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SOCIALITY IN RICHARDSON'S GROUND SQUIRRELS *Spermophilus richardsonii*

by

Lloyd Spencer Davis

A THESIS

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Abstract

Richardson's ground squirrels were examined for behavioural asymmetries based upon kinship at two field sites (1.3 ha each) in Alberta, Canada during a three year study. All squirrels on and within the vicinity of the study areas were live-trapped and marked so that they were individually identifiable. Sex and age class were known for all squirrels, and uterine-kin relationships (i.e., mother-offspring and sibling relationships) were determined when litters emerged at weaning. Scan sampling at 15 minute intervals was used to record locations and activities of individuals. Behavioural interactions were sampled by noting the temporal sequence of behaviours, the identities of the participants, the beginning and end locations, and the outcome of interactions. In all, 731 squirrels were caught and marked, and 636 hours of observation were conducted.

Adult male Richardson's ground squirrels were territorial during the breeding season in places where females emerged from hibernation. Males were not territorial where asynchronous emergence of females, which was correlated with the persistence of snow cover, produced a sparse and unpredictable distribution of females. Some males moved after the breeding period, but some remained in areas in which they had presumably sired some of the offspring. These males gave alarm calls and chased weasels during the period when females were pregnant and lactating.

Adult females were also territorial, and uterine-kin tended to live in greater proximity than did non-uterine-kin neighbours or females that had been neighbours for more than one season. However, effects of spatial proximity to kin on activity budgets and reproductive success were not discernible.

The association of uterine-kin resulted from the perseverance of natal burrow associations after weaning. Male-biased dispersal of juveniles, however, reduced the potential for kin differential behaviour to occur between adult males.

Asymmetries based upon kinship were apparent in interactions. Those between uterine-kin contained a relatively high proportion of "appeasement" and "identification" behaviours and a low proportion of "chasing and fleeing" behaviours compared to interactions involving non-uterine-kin. As a result, uterine-kin usually did not displace each other from the site of an interaction, whereas most often in encounters between non-uterine-kin one participant was displaced.

Kin differential behaviour was also examined in arena tests where cross-fostering experiments demonstrated that an ability to distinguish biological siblings from non-siblings was determined prenatally or soon after birth. Familiarity also affected recognition, but its effects were less obvious.

Alarm calling, elicited by natural stimuli and experimentally, was not equally probable for all age/sex classes. Squirrels were most likely to call when they had offspring or siblings nearby. It did not appear that callers would endanger themselves by calling.

Finally, females in kin clusters on an experimentally treated area where females without uterine-kin had been removed, showed tendencies to feed more, be alert less, suffer reduced predation of litters, and have greater reproductive success than did females without uterine-kin on an adjacent area.

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1. Introduction

1.1 Rationale

Social groups are not random aggregations of animals. Sociality, the association of conspecifics in time and space that is maintained by communication among them, should only be selected for when individuals living in groups do not experience less fitness than solitary living individuals. The benefits that may accrue from group living have been summarized (Alexander 1974, Bertram 1978, Wilson 1975), and chief among them are defense from predators and enhanced utilization of food resources. Sociality may also have various costs associated with it, such as increased likelihood of detection by predators and increased intraspecific competition (Bertram 1978).

The North American ground-dwelling sciurids (Rodentia: Marmotini) are composed of little more than 30 species that vary in the degree of sociality from essentially solitary species (e.g., woodchuck *Marmota monax*, Bronson 1964) to species that live in groups, share the same space, and exhibit mainly cohesive behaviour between all group members (e.g., black-tailed prairie dog *Cynomys ludovicianus*, Hoogland 1981a). Advantages of sociality in ground squirrels have been variously suggested as defense from predators (Carl 1971, Hoogland 1981b, Sherman 1977), protection from intraspecific killing (McLean *in press*, Sherman 1981), and extended care of slow maturing young (Armitage 1981).

Recent reviews (Armitage 1981, Michener *in press*) have proposed that "kin selection" (Hamilton 1963, 1964, Maynard Smith 1964) is the primary mechanism that led to the evolution and maintenance of sociality in the ground-dwelling sciurids. When aid to close relatives may increase an individual's own "inclusive fitness" (Hamilton 1963), the theory of kin selection predicts that such manifestations of sociality will be favoured. Due to the proximity of common ancestors, relatives (kin) have a greater proportion of their genetic make-up (genes) in common than do the less related individuals of the population at large. Selection, while operating on individuals, nevertheless expresses itself as differential survival of genes in the population gene pool and not of individuals *per se* (Dawkins 1976), so that behaviours will be selected for, even if they promote the reproductive success of another, as long as the benefit to the recipient is *k* times the cost to the performer, where *k* is greater than the reciprocal of the degree of genetic relatedness (*r*) between the two, i.e. $k>1/r$ (Hamilton 1963).

For kin selection to be a significant selective pressure, relatives must be able to influence each others survival or reproductive success; that is, there must be some overlap in time and space (Sherman 1980). The common denominator of sociality throughout the Marmotini is the association of adult female kin (Armitage 1981, McLean 1982, Michener 1979a, *in press*, Sherman 1980), so for adult females, at least, there is a potential for influencing kin and the possibility of asymmetrical behaviour based upon the relatedness of the participants.

Also correlated with increasing sociality in these species is the extent to which clusters of females are associated with adult males (Armitage 1981, Michener *in press*). The greater the association and the more exclusive his access to those females, the more likely should a male be to exhibit behaviour which favours the females and their young.

The ground-dwelling sciurids, and Richardson's ground squirrels in particular, are good subjects for a study of sociality. They can be easily observed in the wild, being diurnal, quite large, relatively insensitive to an observer, and occurring at high enough densities that many can be observed from a single location. Richardson's ground squirrels breed when they are one-year old, so length of generations is short, and the female population, at least, is philopatric, resulting in the persistence of individuals at a single location over time. As well, there is a sizeable background literature on aspects of the reproductive biology (Nellis 1969), demography (Hansen 1962, Michener 1979a, 1979b, Michener and Michener 1977, Schmutz *et al* 1979), and social behaviour (Clark and Denniston 1970, Michener and Sheppard 1972, Quanstrom 1971, Wehrell 1973, Yeaton 1972) of *Spermophilus richardsonii*.

It was the aim of this study to examine the potential role of kin differential behaviour in the sociality of Richardson's ground squirrels. The study was divided into seven parts:

1. Male behaviour – I examine adult male behaviour and movements to determine how closely males are associated with females, and what, if any, potential they may have to influence the survival or reproductive success of close kin.
2. Spatial organization of females – It necessary to show that there is spatial overlap

between kin for there to be a potential for kin selection to mediate behaviour, and as well it could be instructive to distinguish between any asymmetries that result from spatial relationships themselves rather than as a consequence of differential behaviour based on genetic relationships. I analyse dispersion patterns to calculate such relationships by comparing the effects familiarity and kinship on the use of space.

3. Socialization - I examine the behaviour and dispersion of juveniles for evidence of asymmetries based upon kinship and sex, since early associations could influence later interactions as adults, and differences in dispersal could influence the potential to interact.
4. Interactions - If sociality is mediated by kin selection in *S. richardsonii* then a predictable outcome should be asymmetrical behaviour based on kinship. In this part I compare behavioural interactions between uterine-kin and between less-related animals for evidence of kin effects.
5. Recognition - If kin differentiated behaviour occurs, there must be a mechanism that allows the ground squirrels to distinguish between kin and non-kin. There need not, but could, be an ability to recognize genetic relatives without requiring prior experience of them; otherwise the mechanism might be based on familiarity through association at some critical time. I tested for effects of post-partum familiarity in a crossfostering experiment.
6. Alarm calling - Since a likely advantage of sociality in ground squirrels is protection from predators, alarm calling in encounters with both real and simulated predators is looked at for any asymmetry based on the likelihood of having kin nearby. Predictably, animals with close kin in the vicinity should be more likely to call than animals without kin around them.
7. Costs/Benefits - The advantages, if any, of associating with kin, and the disadvantages of not associating with kin, were measured by a removal experiment that left one area with all adult females surrounded by non-kin or distantly related neighbours, and another area with all the females having at least one uterine-kin female as a neighbour. If kin association is beneficial, reproductive success and factors that may be related to it should be greater on the latter area.

The relationship between the parts of this study are as follows. A mechanism for recognition of kin is necessary for there to be asymmetries in behaviour. The latter in turn affects, and is affected by, the mating system, socialization, and spatial organization, upon which will rest the likelihood of kin overlapping in time and space and their potential to behave nepotistically. Given that there is a mechanism for determining relatedness that does result in asymmetries based on kinship, the selective advantage of such a system of sociality is that it might provide better predator defense (alarm calling) and should result in increased reproductive success (removal experiment).

1.2 Perspective

Kin selection has become a bandwagon. While I accept that kin selection is an inevitable consequence of natural selection, I remain uncommitted as to its significance in influencing animal social behaviour generally. The purpose of this study was to determine the significance, if any, of kin selection to the sociality of *S. richardsonii*. To accomplish this task I had to concentrate on the potential role of kin selection, but my preoccupation with these ideas was not *a priori* endorsement of them. I attempted to survey the road, not ride the wagon.

1.3 Definition of Uterine-kin

Uterine-kin (UK): mother-offspring and littermate sibling relationships. In effect, these are squirrels that have shared a natal burrow.

Non-uterine-kin (NUK): squirrels known not to be uterine-kin.

Although non-uterine-kin could include some related individuals, on average the members of this group will be much less closely related than uterine-kin. Comparisons between uterine-kin and non-uterine-kin are used to investigate kin-differential behaviour throughout this dissertation.

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2. The Mating System and Behaviour of Male Richardson's Ground Squirrels: territoriality, variability, and sociality

2.1 Introduction

Levels of sociality among species of North American Marmotini correlate with the extent that adult males are associated spatiotemporally with adult females (Armitage 1981, Michener *in press*). Yet, with a few exceptions (Armitage 1974, Barash 1975, 1981, Dobson 1979, McLean *in press*, Murie and Harris 1978, Sherman 1976), the role of males in the social organization of ground-dwelling sciurids has received little direct study.

In general, ground squirrel populations are typical of polygamous mammalian mating systems, exhibiting a female-biased adult sex ratio, female philopatry, and male dispersal (Greenwood 1980). However, the degree to which males defend an area and protect females from access by other males, is a characteristic of the mating system that is variable between species (Armitage 1981, Michener *in press*) and perhaps even within a species (Dobson *in press*).

In the more social species (e.g., *Spermophilus columbianus, S. parryii, Cynomys ludovicianus, Marmota flaviventris, M. olympus*) dominant males defend a territory during and after the breeding season that overlaps the ranges of several females (Murie and Harris 1978, McLean *in press*, Hoogland 1981, Armitage 1974, Barash 1973) and may even exhibit paternal or nepotistic behaviour (McLean *in press*, Barash 1975, Hoogland 1981).

By contrast, amongst the less social species (e.g., *S. beldingi, S. tereticaudus, S. armatus, S. tridecemlineatus*) males do not defend territories after the breeding period, and utilize areas separate from those of females (Sherman 1981, Dunford 1977, Balph and Stoke 1963, Schwagmeyer pers. comm.). It is into this group that *S. richardsonii* has been cast (Armitage 1981, Michener *in press*). Adult males of these species are said not to display paternal (Michener 1979) or nepotistic (Sherman 1980, Dunford 1977b, Schwagmeyer 1980) behaviour.

