagonistic (b.) encounters between juvenile females and their mother (UK) compared to other adult females (NUK), 1981 and 1982 combined. UK = uterine kin; NUK = non-uterine kin.

a.

		Agonistic		
	n	% Chases	% Threats	*P* Value[1]
UK	4	25	75	0.31
NUK	17	59	41	

[1] Fisher Exact Test

b.

		Nonagonistic		
	n	% within 50 cm	% other[1]	*P* Value[2]
UK	29	83	17 (7)	0.63
NUK	8	75	25 (0)	

[1] % of total nonagonistic encounters that were play given in parentheses; [2] Fisher Exact Test

Table 4.7. Percent of nonagonistic encounters among juvenile females and their littermate sisters (UK) compared to other juvenile females (NUK), 1981 and 1982 combined. UK = uterine kin; NUK = non-uterine kin.

		Nonagonistic			
	n	% within 50 cm.	% other[1]	*P* Value[2]	*P* Value[3]
UK	24	38	62 (54)	0.22	0.002
NUK	16	62	38 (19)		

[1] % of total nonagonistic encounters that were play given in parentheses; [2] Yates' X^2 comparing UK to NUK; [3] Fisher Exact Test comparing UK to UK Table 4.6b.

Table 4.8. Percent of agonistic (a.) and nonagonistic (b.) encounters between non-breeding yearling females and adult non-littermate sisters compared to non-breeding yearling females and more distantly related adult females (NSK), 1981 and 1982 combined. NLM sister = non-littermate sister; NSK = non-specified kin; UK = uterine kin.

a.

		Agonistic				
	n	% Fights	% Chases	% Threats	*P* Value[1]	*P* Value[2]
NLM sister	22	5	77	18	0.54	0.20
NSK	135	7	65	27		

[1] Yates' X^2 comparing NLM sister to NSK; [2] Yates' X^2 comparing NLM sister to UK Table 4.4a, combining fights and chases

b.

		Nonagonistic			
	n	% within 50 cm	% other[1]	*P* Value[2]	*P* Value[3]
NLM sister	11	36	67 (27)	0.12	0.67
NSK	17	71	29 (0)		

[1] % of total nonagonistic encounters that were play given in parentheses; [2] Fisher Exact Test comparing NLM sister to NSK; [3] Fisher Exact Test comparing NLM sister to UK Table 4.4b.

Table 4.9. Activity budgets of adult females with and without uterine kin by time period as percent scans, 1981 and 1982 combined. Asterisks indicate groups significantly different (Pearson or Yates' X^2 or Fisher Exact Test, $P < 0.05$). UK = females with uterine kin, in this case mothers and breeding daughters (n = 16); NO UK = females without uterine kin (n = 3); PJE1 = Early Post Juvenile Emergence; PJE2 = Late Post Juvenile Emergence.

	Time Period										
	Breeding		Gestation		Lactation		PJE1		PJE2		
Behaviour	UK	NO UK	UK	NO UK	UK	NO UK	UK	NO UK	UK		NO UK
Feeding	38	41	44	54	42	38	36	40	59	*	42
Resting/ Maintenance	27	32	23	17	21	22	15	19	19		20
Moving	13	10	13	17	14	17	21	23	11		15
Alert	4	7	4	6	8	10	15	12	7		9
Interacting Agonistically	7	4	7	0	11	12	6	2	3	*	9
Interacting Nonagonistically	5	4	1	0	1	0	2	0	0		1
Nesting	5	2	7	6	2	0	2	2	1		3
Scentmarking	1	0	1	0	1	1	3	2	0		1
(n scans)	319	69	173	53	393	69	302	64	275		80

Table 4.10. Reproductive success of adult females with or without mother, breeding daughter or breeding littermate sister (UK) and of adult females with or without mother, breeding daughter, breeding littermate or non-littermate sister (SK), 1980-1982 combined.

