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Inheritance of nest sites in female Columbian ground squirrels

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Summary. Home ranges, areas of intensive use, and locations of nest sites were determined for female Columbian ground squirrels and their daughters over seven years from a low-density population in southwestern Alberta. Adult females usually retained similar home ranges from year to year. However, they moved their nest sites more often than expected in years when a yearling daughter was present. Core areas and centres of activity also changed when the nest site was moved. Most daughters settled on their natal areas. The relinquishing of nest sites by females to their daughters is seen as a form of parental investment.

Introduction

It has been proposed that sociality in the ground-dwelling sciurids is based on genetic relatedness between females (Michener 1983). Closely related females tend to live in spatial proximity, forming "kin clusters". This tendency is promoted by site fidelity among females and extension of the mother-infant bond into adult life. Males, on the other hand, usually disperse off their natal area. Differential treatment of kin and non-kin by females in the field has been documented for some species (Dunford 1977a; Sherman 1981a; McLean 1982; Davis, in press). Recognition of kin has also been demonstrated in experimental situations (Michener and Sheppard 1972; Holmes and Sherman 1982; Davis 1982).

Despite their tendency to live in kin clusters, females of even the most social of the ground-dwelling sciurids usually raise their litters in isolation (e.g. King 1955, pp. 84–85). The young are altricial and spend the first few weeks of life underground, potentially easy prey for predators or infanticidal members of their own species (Sherman 1981b; McLean 1982). Lactating females tend to behave in a protective and secretive manner around their nest burrows, they often choose nest sites peripheral to their regularly used burrow systems, and they may defend these sites against members of their own and other species (e.g. O'Shea 1976; Betts 1973, p. 180; McLean 1978; Harris 1981). Thus nest sites appear to be individually held and protected resources for these animals.

Like other sciurids, Columbian ground squirrels (*Spermophilus columbianus*) show male-biased dispersal (Boag and Murie 1981b; Murie and Harris in press). Adult females tend to retain the same home ranges from year to year and most young females settle near their natal area (Festa-Bianchet 1981; Festa-Bianchet and Boag 1982; Murie and Harris in press). These characteristics are shared with other sciurid species (see, for example, Rongstad 1965; Slade and Balph 1974; Michener 1980). However, Columbian ground squirrels have relatively high rates of survival and recruitment and relatively small litter sizes compared to other species (Murie et al. 1980). Also, unlike other ground squirrels, reproductive maturity is usually delayed until the age of two (exceptions occur in some populations; see Festa-Bianchet 1981), and dispersal is delayed until the age of one. Thus a yearling cohort of non-reproductively active animals exists in most populations, a factor that may promote the development of sociality (Armitage 1981; Michener 1983).

Our aim was to determine whether the use of space, particularly choice of nest sites, by adult female Columbian ground squirrels in the field was affected by the presence of daughters, and to compare the use of space by daughters with that shown by their mothers. To this end, we documented locations of nest sites, areas of intensive use, and home ranges for females and their surviving daughters from a single population over seven years. If the social organization of Columbian ground squirrels is indeed influenced by kinship and matrilineal inheritance of space, one might expect the patterns of space use exhibited by females to be modified in the presence of close female relatives.

Materials and methods

The study took place from 1976 to 1982. The study area was a meadow of about 5 ha along the Sheep River drainage in southwestern Alberta (50°39′ N, 114°38′ W; elevation 1,500 m). Densities of adult females were lower (about 5/ha) and home ranges were larger (about 2,800 m^2) than noted for some other populations (Festa-Bianchet and Boag 1982). Rates of aggressive interactions between adult females were low (averaging about 0.1/h of observation) and no pronounced peaks in aggression between females were noted post-breeding or prior to emergence of juveniles (cf. Festa-Bianchet and Boag 1982). Distances between nest sites of neighboring females were relatively large, averaging 35 (range 5–80) m.

All squirrels on the study area were live-trapped (National Live Traps), tagged through each ear with a numbered metal band (National Band and Tag Co., Monel No. 1), and painted on the fur with individually distinctive black dye markings (Lady Clairol blue-black hair dye). During 1976 to 1980, behavioral observations were performed over most of the study area from late April (when adults first emerge from hibernation) to mid-June (just prior to the emergence aboveground of juveniles). Locations of each animal visible were recorded at 5-min intervals and all interactions were noted. Total observation time was about 900 h.

Locations of *nest sites* were usually determined by noting the burrow at which newly-emerged juveniles were first trapped (52 cases). In years when observational data were available, locations of some nest sites were determined by noting where a lactating female first emerged in the morning (21 cases). If no observational data were available and no litter was trapped for a particular female, no specific nest site was assigned.