The behaviour of males in this latter group has been studied in detail only for *S. beldingi*. Belding's ground squirrel males do not form territories during the breeding period, and instead have a 'lek'-type mating system, with males travelling extensively during the breeding period (Sherman 1976). Michener and Michener (1977:366) and Michener (1979:129) concluded that males of *S. richardsonii* also range over a large area before and during the breeding season, and do not actively defend an area (Michener 1979:134). By contrast, Yeaton (1972:141) reported that Richardson's ground squirrel males established territories which encompassed the nest burrows of three to five females, although he did not present any evidence of territorial behaviour.

The aims of this study were to determine the nature of the Richardson's ground squirrel mating system by examining male behaviour particularly during the breeding period, to assess the degree of association of males with females relative to other ground-dwelling sciurids, and to look at the potential for paternal or nepotistic behaviour.

In this paper I present the results of direct observation of 20 *S. richardsonii* males during the breeding period at two localities in Alberta, Canada. I examine home ranges, evidence for territoriality, access to females, activity budgets, and overlap between breeding and post-breeding ranges.

2.2 Methods

Squirrels on the 1.3 ha Highwood River study area (HRSA), situated on flat fescue grassland 6 km northwest of Longview (50°34'N, 114°18'W; elevation 1235m), were observed from 20 March to 20 August 1979, and 17 March to 13 August 1980. The 1.3 ha Roi Lakes study area (RLSA) was located in a rolling, grassy clearing amid aspen forest 12 km northwest of Stony Plain (53°35'N, 114°05'W; elevation 730m), and studied between 11 May to 14 August 1980, and 15 March to 9 August 1981. Both areas were sometimes grazed by cattle.

All ground squirrels on or near the study areas were live-trapped and marked for individual identification, using numbered metal ear tags, coloured plastic discs or strips attached to one ear tag, and dye-marks made with human hair-dye on their fur. Squirrels were weighed (±5 g) with a spring balance, and released at the point of capture. Thereafter squirrels were retrapped usually only as necessary to renew their dye-marks. In all, 447 squirrels were caught and marked at the HRSA and 284 at the RLSA.

Numbered flags or stakes were used to mark the co-ordinates of a grid with 10m x 10m squares on each study area. Squirrels were observed using 10 x 50 binoculars from a 2.5m observation stand (HRSA) or a chair situated on elevated ground (RLSA). Squirrels could be observed at the HRSA in a further 5 ha that was marked with a grid of 50 x 50m squares, and at the RLSA over a further 2 ha. Overall, 636 hours of behavioural observations were made.

The 'breeding period' was defined after Michener (1979) and was taken as the two weeks following the first emegence of females from hibernation. In both 1980 (HRSA) and 1981 (RLSA), females first emerged from hibernation on 25 March, and consequently the 'breeding period' for both years was taken as being from 25 March to 7 April.

During the breeding period I followed the movements and activities of adult males (*n*=11 HRSA, *n*=9 RLSA) from daily instantaneous scan sampling (Altmann 1974) taken at 15 minute intervals (*n*=101 scans [HRSA], *n*=93 scans [RLSA]). Four of the males at HRSA were fitted with small radio transmitter collars (AVM SM1 transmitter with "R" collar; weight = 4 g) throughout the breeding period, and six of the males at the RLSA were fitted with radios from 4 to 27 April. Locations of radio-tracked squirrels were noted to the nearest 10m at about 1400h (HRSA) or 1500h (RLSA) daily. Interactions observed during the breeding period were recorded using sequence sampling (Slater 1978), and I noted the identities of the initiator and responder, the starting location (defined as the location of the responder when the interaction was initiated), the end location (location of the responder when the interaction terminated), and the outcome.

All home ranges were calculated using the minimum polygon method (Mohr and Stumpf 1966), and unless otherwise indicated comparisons between groups were made using the non-parametric Mann-Whitney *U*-test. Means are given with plus or minus one standard deviation throughout.

2.3 Results

2.3.1 Mating system and male territoriality

In spring Richardson's ground squirrel males emerge from hibernation before females. Males were first caught on 17 (HRSA) and 15 (RLSA) March. Thereafter the number of emergent males increased rapidly, and 78% (HRSA) and 85% (RLSA) of males on the study area emerged by the time the first females appeared on 25 March. Females came up as the snow cover receded. At RLSA snow melted quickly so that by 31 March the area was completely snow-free. By contrast, at HRSA the melt was slower and dampened by two heavy snow falls (10.0 cm on 23/24 March and 7.5 cm on 29 March), so that by 7 April a quarter of the area was still under snow. As a result, female emergence was less synchronous at HRSA than at RLSA; whereas 98% of females at RLSA emerged by 7 April, only 39% had emerged at HRSA (Fig. 2.1).

Sizes of male ranges during the breeding period varied considerably, 0.18 - 16.57 ha at HRSA and 0.16 - 0.76 ha at RLSA (Table 2.1). The sample was biased towards those males with restricted ranges of movements that could be observed throughout the breeding period. Seven (HRSA) and 10 (RLSA) males emerged from hibernation on the areas trapped and disappeared soon afterwards. Five of these males were sighted subsequently, and it was likely that many of these males were simply moving over wide ranges that took them beyond the limits of observability in this study. The two largest ranges (HRSA) were those of radio-tracked individuals (16.57 and 3.58 ha), but as the other two radioed squirrels had small ranges (0.18 and 0.57 ha), it seems unlikely that the radios were responsible for the animals' movements.

Yeaton's (1969:10) largest male territory size was 0.57 ha[1], and I arbitrarily categorized males as 'localized' in this study if their ranges were less than or equal to 0.57 ha. Localized males tended to feed less, move about more, be alert more, and interact agonistically more than did non-localized males (Fig. 2.2). Localized males at RLSA spent much less time feeding, and more time on the other three activities than did their counterparts at HRSA. RLSA males lost weight at an average rate of 3.9 g/day during the breeding period (SD = 1.2, n = 6). At HRSA, where there was a broad distribution of

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[1] The figure of 0.058 ha quoted in Yeaton (1972:141) is in error by an order of magnitude

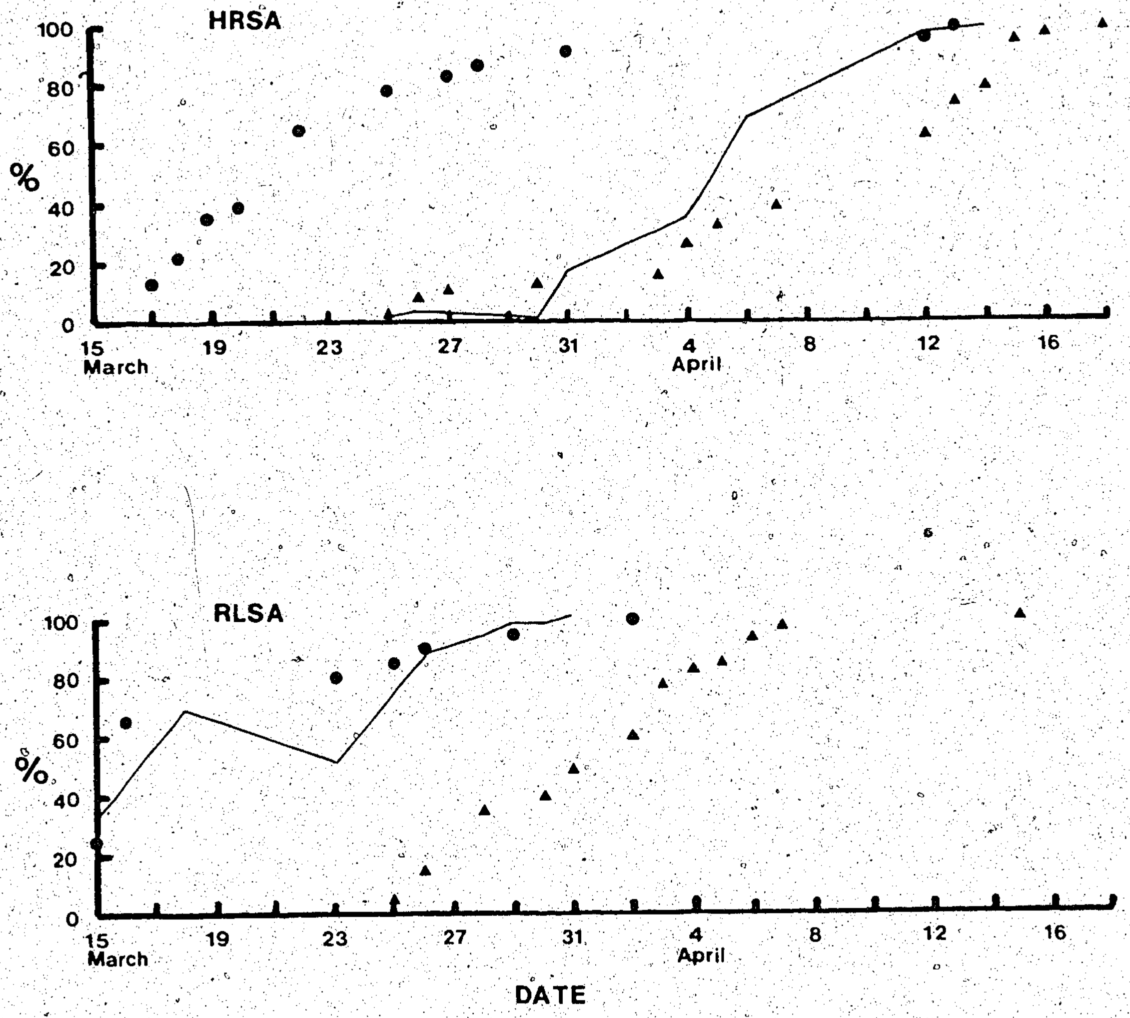

Fig 2.1. Vernal emergence from hibernation of male and female Richardson's ground squirrels at the Highwood River study area (HRSA) in 1980 and Roi Lakes study area (RLSA) in 1981. Dots show the percentage of males that had emerged by a given date (*n* = 23 HRSA, 20 RLSA), and triangles show the percentage of females that had emerged (*n* = 38 HRSA, 40 RLSA). At HRSA males and females were trapped on 2.56 and 2.40 ha respectively, and at RLSA on 1.98 and 1.83 ha respectively. The solid lines show the percentage of the study area that was free of snow cover.

Table 2.1. Breeding period ranges of adult male Richardson's ground squirrels at HRSA in 1980 and RLSA in 1981. Each range is calculated from a mean of 48±17 (HRSA) or 49±23 (RLSA) observations per individual.