	UK			SK			
	With	Without	*P* Value[1]	With[2]	Without[2]	*P* Value[1]	Test
% raising a litter (n females)	76 (21)	56 (9)	0.39	68 (37)	50 (6)	0.65	F
No. juveniles produced per year (n females)	3.00 (21)	1.89 (9)	0.13	2.62 (37)	1.33 (6)	0.10	MW
Litter size (n litters)	3.94 (16)	3.40 (5)	0.27	3.88 (25)	2.67 (3)	0.04	MW
% survival juveniles to yearling age (n juveniles)	38 (63)	41 (17)	1.00	38 (63)	50 (2)	--	Y

[1] Fisher Exact Test (F), Mann-Whitney U Test (MW) or Yates' X^2 (Y); [2] includes data from 1984, except for % survival juveniles

5. Concluding Discussion

Adult female Columbian ground squirrels are likely to co-occur with adult matrilineal kin, making it possible for nepotistic behaviour to play a prominent role in their social organization. Squirrels formed female kin groups as a result of philopatry so that matrilineal kin were available in both time and space. However, the behaviour of adult females with kin was mostly hostile, with each female defending an individual area but exhibiting some tolerance within proximity of neighbouring relatives. Encounters between close kin sometimes resulted in no displacement of the participants, while those between distant kin almost always resulted in displacement. Immature females associated in space with littermate sisters with which they had cohesive relationships typified by play. Relationships with more distant relatives were mostly agonistic. Mother/ daughter pairs did not form cohesive units in either spatial or behavioural relationships but exhibited some tolerance.

It appears that the social structure of *S. columbianus* has been inappropriately described by both Armitage (1981) and Michener (1983). Both authors considered this species to be among the most social of *Spermophilus*. Armitage assumed that for "social species", such as *S. columbianus*, cohesive behaviours predominated among kin, and that kin were also often burrowmates, while agonistic behaviour characterized social behaviour of non-kin. Michener supposed that for species like *S. columbianus* with "multiple-family female kin clusters", litter distinctions were relaxed so that females from adjacent litters associated as adults and mothers showed no strong discrimination between their own offspring and those of adjacent litters. Neither description is in accord with my results. Of *S. richardsonii, S. tereticaudus, S. beldingi, S. parryii* and *S. columbianus* (Yeaton 1972, Davis 1982; Dunford 1977; Sherman 1981; McLean 1982; my results), cohesive behaviours seem to predominate among adult kin only in *S. beldingi* and cooperative defense has been suggested only for *S. beldingi* and *S. parryii*. Relationships between adult females are usually agonistic, whether between close kin or not. Whether adult female kin are regularly burrowmates is largely unknown but seems unlikely for any species, particularly during gestation and lactation. In all species, adult females had fewer agonistic encounters with close kin (including daughters) than with distant kin (including daughters of other females). In no species have females from adjacent litters been shown to associate as adults. I consider systematic association of close kin, typified by cooperation, and cooperation and competition resulting in alliances and dominance relationships to be important factors in considering level of sociality, as does Wrangham (1983). Those species showing cooperative relationships between kin and a predominance of cohesive behaviours between individuals that could result in alliances should be deemed more social. By these criteria, *S. columbianus* is certainly not more social than either *S. beldingi* or *parryii*.

In Columbian ground squirrels, tolerance towards relatives must have a greater benefit than cost in fitness; otherwise it would not occur (Hamilton 1964). Inclusive fitness can be extremely difficult to measure in field studies, but measures of reproductive success do take into account effects of kin-differential behaviour (Grafen 1982). Still, a rigorous evaluation of fitness requires measures of lifetime reproductive success. Studies over longer time periods and with larger sample sizes might indicate that significant advantages in reproductive success accrue through nepotism. Additionally, tolerance towards relatives may increase inclusive fitness if females thereby allow relatives to recruit successfully in favourable habitat rather than causing settlement in submarginal habitat or precipitating a potentially risky dispersal movement to another population. A similar idea has been proposed to explain tolerance of female relatives in red deer (Clutton-Brock *et al.* 1982).

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