When observational data were available, other use of space was also determined for many females. *Home ranges* comprised all squares on a 10 × 10 m grid of the area in which an animal was seen during regular observations. *Core areas* were those squares in which an animal was seen on at least 25% of all days of observation (see Murie and Harris 1978 for details). *Overlap* of home ranges and core areas between years was calculated as the number of squares used in both years divided by the total number of squares used. Geometric *centres of activity* were determined by taking the weighted means of x and y coordinates of all grid squares used.

Between years, females were considered to have *moved* their nests if the new location was more than 20 m from the location used in the previous year (at this distance two different sites were not likely to be connected through underground burrow systems). Sites were considered to be *vacant* if no female's nest was within 20 m in that year and in the previous year as well. Sites were considered to be *available* to a particular female if they were within 45 m of her previous nest (and thus probably within an area that was familiar) and if they were known nest sites (a nest was recorded within 20 m of there in some year of the study).

Results

We documented locations of nest sites for a given female on two or more successive years in a total of 49 cases. These involved 26 different females, who were followed for an average of 3.6 years (maximum 5 years) per individual. In 9 instances, no young appeared aboveground, although the female lactated for at least some length of time. In the remainder, at least one juvenile eventually emerged aboveground; average litter size at emergence was 2.8 (range 1–5). In 22 cases, at least one member of the litter was recaptured the following spring as a yearling; average number of yearlings produced per weaned litter was 1.0 (range 0–2). Nest sites for 13 daughters were known when they first bred (11 as two-year-olds, 2 as three-year-olds). The mothers of 7 of these 13 daughters were still alive and also bred that same year.

Females moved their nest site in 19 out of 49 cases (39%; see Table 1). Of these 19, 13 went to sites that had not been used the previous year, four went to sites from which the previous year's occupant had disappeared, and two went to sites from which the previous occupant had moved. Thus, females who moved their nest sites went to vacant or currently unoccupied sites. For females for whom observational data were available ($n=7$), the new site was within (5 cases) or immediately adjacent to (2 cases) their previous year's home range. The maximum distance that nest sites were moved was 75 m.

Females who moved their nest sites did not show significantly less overlap in their home ranges between years than females who did not move (Table 2). However, they showed significantly less overlap in their core areas and greater distances between centres of activity. Thus, while home ranges remained approximately the same for any given female from year to year, her areas of greatest use shifted when she moved her nest site.

Moves were most likely to occur when a surviving yearling daughter was present. Females moved in 11/17 cases (65%) when a yearling daughter was present, but in only 8/32 cases (25%) when no yearling daughter was present ($P=0.01$, Fisher's exact test). This same pattern held if each individual was included in the results only once, using the first occasion she was sampled ($n=26$; $P=0.02$, Fisher's exact test). Females were also more likely to move when there was an available vacant site (16/32 cases or 50%) than when there was not (3/17 cases or 18%; $P=0.03$, Fisher's exact test). For females with an available vacant site, a move was more likely if she had a yearling daughter

Table 1. Frequency with which adult females moved their nest site in relation to success of their previous year's litter

	Female lactated, but no litter emerged	Litter emerged, but none survived	Only yearling son(s) survived	Only yearling daughter(s) survived	Yearling son and daughter survived
Move	2	5	1	8	3
No move	7	13	4	4	2

Table 2. Use of space by adult females. Comparisons are made between years in which they moved or did not move their nest site. Median values are given, with ranges in parentheses

	Home range overlap	Core area overlap	Distance (m) between centres of activity
Move ($n=7$)	0.35 (0.17–0.64)	0.00 (0.00–0.56)	14 (0–23)
No move ($n=19$)	0.48 (0.24–0.59)	0.57 (0.29–1.00)	10 (0–14)
Mann-Whitney *U* Test	$P>0.20$	$P<0.01$	$P=0.02$

Table 3. Use of space by daughters, compared with use of space by their mothers and the nearest other adult female in the daughters' natal year: a) for daughters as yearlings ($n=7$); b) for daughters as adults, in the year they first lactated ($n=4$). Median values are given, with ranges in parentheses

Daughter compared to	Home range overlap	Core area overlap	Distance (m) between centres of activity
a) Mother	0.41 (0.09–0.50)	0.19 (0.00–1.00)	15 (0–23)
Other ♀	0.17 (0.06–0.40)	0.00 (0.00–0.25)	30 (23–47)
Wilcoxon matched-pairs test	$P=0.03$	$P=0.05$	$P=0.02$
b) Mother	0.38 (0.29–0.61)	0.15 (0.00–0.38)	12.5 (0–23)
Other ♀	0.13 (0.04–0.28)	0.04 (0.00–0.08)	28 (20–37)

(10/14 cases or 71%) than if she did not (5/18 cases or 28%; $P=0.03$, Fisher's exact test). Thus, while presence of available vacancies probably influenced likelihood of moving, it did not account for the frequency of moving by females with daughters.