HRSA		RLSA	
Male	Range (ha)	Male	Range (ha)
Q[1]	0.18	D[2]	0.16
Z	0.27	B[2]	0.17
K	0.40	X	0.29
Y	0.41	F[2]	0.30
J[1]	0.57	A[2]	0.31
C	0.66	N[2]	0.36
4	0.76	Q[2]	0.39
B	0.91	K	0.47
0	1.51	J[2]	0.76
A[1]	3.58		
H[1]	16.57		

[1] radio–tracked throughout the breeding period

[2] radio–tracked from 4 to 27 April

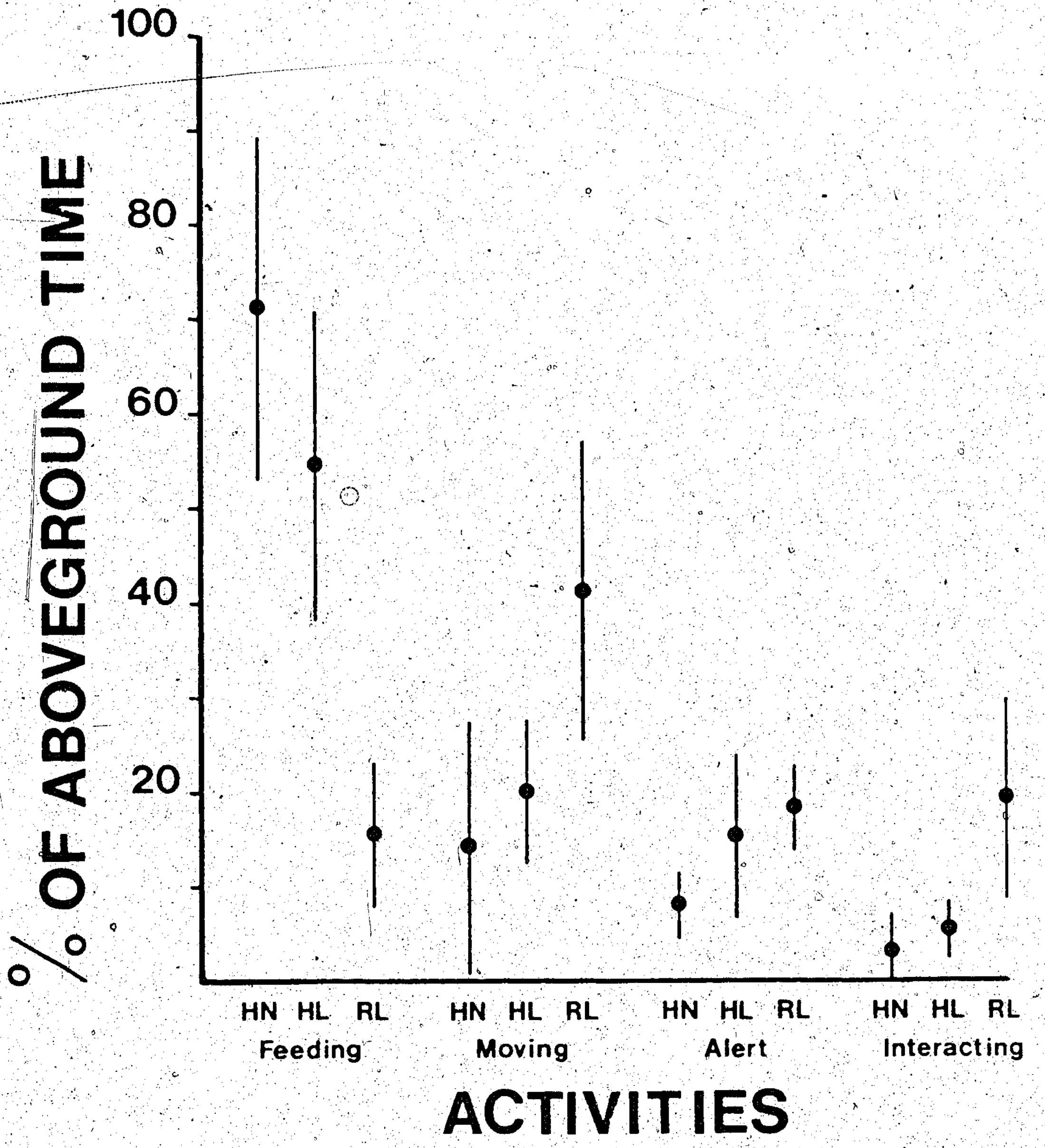

Fig. 2.2. Percentage of aboveground time during the breeding period spent feeding, moving, alert, and interacting agonistically for non-localized males (HN, n = 6) and localized males (HL, n = 5) at HRSA, and localized males at RLSA (RL, n = 8). Number of observations per individual averaged 35±23 (HN), 48±17 (HL), 45±23 (RL). Differences between HL and RL were either significant (Feeding and Moving, $P<0.01$; Interacting, $P<0.05$) or nearly so (Alert, $0.05<P<0.1$). Between HN and HL Alert ($P<0.05$) and Feeding ($0.05<P<0.1$) were different or nearly so.

range sizes, range size was significantly correlated with time spent feeding (*r* = 0.63, *P*<0.05, n = 11) and moving about (*r* = −0.57, *P*<0.05, n = 11).

The proportion of a localized male's total range that overlapped with the range of his nearest localized neighbour averaged 37±18 % (HRSA) and 30±17 % (RLSA). The small amount of overlap suggested localized males were spacing themselves out. Range area was related geometrically to usage (Fig. 2.3), so that the area where males spent 80% of their time was approximately only half that of their total range size [0.18±0.09 ha (HRSA), 0.14±0.04 ha (RLSA)]. There was little overlap between 80% usage polygons of localized males, and locations and directions of interactions (Fig. 2.4) reveal that the resident was dominant within his 80% area and repelled other males from it by chasing them out. Localized males chase other males within their 80% usage areas more often than they are chased by other males, whereas the reverse is true outside their 80% areas (Fig. 2.5). Further, when localized males chased other males that had intruded into their 80% areas, the intruders were chased *out* of the 80% area on 72.2% (13/18: HRSA) and 79.6% (43/54: RLSA) of those occasions. In those instances where localized males that were outside of their 80% areas began chasing other males, 100% (5/5: HRSA) and 80.6% (25/31: RLSA) ended in the other male being further from the border of the localized male's 80% area than it was at the start of the chase.

2.3.2 Spatial association of males with females

At RLSA localized males spaced themselves evenly across the entire area, whereas at HRSA these males were found only on the southern and south-eastern flanks of the study area. Yet density of males emerging on the two areas was about the same for HRSA (9 males/ha) as RLSA (10 males/ha).

As noted above, there appears to be a relationship between snow cover and the rate of female emergence (Fig. 2.1). At HRSA, during the two weeks arbitrarily defined as the 'breeding period', females emerged along the southern and south-eastern flanks of the study area, as these were the areas first to lose their snow cover. Since it was in these snow-free areas that localized males established their territories, the likely resource they were protecting was access to females (Fig. 2.6). There were males in the snow covered areas, but faced with few females they moved over large areas, often

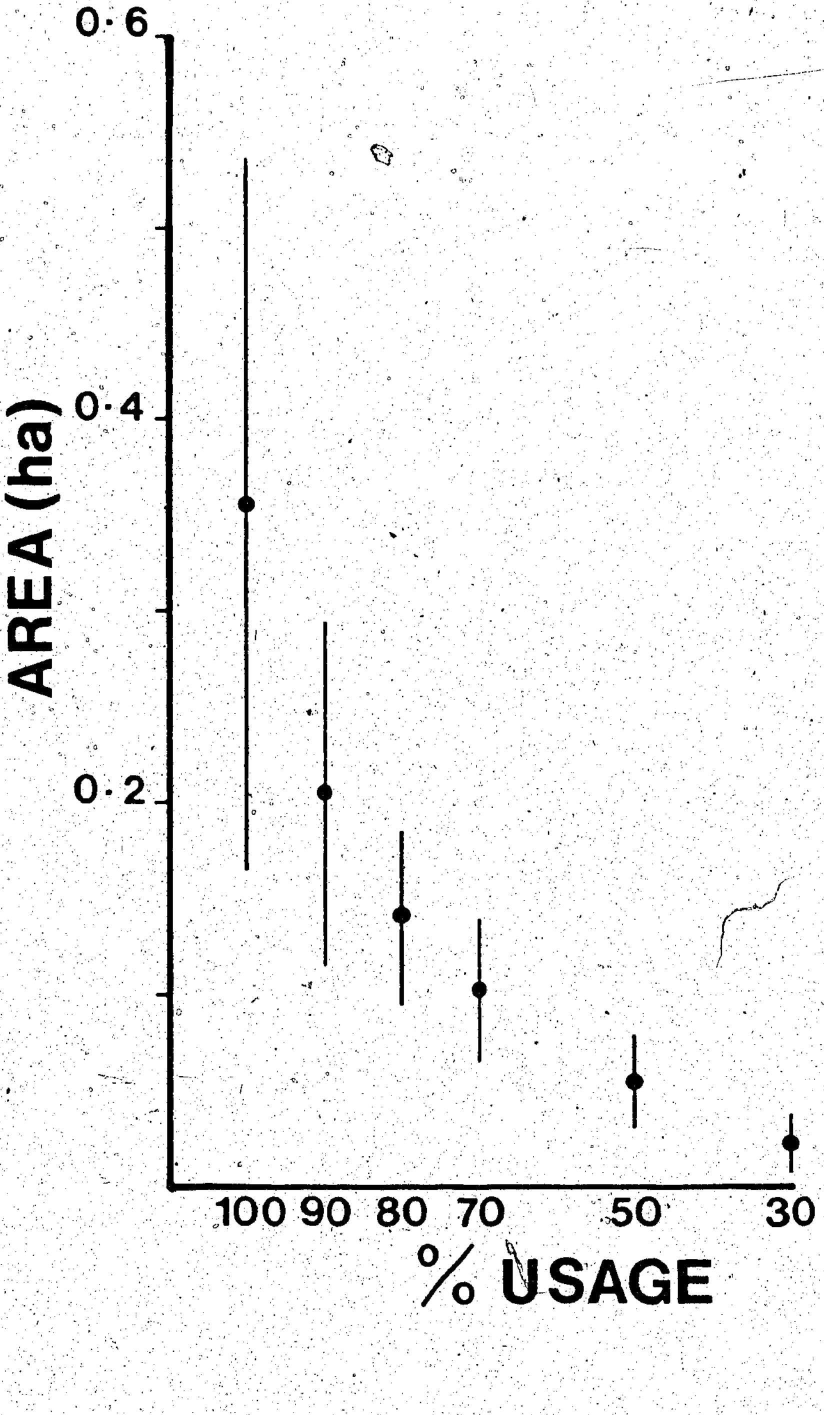

Fig. 2.3. Minimum area polygons in which adult males at RLSA spent a given percentage of their time during the breeding period. (n = 9, # observations/individual = 49±23). ln A = 4.33 + 0.037x, where A is area and x is % usage (r^2 = 0.994).

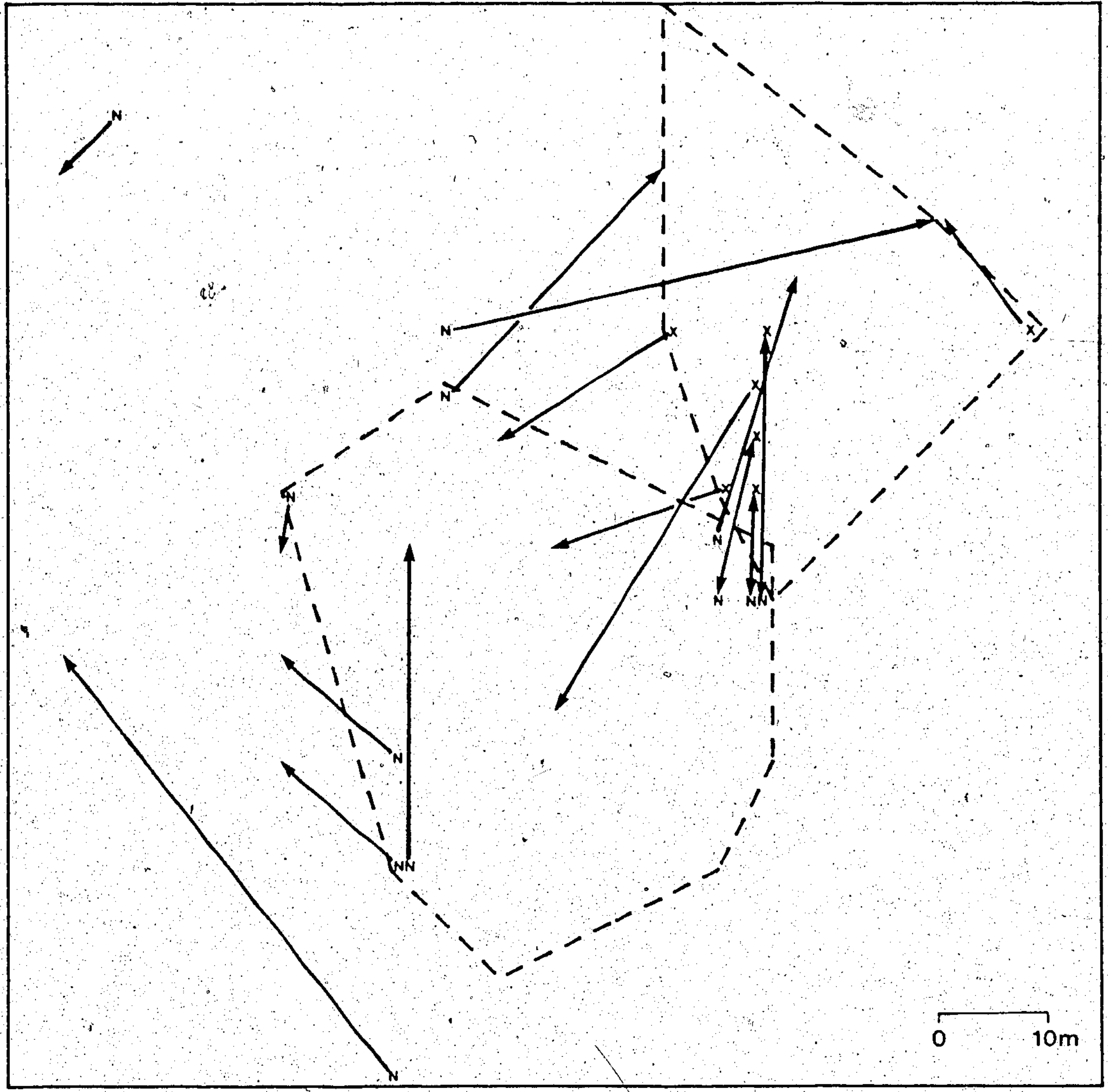

Fig. 2.4. Locations from which males N and X chased other males during the breeding period at RLSA. The direction and length of a chase are shown by the arrow. Double-headed arrows indicate "reverse chases", where males alternatively displaced each other. 80% usage areas of N (lower) and X (upper right) are outlined with dashed lines.

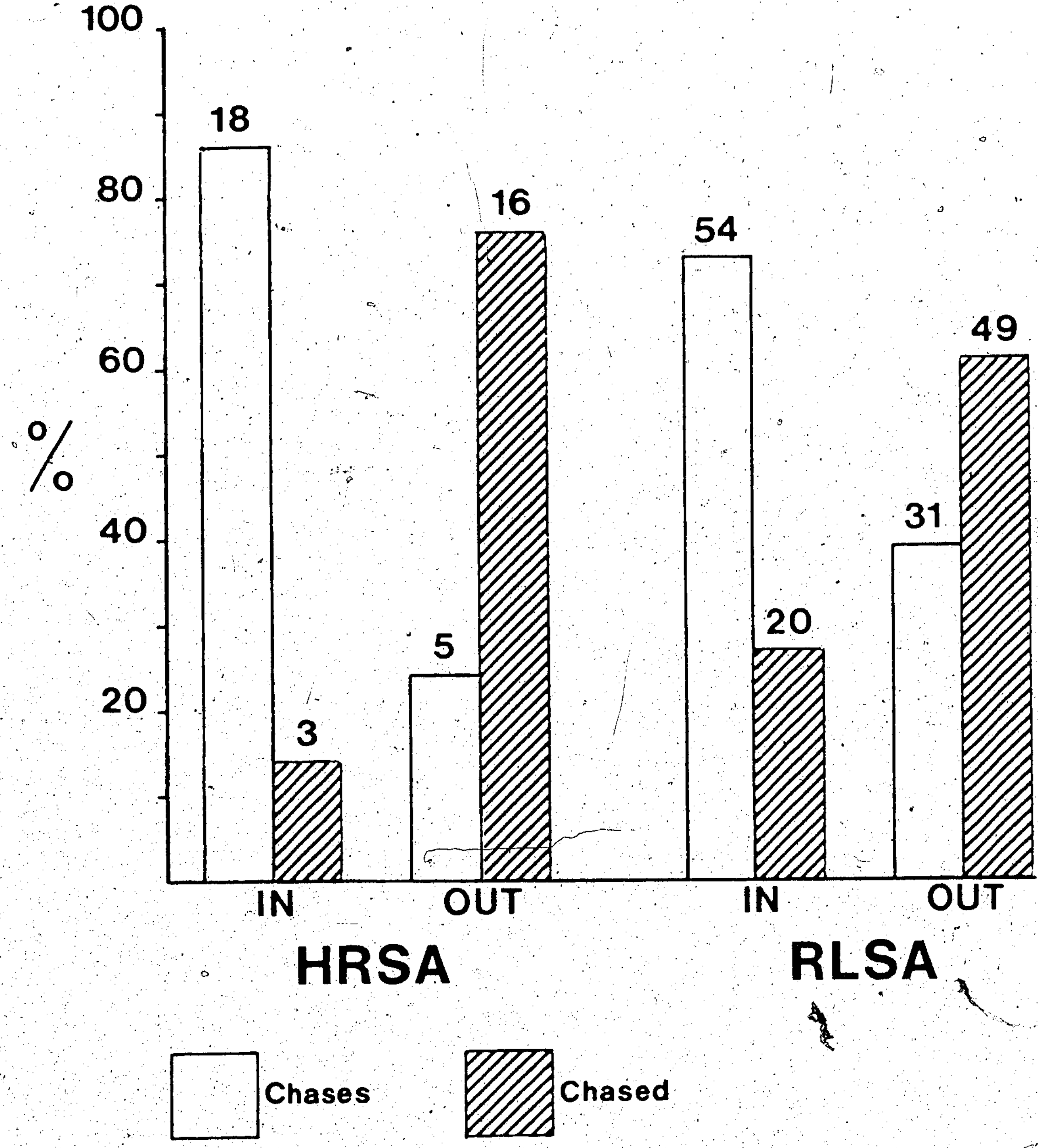

Fig. 2.5. Percent of interactions in which localized males chase, and are chased by, other males inside and outside their 80% usage areas during the breeding period at HRSA and RLSA. Numbers of interactions are given atop the bars.

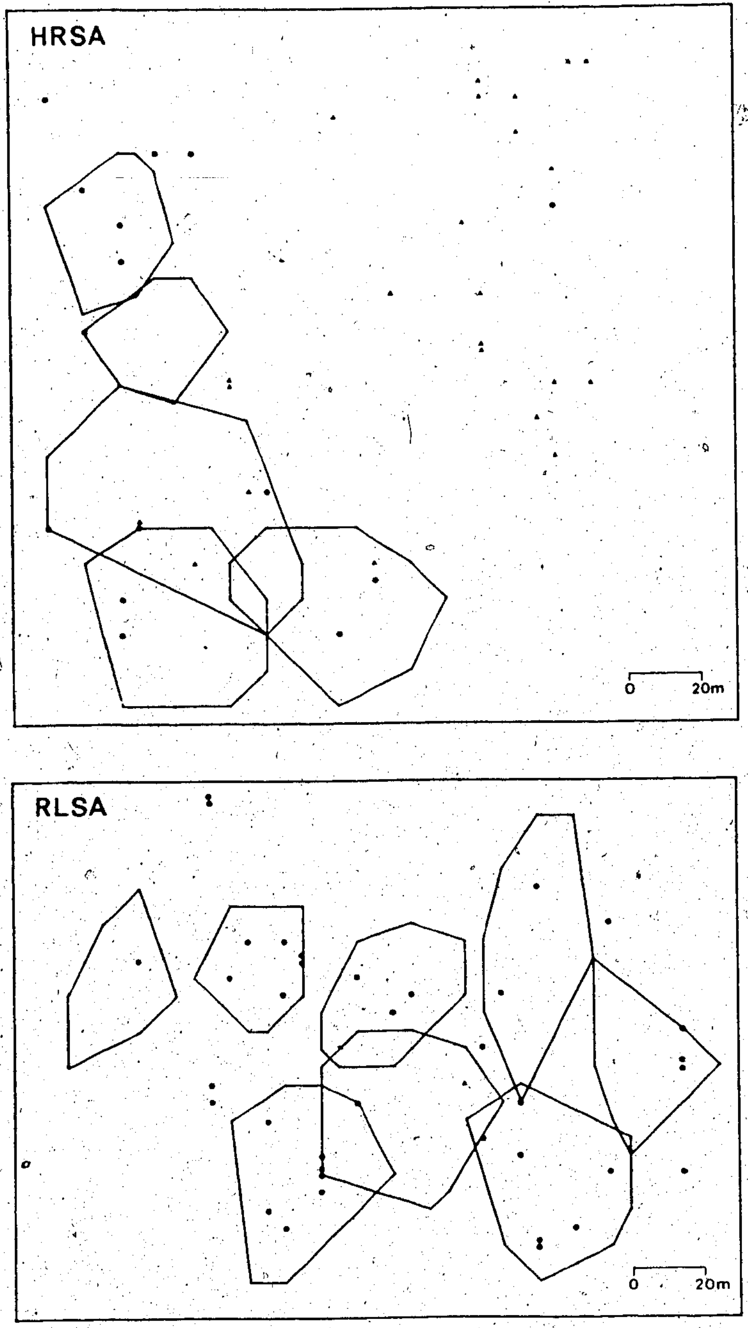

Fig. 2.6. 80% usage polygons of localized males at HRSA and RLSA during the br period. Dots indicate locations at which females emerged from hibernation on or 7 April. Triangles show locations of those females that emerged after 7 April. (Lo were the site at which the female was first captured).

trying to challenge established localized males for their territories. By contrast, at RLSA nearly all females (98%, n = 40), emerged within the two-week 'breeding period' and were spread throughout the study area (Fig. 2.6).

Density of females at RLSA (22/ha) was 38% higher than at HRSA (16/ha). This may have accounted for the slightly smaller territory size (i.e., 80% usage polygon) of males at RLSA, (although this difference was not significant, U = 29, P>0.1), since males at RLSA still had twice as many females (x = 4.4, SD = 2.4, n = 8) emerging within their territories, compared to HRSA (x = 2.2, SD = 0.8, n = 5). The higher density and synchronous emergence of females at RLSA may explain the intensification of male-male conflict at RLSA relative to HRSA, as the increased density of the resource (i.e., females) would be harder to defend from other males, requiring more alertness and moving about, and resulting in there being more agonistic interactions and less time for feeding (Fig. 2.2). Male-male interaction rates averaged 0.90 interactions/hour/male aboveground at RLSA during the breeding period, compared to 0.25 interactions/hour/male aboveground at HRSA.

Only some of the males remained resident on the study areas in the post-breeding period (defined here as beginning on 21 April, or approximately the time of birth of young on the area). At HRSA, 7 of the males were not seen on the study area after 21 April, and presumably had moved away. Four remained resident. At RLSA, one male was killed by a hawk two days after the end of the breeding period, another disappeared (perhaps to the same fate) and had his territory taken over by a new localized male, 78% of whose range overlapped that of his predecessor's. Two males moved off the study area and established post-breeding ranges that did not overlap their breeding period ranges, and three others were seldom observed during the post-breeding period, presumably having established residencies near, but not on, the study area. Three males remained resident. For those males that remained resident on the study areas, the nest burrows of an average of 4.5 females (SD = 2.6, n = 6) were included in their home ranges.