It was unlikely that moves resulted from high degrees of agonism between mothers and offspring. Probably owing to the low density of squirrels on this study area, we recorded few interactions of any kind between females and their yearling offspring. Of the interactions that did occur, some (6/15) were amicable (naso-oral sniffing, playing) and some (9/15) were agonistic (mother chased her offspring). In comparison, only agonistic (33/33) interactions (female chased yearling) were seen between adult females and unrelated yearlings (these proportions differed significantly; $P<0.01$, Fisher's exact test). Adult females were never observed to be chased by yearlings. Treatment of yearling sons did not differ in any obvious way from treatment of yearling daughters (no significant difference in proportions of amicable and agonistic interactions; $P=0.61$, Fisher's exact test).

Yearling females tended to live on the areas used by their mothers in the previous year. Overlap of yearling daughters' home ranges and core areas were greater with their mothers' previous areas than with those of the nearest other adult female, and centres of activity were closer to their mothers' (Table 3a). It also appeared that when they first bred as two- or three-year-olds, daughters used areas similar to those their mothers had used in the natal year (Table 3b), though sample sizes were too small to permit statistical tests. In contrast, although yearling males ($n=9$) also tended to remain on their mothers' areas, sons did not use their natal range when they became adults (in all cases the core areas were widely separated, and only one male showed a slight overlap of his adult home range with his mother's former range). Since our observations stopped in mid-June, about the time

Table 4. Use of space by daughters as adults, compared with their mothers and the nearest unrelated female in the year the daughter first lactated ($n=4$). Median values are given, with ranges in parentheses

Daughter compared to	Home range overlap	Core area overlap	Distance (m) between centres of activity
Mother	0.31 (0.17–0.41)	0.11 (0.00–0.29)	22.5 (15–44)
Other ♀	0.13 (0.09–0.23)	0.05 (0.00–0.13)	34 (22–46)

that yearling dispersal begins (Boag and Murie 1981), any movements by yearling males were probably not sampled in our study.

Nest sites were determined for 13 daughters with known natal sites. In 7 (54%) of these cases, the nest site in the first year of breeding was within 20 m of the natal site. In 9 (69%) of the cases, daughters nested closer to their natal site than to the nearest vacant site, but differences were not significant (median distance of the natal site from the nest site was 18 m (range 5–75) m, and of the natal site from the nearest vacant site was 30 m (range 20–90) m; $P>0.10$, Wilcoxon matched-pairs test).

When mothers survived and bred in the same year that their daughters first bred ($n=7$), the daughters nested closer to their mothers (median 40 m, range 7–68 m) than to the nearest unrelated female (median 56 m, range 17–78 m; $P=0.03$, Wilcoxon matched-pairs test). The daughters' use of space in that year also appeared to be more similar to their mothers' than to that of the nearest unrelated female (Table 4), although numbers were too low to test statistically.

There was a suggestion that mothers might increase the likelihood of success of their daughters by moving. Eight of 11 (73%) yearling daughters whose mothers moved were eventually successful (lactated) on the area, but only 2/6 (33%) daughters whose mother did not move eventually lactated ($P=0.16$, Fisher's exact test). Of the seven unsuccessful daughters, four were not recaptured as two-year-olds; the three that were recaptured did not lactate and were not recaptured in subsequent years. Of the ten successful daughters, eight lactated as two-year-olds and two lactated for the first time as three-year olds. Whether or not adult females moved did not seem to affect their own success in subsequent years (8/15 females who moved and 15/25 females who did not move lactated the following year; $P=0.75$, Fisher's exact test).

Discussion

This study has shown that despite their relatively stable home ranges, the nest sites and areas of intensive use of adult female Columbian ground squirrels often shifted between years. Changes in nest sites were related to the presence of offspring, females moving more often in years when a yearling daughter was present. This phenomenon has not been previously reported for a ground squirrel, and is probably most likely to be recognized in a relatively long-lived species where nest sites of individual females can be recorded over several years. Changes in burrows used by adult females of Belding's ground squirrel (*Spermophilus beldingi*) have been reported, but were associated with killing of young by predators (Sherman 1981b). No such correlation was evident in this study. In fact, our results indicated that females whose litters disappeared usually remained at their former sites (Table 1). The distances moved by female Belding's ground squirrels were also greater (average 114.7 m) than found in this study (maximum 75 m), suggesting that their home ranges may have shifted as well.