2.3.3 Are males likely to reside near kin?

Of the four males resident at HRSA, one had a post-breeding period range that did not overlap at all the area he occupied during the breeding period, and can therefore be included with those that established post breeding-period residencies off the study area. On average, 46±22% of the post-breeding ranges of the other three resident males at HRSA overlapped their breeding period ranges; and for resident males at RLSA the overlap was 90±10%. During the post-parturition period, these males spent 66±33% (HRSA) and 97±3% (RLSA) of their time in areas they had occupied during the breeding period. Hence, if males sired at least some of the progeny within their breeding period ranges, it is likely that those males that remained after the breeding period had some of their progeny nearby.

Activity budgets in the post-breeding period were similar for males at both HRSA and RLSA (Fig. 2.7), further suggesting that differences between the two areas during the breeding period were the result of differences in the intensity of male-male competition for females, and not due to physiographic differences. However, time spent alert remained high for males at both areas, and perhaps these males aided the survival of young being raised on the area by keeping a watchful eye for predators and excluding strange ground squirrels from the vicinity. Data were available on the post-breeding activities of only one male whose post-breeding range did not overlap his breeding period range. He spent only 9% of his time alert. Three of the post-breeding residents had been localized and three had been non-localized during the breeing period, and the localized males tended to spend more time alert (16.0±3.5%) than did the non-localized residents (12.0±3.0%). During the same period adult females spent on average 15.0% (HRSA) and 18.4% (RLSA) of their time alert (see Chapters 3 and 8).

If males spent the breeding period either near their natal areas or the previous year's breeding range, the potential for inbreeding would exist. Male juvenile's disperse in the fall of their first year (see Chapter 4). The difference in weight between localized and non-localized males (Table 2.2) suggests that non-localized males were probably yearlings, since yearlings usually weigh less than older males at emergence (unpul. data). If the number of male-male interactions in which a male chased another male minus the number of interactions in which it was chased is used as an index of dominance, then

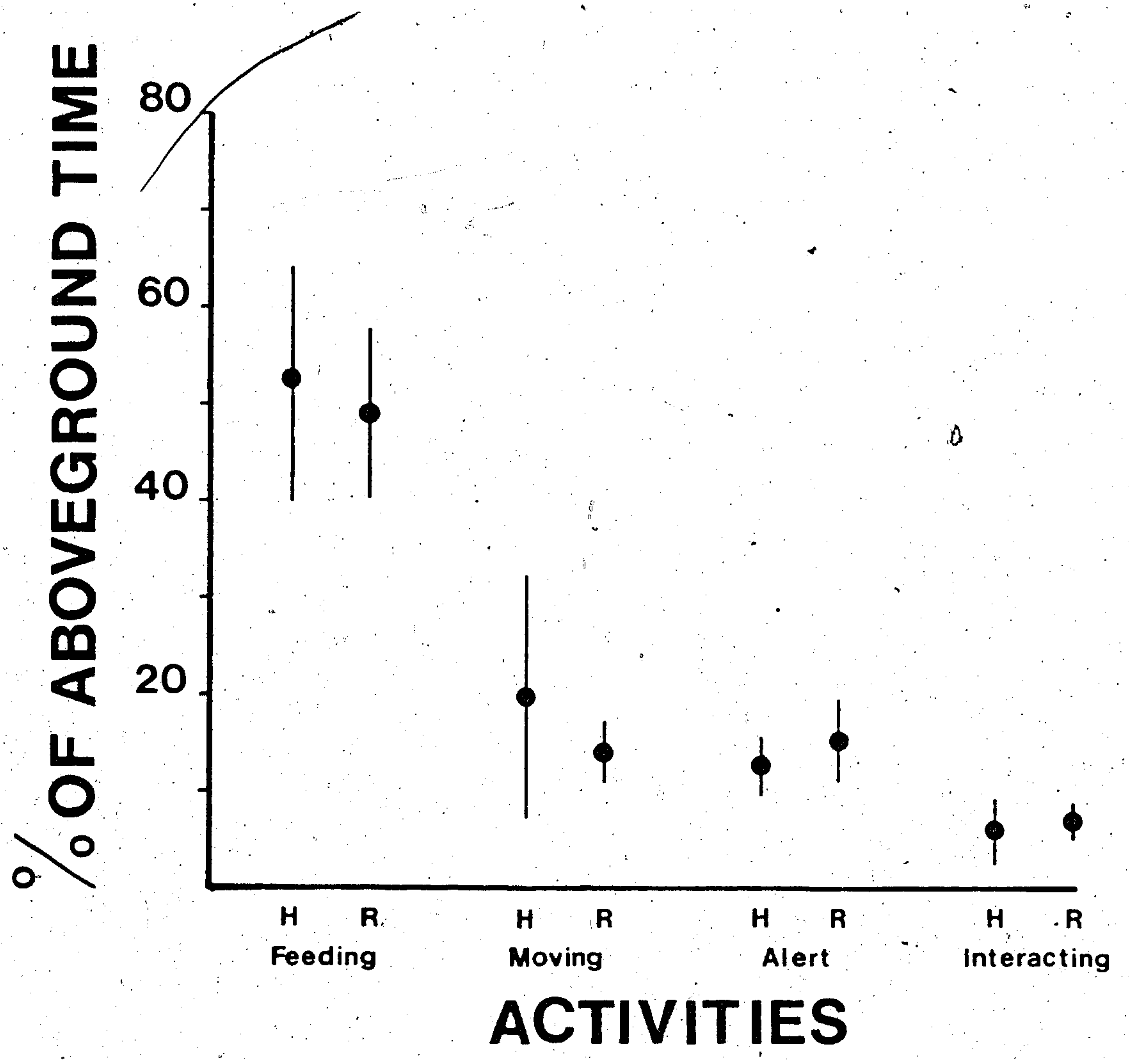

Fig. 2.7. Percentage of aboveground time during the post-breeding period spent feeding, moving, alert, and interactiing, for adult males at HRSA (H, n = 6) and RLSA (R, n = 3). Observations/individual averaged 206±170 (HRSA) and 130±38 (RLSA). Differences between HRSA and RLSA were non-significant for all activities.

Table 2.2. Weights (in grams) of localized males and non-localized males at emergence from hibernation at HRSA (n = 8 and 10 respectively) and RLSA (n = 5 and 13 respectively).

	Localized	Non-localized	P
HRSA	330±42	276±42	*
RLSA	485±23	403±49	**

* $P = 0.05$, Mann-Whitney U-test (2-tailed)

** $P<0.01$, Mann-Whitney U-test (2-tailed)

Table 2.3. Numbers of adults caught and tagged on 10 ha at HRSA in the spring of 1979 and the number recaptured in the spring of 1980.

	# Tagged	# Recaptured	% Recaptured	
Males	43	15	35	ns
Females	76	30	39	

$X^2 = 0.13$

localized males ($x = 4.9 \pm 5.5$, $n = 14$) were more dominant ($U = 107.5$, $P<0.01$) than non-localized males ($x = -0.7 \pm 2.8$, $n = 9$). The low dominance of non-localized males (many of which were probably yearlings) and their tendency to be chased may correlate with spring dispersal of some yearling males. However, recapture rates between years on a 10 ha area were the same for adult males as adult females (Table 2.3), and all 15 males recaught in 1980 were less than 100m from their location during the breeding period in 1979. Further, seven males that had been trapped on the area before 1978 were caught in 1979 or 1980 less than 200 m from their point of initial capture. Thus, most adult males appear to remain in the same general vicinity in successive breeding seasons.

2.4 Discussion

Two main points arise from the results of this study. Firstly, the mating system in Richardson's ground squirrels and individual mating strategies of males are variable, and the behavioural variability observed had ecological correlates. Secondly, the behaviour of male *S. richardsonii* more closely resembles that of the more social species of ground-dwelling sciurids than those with which it traditionally has been considered to be similar.

2.4.1 The mating system

During the breeding period dominant male Richardson's ground squirrels spaced themselves out. Spacing was maintained through overt defense, as localized males were likely to repulse intruding males from an area in which they spent 80% of their time. The reversal of dominance in relation to site, coupled with the active expulsion of male intruders from the area of dominance, is unequivocal evidence of territoriality (Wilson 1975).

The resource being defended was unlikely to have been food (Murie and Harris 1978), as is the function of territoriality in many mammalian species (Wilson 1975), but was access to females. Copulations are rarely observed in Richardson's ground squirrels (Davis *in press*), but each dominant male probably had priority of access, although not exclusive access, to the females that emerged within his territory. Hence, the mating system of *S. richardsonii* can be described as male defense polygyny (Emlen and Oring 1977).

Male defense was most evident at RLSA, where territories were small and distributed throughout the study area; while at HRSA over half of the males studied adopted a non-defense strategy. This variation in the level of male-male competition cannot be attributed to differences in the density of males, as has been suggested for other species of vertebrates (LeBoeuf 1974, Bradbury 1980, Davis 1979). The longer mating season at HRSA, resulting from the asynchronous emergence of females, produced a patchy and unpredictable spatial pattern of the resource (i.e., females). For those males on areas without females, the benefit of territorial defense would be low relative to the cost, and it was probably more adaptive to range widely seeking either to displace residents territorial in areas with females or to obtain sneak copulations (Dawkins and Krebs 1978). Such behaviour has been referred to as a 'satellite male strategy' (Emlen 1976), and as 'gallivanting' (Barash 1981). The observation of a non-localized male at RLSA copulating aboveground (Davis *in press*) suggests that non-localized males are able to successfully obtain copulations.

While the asynchronous emergence of females at HRSA increased the operational sex ratio (i.e., the number of males relative to the number of females), the differences between the two study areas did not support the predictions of the theory (Dobson *in press*, Emlen 1976), since where females did emerge along the southern and south-eastern flanks of the HRSA, dominant males still maintained territories instead of evincing a lek-type of mating system as found in Belding's ground squirrels (Sherman 1976).

Some quality of the habitats may have influenced the form of the mating system. Squrrels at RLSA were heavier than those at HRSA, despite a shorter growing season (unpubl. data) and higher densities This implies food quality was perhaps better at Roi Lakes, ultimately accounting for the density of females emerging upon the area. Thus, if male behaviour during the breeding period is dependent on the distribution and abundance of females, this will be affected by:

1. the synchrony of female emergence, which is influenced by snow-cover, and
2. the density of females, which is influenced by habitat quality.

2.4.2 Sociality

Adult male Richardson's ground squirrels defend territories during the breeding season that overlap the ranges of several females, and some continue to maintain post-breeding ranges that encompass the nest burrows of several females. This association of adult males with adult females resembles the pattern found in Arctic ground squirrels (McLean *in press*), Columbian ground squirrels (Murie and Harris 1978), black-tailed prairie dogs (Hoogland 1981), hoary marmots (Barash 1981), and yellow-bellied marmots (Armitage 1974). Such an association is characteristic of high levels of sociality in the North American Marmotini (Armitage 1981, Michener *in press*). By contrast, a lack of male territoriality and post-breeding association of males with females is characteristic of the less social species of ground squirrels (Balph and Stoke 1963, Dunford 1977, Sherman 1976). The results of this study show that the classification of Richardson's ground squirrels as belonging to the latter group (Armitage 1981, Michener *in press*) is inappropriate.

In the less social ground squirrel species males compete for access to females (Sherman 1976), and in Belding's ground squirrels females usually mate with more than one male and most litters are multiply sired (Hanken and Sherman 1981). As well as ensuring access to females, male territoriality in the more social species probably functions as "mate guarding" (Barash 1981) so that the incidence of multiple matings is reduced. Mate guarding could then provide some assurance of paternity, such that a territorial male that continues to reside in the area where it bred is likely to have sired at least some of the offspring in that area. Given a likelihood of paternity there is the potential for paternal investment (Grafen 1980), which could be expressed through watching for predators and giving alarm calls. Males do alarm call and/or chase predators in the more social species (Barash 1975, 1981, Hoogland 1981, McLean *in press*), but not in the less social species (Dunford 1977b, Schwagmeyer 1980, Sherman 1977). Adult male Richardson's ground squirrels do alarm call and chase predators from areas in which they are likely to be related to the young present there (see Chapter 7).

2.5 Acknowledgements

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3. Territoriality, Familiarity, and Kinship in Adult Female Richardson's Ground Squirrels *Spermophilus richardsonii*

3.1 Introduction

The common denominator of sociality throughout the Marmotini is the association of adult female kin (Armitage 1981, Michener *in press*), and kin selection (Hamilton 1963, Maynard Smith 1964) has been proposed as the primary mechanism that led to the evolution and maintenance of sociality in these species (Barash 1974; Dunford 1977; Michener *in press*). For nepotism, the favouring of relatives, to occur, degrees of relationship and the costs and benefits of such behaviour (Hamilton 1964) are not the only conditions upon which kin selection is contingent, since there must also be the opportunity for related individuals to influence each others survival and/or reproductive success. Favouritism is not likely to be selected for among relatives that overlap in time and space infrequently (Sherman 1980).

Males of the genus *Spermophilus* normally disperse before they breed (natal dispersal) and sometimes after they breed (breeding dispersal) (Armitage 1981, Greenwood 1980, see Chapters 2 and 4). By contrast, females are philopatric, maintaining a high level of site fidelity between years to their natal area. As a consequence of this dispersal pattern, closely related adult females (i.e., mother and daughter, sisters) have adjacent and overlapping home ranges when simultaneously present in the population (*S. beldingi* Sherman 1980, *S. columbianus* W.J. King pers. comm., *S. parryii* McLean 1982, *S. richardsonii* Michener 1979, *S. tereticaudus* Dunford 1977).

Kin selection could operate even if kin association resulted solely from minimal female dispersal from a common natal site; however, it would be stronger evidence for the likelihood of nepotistic behaviour occurring if it could be shown that adult female kin associate preferentially. Only McLean (1982) has examined the overlap of home ranges between closely related females and that between distantly related or unrelated female neighbours. However, he considered all neighbours (even non-overlapping neighbours) together, and because the dispersal pattern made it statistically more likely that kin would overlap more than any two contiguous neighbours, his results were biased towards greater overlap between kin. The question of importance in determining preference for kin is, do adult female ground squirrels associate more with their nearest kin than their nearest non-kin?

Since uterine-kin share common experiences in the nest burrow, it is possible that subsequent association and preferential treatment between adult female kin could be the result of familiarity (Bekoff 1981, Davis 1982). Although such a mechanism would still permit the operation of kin selection, a question that arises is, does familiarity through length of association of adults affect the likelihood of preferential treatment? Sherman (1980, 1981) presented evidence that it did not in Belding's ground squirrels.

Whereas adult females of Belding's (Sherman 1980, 1981), Columbian (Festa-Bianchet and Boag 1982), and round-tailed (Dunford 1977) ground squirrels defend territories, Michener (1979) has argued that Richardson's ground squirrel females do not defend territories, instead having core areas in which they are unlikely to be submissive while being equally likely to be aggressive anywhere within their range. Yeaton (1972), on the other hand, reported that kin of *S. richardsonii* were "allowed preferential access to defended areas".

Thus, the aims of this study were to examine the pattern of social organization in adult female Richardson's ground squirrels and the potential for kin association, to deduce the effect of relatedness (kinship) and length of association (familiarity) on behaviour towards neighbouring conspecifics, and to examine evidence for female territoriality and overlap of defended areas.

3.2 Methods

Richardson's ground squirrels were studied during 1979 and 1980 at a site (the Highwood River Study Area, HRSA) located on flat, open, fescue grassland 6 km northwest of Longview, Alberta, Canada (50°34'N, 114°18'W; elevation 1235 m). The area was occasionally grazed by cattle. A 1.3 ha study area had a grid of 10 x 10 m squares superimposed upon it by using painted flags and stakes to mark the co-ordinates. In addition squirrels could be observed in a further 5 ha, which in 1980 was marked with a grid of 50 x 50 m squares. During the spring emergence from hibernation in both years, squirrels were trapped over an approximately 10 ha area that extended in all directions from the study area.

All ground squirrels on and surrounding the study area were live-trapped and marked for individual identification by using numbered metal ear tags in both ears, a coloured plastic disc or strip attached to one of the metal ear tags, and letters or numbers painted on the pelage with "blue-black" human hair-dye. Thereafter, squirrels were retrapped usually only as necessary to renew their dye marks. Juveniles were trapped at the time of emergence coincident with weaning, while they were still associated with their natal burrow and mother. From this, matrilineal kinship was obtained for all young brought up on the area during the course of this study. When caught, all squirrels were transferred to a bag and weighed (±5g) using a spring balance. Squirrels were released at the point of capture. In all, 178 adults and 269 juveniles were caught and marked during the two years of the study.

Observations were made from a 2.5 m high stand using 10 x 50 binoculars. All observations were recorded directly onto paper using a "shorthand" code, and later transcribed for computer analysis. Instantaneous scan sampling (Altmann 1974) at 15 minute intervals, on the quarter hour, was used to obtain data on spatial organization, movements, and activity budgets. When a squirrel was seen in a systematic search of the area, its identity, location (locations were recorded as being within a specific 5 x 5 m square), and activity at that instant were recorded. All-occurrences (Altmann 1974) sequence sampling (Slater 1978) was used to record interactions; the identities of the participants, the beginning and end locations of the interaction, and the temporal sequence of behaviours were noted (see Chapter 5).

Observations were conducted between 8 May and 20 August 1979, and between 25 March and 13 August 1980. In all, 397 hours of behavioural observations were made (1979: 90 hours, 1980: 307 hours), and adult females were seen in 228 scans in 1979 and 1168 scans in 1980. Observations were conducted between 0700 and 1900 hours Mountain Daylight Time, with the majority of hours spent on observation in the early morning (0700 to 1100 hours) or late afternoon (1500 to 1800 hours). Observation periods usually lasted for 2 to 4 hours.

For the purposes of analysis, the active season was divided into three parts which correspond to significant biological events taking place in the population (after Dunford

1977 and Michener *in press*). The first phase, the *breeding period*, was defined as that period from the first emergence of females from hibernation until at least 96% of females had emerged. Richardson's ground squirrel females usually copulate in the first 3 or 4 days following emergence (Michener 1980a, Davis *in press*). The *gestation/lactation* period was the time from the end of the breeding period until all litters of young had emerged on the area. It was the period when most females were pregnant and suckling their young, which first emerge aboveground about the time of weaning (Michener 1977). The *postemergence period* was from the time of juvenile emergence until entry into hibernation or the end of this study. Both Dunford (1977) and Michener (*in press*) recognized a fourth, prehibernation phase; but as elements of the population go into hibernation, depending upon sex, age, and reproductive status, from about the time of juvenile emergence, it seemed unwarranted to further sub-divide the postemergence phase.

In 1980 periods were from 25 March to 16 April (breeding), 17 April to 17 June (gestation/lactation), and 18 June to 13 August (postemergence). In 1979, observations did not begin until 8 May which was near the end of the gestation/lactation period (9 June). Hence, for this paper, 1979 data are treated as a whole, and used only for the purposes of examining between-year movements.

Home ranges were computed using the minimum convex polygon method (Mohr and Stumpf 1966). Area calculations were made for each period only for those females with more than 20 locations within the period. A given percentage of the most outlying locations from the geometric centre of activity, was excluded when calculating percentage usage areas (i.e., the minimum area in which an animal spent a given percentage of its time).

In this paper, the following three categories of relationship between neighbouring females are recognized: a) uterine-kin (mothers and daughters, or sisters), b) familiar (females that have been neighbours as adults for more than one year), c) unfamiliar, non-uterine-kin (a yearling female and her nearest non-uterine-kin neighbour). Female Richardson's ground squirrels first breed as yearlings (Michener 1980a, 1980b), so that any female emerging from hibernation was considered to be an adult in this study.

Non-parametric statistics were employed (Sokal and Rohlf 1969), and the 0.05 probability level of a Type I error is considered significant. Throughout means are given with plus or minus one standard deviation.

3.3 Results

3.3.1 Home range size and site fidelity of adult females

Home ranges of adult females at HRSA in 1980 were smallest during the breeding period, increased during gestation and lactation, and decreased again after the emergence of the young (Fig. 3.1). However, there was a positive correlation between number of sightings of a squirrel and its calculated home range in all periods (breeding: r = 0.26, P>0.05; gestation/lactation: r = 0.52, P<0.01; postemergence: r = 0.69, P<0.01), so that home range may be underestimated for those animals sighted least frequently. Small sample sizes occur particularly during the breeding and postemergence periods.

For females that had been resident on the area as adults in 1979, their 1980 home ranges included, on average, 96% (SD = 10, n = 11) of their 1979 ranges, and the difference between their geometric centres of activity for 1979 and 1980 averaged only 8.6 m (SD = 4.6, n = 11). Hence, adult females were extremely faithful to the site they had occupied the previous year.

3.3.2 Territoriality

If females exhibit such extreme site tenacity, are they also dominant within their areas, or parts of it, and do they actively exclude other females from their area? In other words, is the pattern of their spatial organization maintained through territorial behaviour?

Females spent little time in the bulk of their home range (Fig. 3.2), on average spending 80% of their time within an area that made up only 18% of their home range. For minimum areas (usage polygons) in which they spent less than 80% of their time (Fig. 3.2), the reduction in area was almost directly proportional to the reduction in usage (r = 0.97).

Plots of locations where females initiated interactions against other adult females that resulted in the displacement of the responder (i.e., the responder fled, usually chased

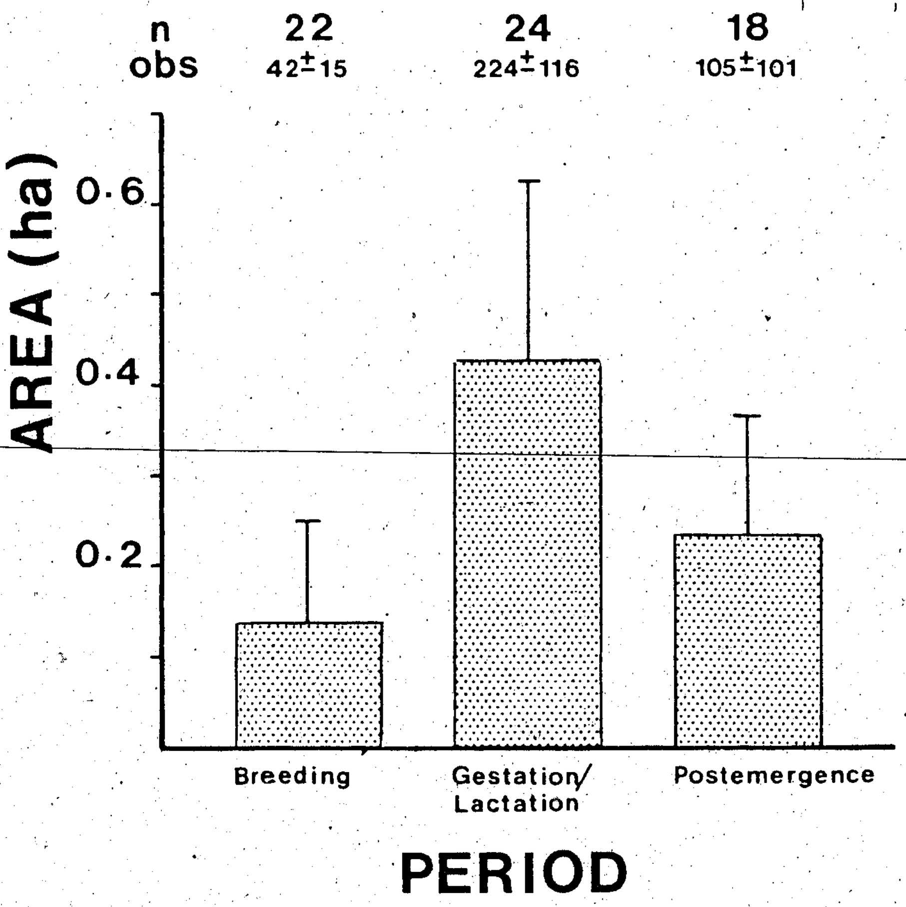

Fig. 3.1. Home range sizes of adult female Richardson's ground squirrels at HRSA during the breeding period (25 March–16 April), gestation/lactation period (17 April–17 June) and postemergence period (18 June–13 August). Number of females and average number of observations per female are given for each period.