As indicated by the direction of chases, mothers were dominant to their yearling daughters (also noted for the yellow-bellied marmot, *Marmota flaviventris;* Armitage 1975). Therefore, mothers were probably not forced to move by their daughters, so must have relinquished their former nest sites voluntarily. Females are unlikely to benefit directly from shifting their nest sites, however. If food resources were richer or predation less probable at a new site, they should move whether or not they have a surviving daughter, but that was not the case. Females will be more familiar with the burrows at their former sites, an advantage in escaping predators. Also, since the nest sites are defended, particularly against other females (Betts 1973, p. 180; unpublished data), a change in site would require that energy by expended in establishing new boundaries, possibly against new neighbors. At best, there might be little cost to moving to a site that is within the home range, that is already somewhat familiar, and that is not defended by another squirrel.

Nevertheless, females could benefit indirectly by moving their nest sites when they leave a daughter with the natal site. Such behavior could be a form of parental investment, if the daughter were thereby more likely to breed the next year. Daughters might have more difficulty in establishing a new site than their mothers would, because they will be less familiar with the area and the other squirrels. Daughters might also have more difficulty protecting a new site. In male Columbian ground squirrels, older individuals tend to be dominant to younger ones (Murie and Harris 1978), and the same may hold true for females (Festa-Bianchet 1982, p. 81; see also Dunford 1977a for round-tailed ground squirrels, *Spermophilus tereticaudus*). Certainly, two-year-old females are usually lighter in weight than older females (Boag and Murie 1981 a), and thus might be at a disadvantage if it became necessary to defend a new site. It may be advantageous for mothers to move when their daughters are yearlings if young females must first establish residence as yearlings where they will later breed (as suggested for yellow-bellied marmots, Armitage 1975).

The changes in nesting location that we found may have been related in part to the low density of ground squirrels on the study area, and the existence of seldom-used burrow systems. When there are vacant sites that are some distance away from other nests, females have the opportunity of moving to a new location without infringing on sites used by other squirrels. The same may not be true for other populations. Columbian ground squirrels can occur in much higher densities than noted here (Festa-Bianchet and Boag 1982), possibly because of more favorable habitat (Festa-Bianchet 1981). In such populations, the nests of neighboring females are often closely spaced (W. King and J. Waterman, personal communication). When nest sites are limited, it might not be advantageous for females to move even if they have surviving daughters. Without suitable alternative sites, they would benefit more by retaining the breeding sites for themselves rather than releasing them to their daughters. Therefore, on densely populated areas one might expect adult females to retain similar nesting sites from year to year, and their daughters to nest either in close proximity to them or in less desirable peripheral locations.

In this study, daughters' nest sites were found to be closer to their mothers' than to nest sites of unrelated neighbors, suggesting the existence of female kin clusters. Nevertheless, the nests of daughters and mothers were usually some distance (median 40 m) from one another. Both results are similar to those reported for the Arctic ground squirrel, *Spermophilus parryii* (McLean 1982).

The loosely organized and spatially dispersed aggregations of female kin found in this and other sciurid species seem unlike the more cohesive, behaviorally integrated bands of related females found in some primates (e.g. Kurland 1977; Olivier et al. 1981), although both types of social systems are apparently organized matrilineally. Perhaps for species like ground squirrels that raise their young underground in a fixed location, it might not be advantageous for females to live too closely together. Food resources around their nests are probably limited and if nests are too closely spaced the litters might become vulnerable to predation (McLean 1982). However, related females may benefit by living in loose associations. Individuals could then increase their inclusive fitness as well as their direct fitness by engaging in alarm and other anti-predator behavior (Dunford 1977b; Sherman 1977; Schwagmeyer 1980). Nepotism occurs in many sciurids, in the form of less agonism among relatives, cooperative chasing, clumping of different litters, sharing of resources, and anti-predator alarm calling (e.g. Hoogland 1981; Sherman 1981a; McLean 1982; review by Vestal and McCarley in press). The phenomenon documented in this population of Columbian ground squirrels, that mothers move and leave their former nest sites to their daughters, can be viewed as part of this overall tendency toward preferential treatment of close kin.

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