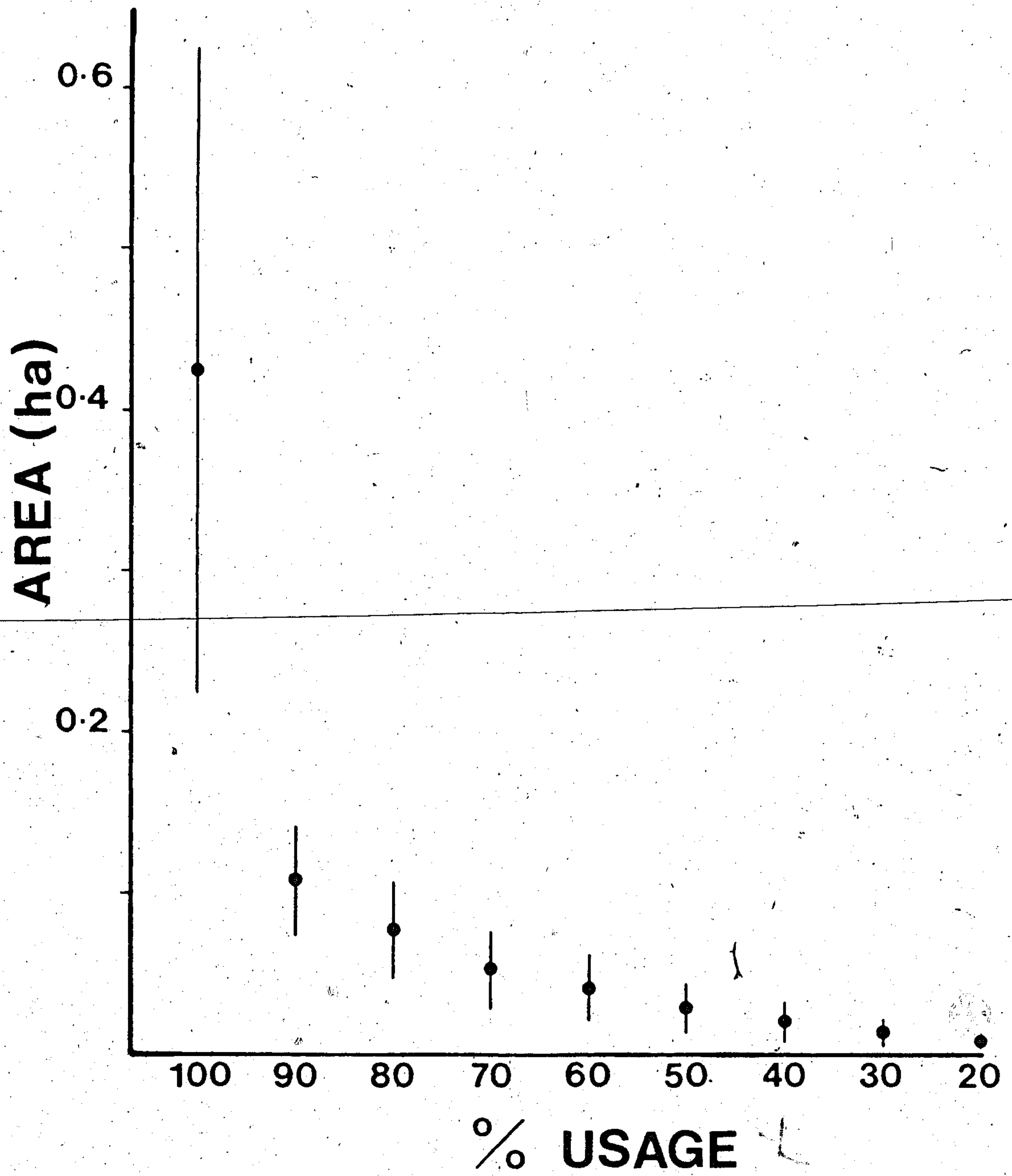

Fig. 3.2. Minimum areas in which adult females at HRSA spent a given percentage of their time during the gestation/lacatation period. (*n* = 24, # observations/female = 224±116).

by the initiator) show a considerable amount of spatial segregation for different individuals (Fig. 3.3). The areas where females were initiating and winning interactions against other females were probably representative of territories, since females were demonstrably dominant within them and actively (by initiating the interactions) excluded others. Visual inspection of the boundaries of usage polygons showed that for individual females, the 80% usage polygon most closely approximated the area in which interactions were initiated and won. Based upon interactions, irrespective of which squirrel was the initiator, females were much more likely to chase other females within their 80% usage areas than they were to be chased by them, whereas the reverse was true for interactions occurring outside the 80% usage area (Fig. 3.4). A preponderance of chasing other females within the 80% area, coupled with the reversal of dominance outside the area, is strong evidence for territoriality. However, 80% usage areas are only approximations of the actual territory, since they are defined by the probability of occurrence within the area and not the probability of defense. While for some females the approximation to the defended area was very close, some females did not defend all their 80% area, and some defended areas outside of it. Nevertheless, henceforth in this paper, 80% usage areas are employed as the best available approximations of territories.

Territories were probably established at the outset of the season, immediately following copulation and the start of gestation, since interaction rates between adult females were highest in the breeding period (0.24 interactions/hour/female aboveground), and decreased thereafter in the gestation/lactation (0.19 interactions/hour/female aboveground) and postemergence (0.11 interactions/hour/female aboveground) periods. The mean territory size during the gestation/lactation period was 784 m^2 (SD = 299, n = 24), and was not as dependent as home range estimates on sample size (r = 0.29, P>0.05). Also, territory size remained relatively constant between the gestation/lactation period and postemergence period (x = 822 m^2, SD=390, n = 18). Territory overlap between years was high for adult females resident in 1979 and 1980, and on average their 1980 territories contained 85% (SD = 20, n = 9) of their 1979 territory.

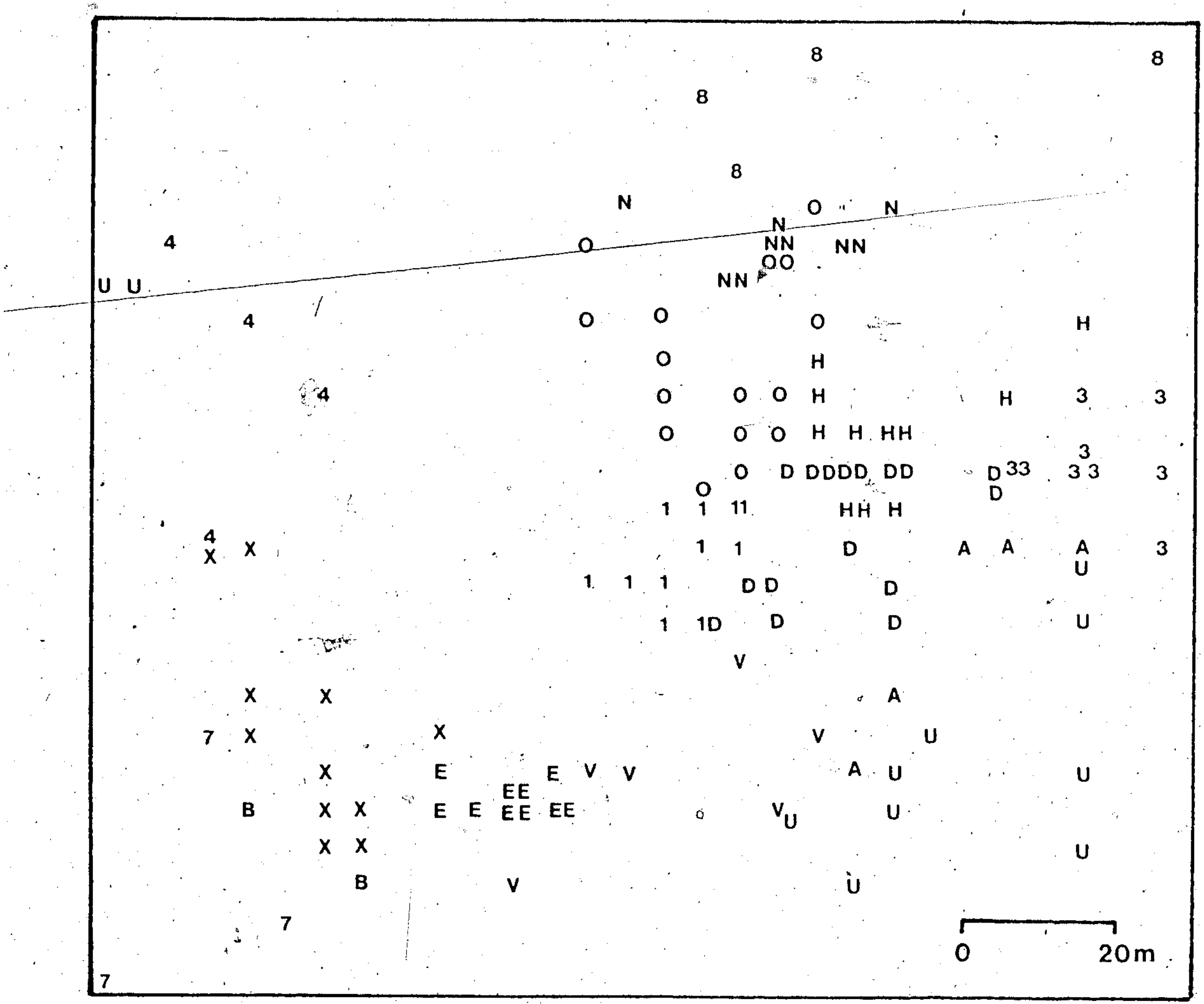

Fig. 3.3. Locations where 16 adult females initiated and won interactions during the gestation/lactation period. Individual females are identified by a letter or number.

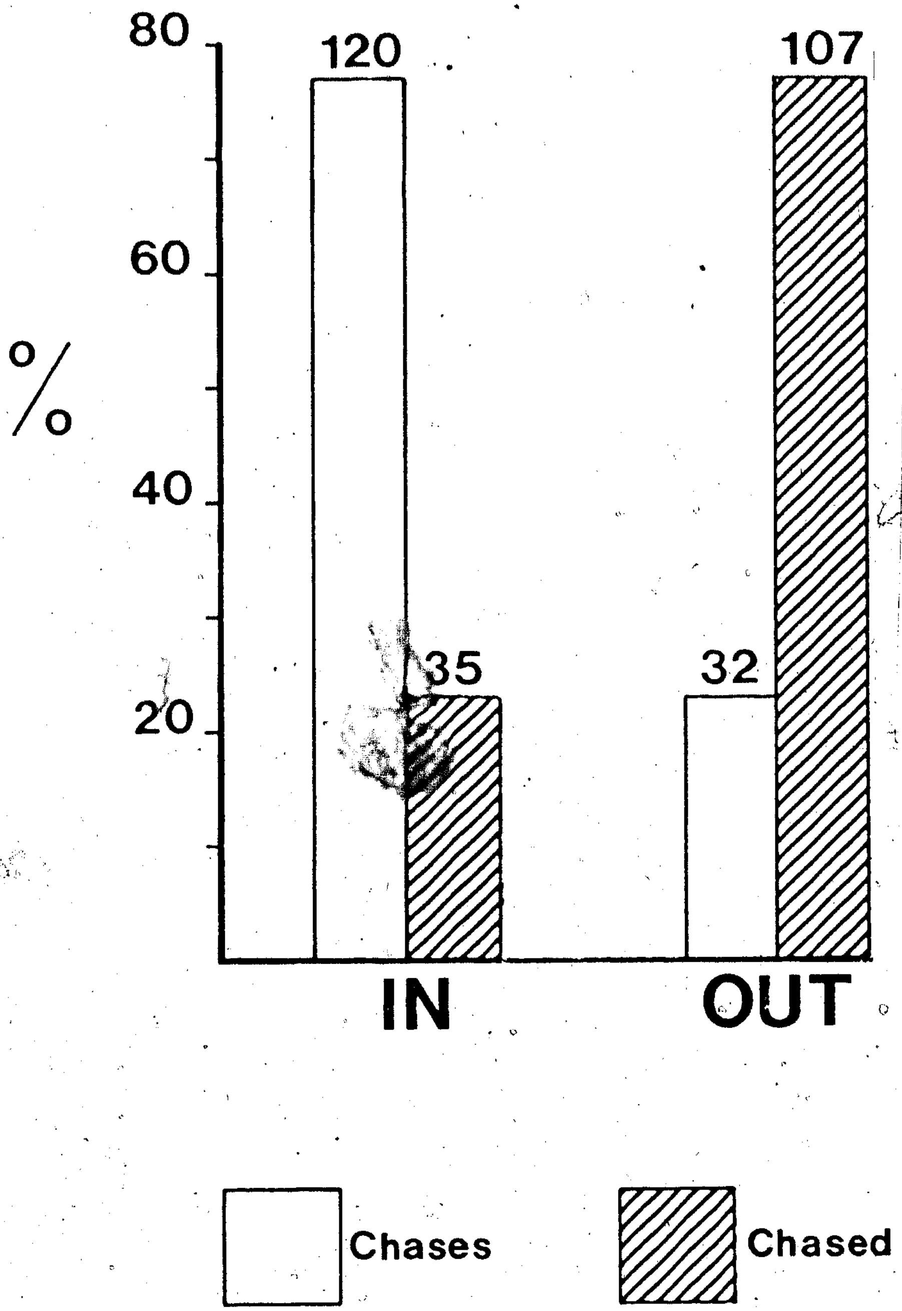

Fig. 3.4. Percent of interactions in which adult females chase, and are chased by, other females inside and outside of their 80% usage areas during the gestation/lactation period. Numbers of interactions are given atop the bars.

3.3.3 Association based upon kinship and familiarity

Only seven females born on the area in 1979 survived and established residency on the area as yearlings, and for only three of these was their mother also present in 1980. One yearling had a sister present in 1980, but although she occupied a contiguous area, it was off the study area. An adult female moved onto the area in 1980 from about 30 m away, while her daughter remained near the natal area. The mother made frequent excursions over to her daughter's area. However, in both cases the sample sizes were so small as to preclude accurate measurement of spatial overlap. Hence, measures of kin association are restricted here to the three mother–daughter pairs.

The mean distance between activity centres of the mother–daughter pairs in 1980 was 12.7 m (range: 7 – 21). By contrast, the average distance between the activity centres of 26 other females and their *nearest* neighbour was 16.2 m (SD = 6.0). Between a female and her nearest familiar neighbour, activity centres were a mean distance of 19.4 m apart (SD = 6.3, n = 16). The average distance between the activity centres of a yearling female and her closest unfamiliar, non–uterine–kin was 18.9 m (SD = 6.8, n = 7).

Hence, adult female kin tended to reside near each other, and they appeared to be closer together than non–uterine–kin nearest neighbours (sample sizes were too small to conduct any meaningful statistical comparisons). Familiar adults were no more likely to be closer together than unfamiliar neighbours (Mann–Whitney U–test: U = 60.5, P>>0.05). Indeed, daughters' home ranges in 1980 included 99% (SD = 2, n = 5) of their mother's 1979 home range, and their territory overlapped 85% (SD = 18, n = 4) of their mother's territory in 1979, irrespective of whether the mother was still alive in 1980.

Overall, mean overlap of home range and territories was higher between nearest uterine–kin, than nearest familiar, or nearest unfamiliar, non–uterine–kin neighbours (Fig. 3.5). However, differences between the groups were not statistically significant because of the large amount of individual variation within the groups and small sample sizes. The amount of overlap increased throughout the season between uterine–kin, while remaining relatively constant between familiar neighbours. Time spent within the overlap area of the home ranges during the gestation/lactation period was not statistically different (Kruskal Wallis H = 2.50, df = 2, P = 0.29) between the groups, and did not indicate increased attraction between related or familiar females (uterine–kin: $\bar{x}$ = 70.2%, SD = 29.0, n = 6;

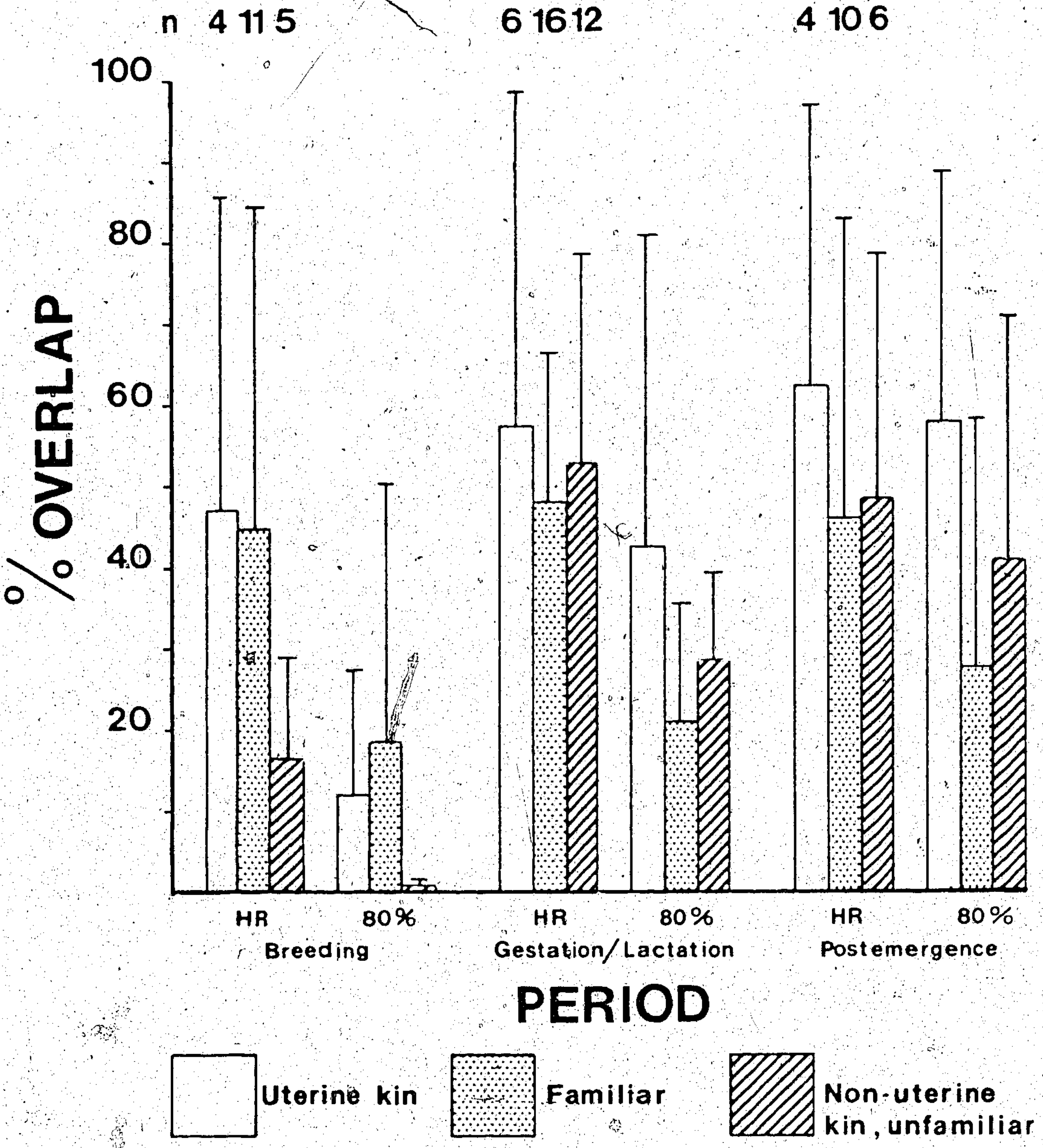

Fig. 3.5. Overlap of home ranges and 80% usage areas (approximations of territories) between uterine-kin, familiar neighbours, and unfamiliar, non-uterine-kin neighbours, during the breeding, gestation/lactation, and postemergence periods.

familiar: x = 63.8%, SD = 24.7, *n* = 16; unfamiliar, non-uterine-kin: x = 77.3%, SD = 13.5, *n* = 12).

However, when both members of a pair were simultaneously above ground, uterine-kin were closer together (x = 16.8 m, SD = 10.8, *n* = 3) than unfamiliar, non-uterine-kin neighbours (x = 24.9 m, SD = 5.7, *n* = 7) ($U = 2$, $P = 0.05$), whereas familiar neighbours were not closer (x = 26.8 m, SD = 4.4, *n* = 11) ($U = 45$, $P >> 0.05$).

In conclusion, when close female kin are simultaneously alive in the population, they are likely to be near each other. However, there is only slight evidence that they may exhibit a preference for each other by associating more than do non-uterine-kin neighbours, or females that also had been neighbours in the previous year.

3.3.4 Female behaviour and reproductive success

Adult females apportioned their time differently throughout the active season. In the breeding period, which corresponded with the period of smallest home ranges, they fed nearly two-thirds of their aboveground time, and spent little time moving about or being vigilant (Fig. 3.6). During gestation and lactation, time spent moving and being alert increased, while the proportion of time feeding was reduced. Relative amounts of time spent feeding were further reduced by females after their young had emerged, when they increased the percentages of their aboveground time spent moving and being vigilant. However, females that did not bring up any young spent more time feeding (x = 62.8%, SD = 7.5, *n* = 4) than did parous females (x = 40.4, SD = 13.5, *n* = 14) ($U = 55$, $P < 0.005$) in the postemergence period. Most females that did not bring up young disappeared from the population, presumably into hibernation, early in the postemergence period, so that accurate activity budgets could be calculated for only four of them. Females with uterine-kin as neighbours did not differ significantly from the rest of the population for time apportioned to any behaviour during any period.

Breeding success was low; 2.8 young per female (SD = 2.4, *n* = 32) emerged at weaning, and litter size did not differ significantly for those with uterine-kin, those with familiar neighbours (which were by definition all 2 years or older), or yearlings.

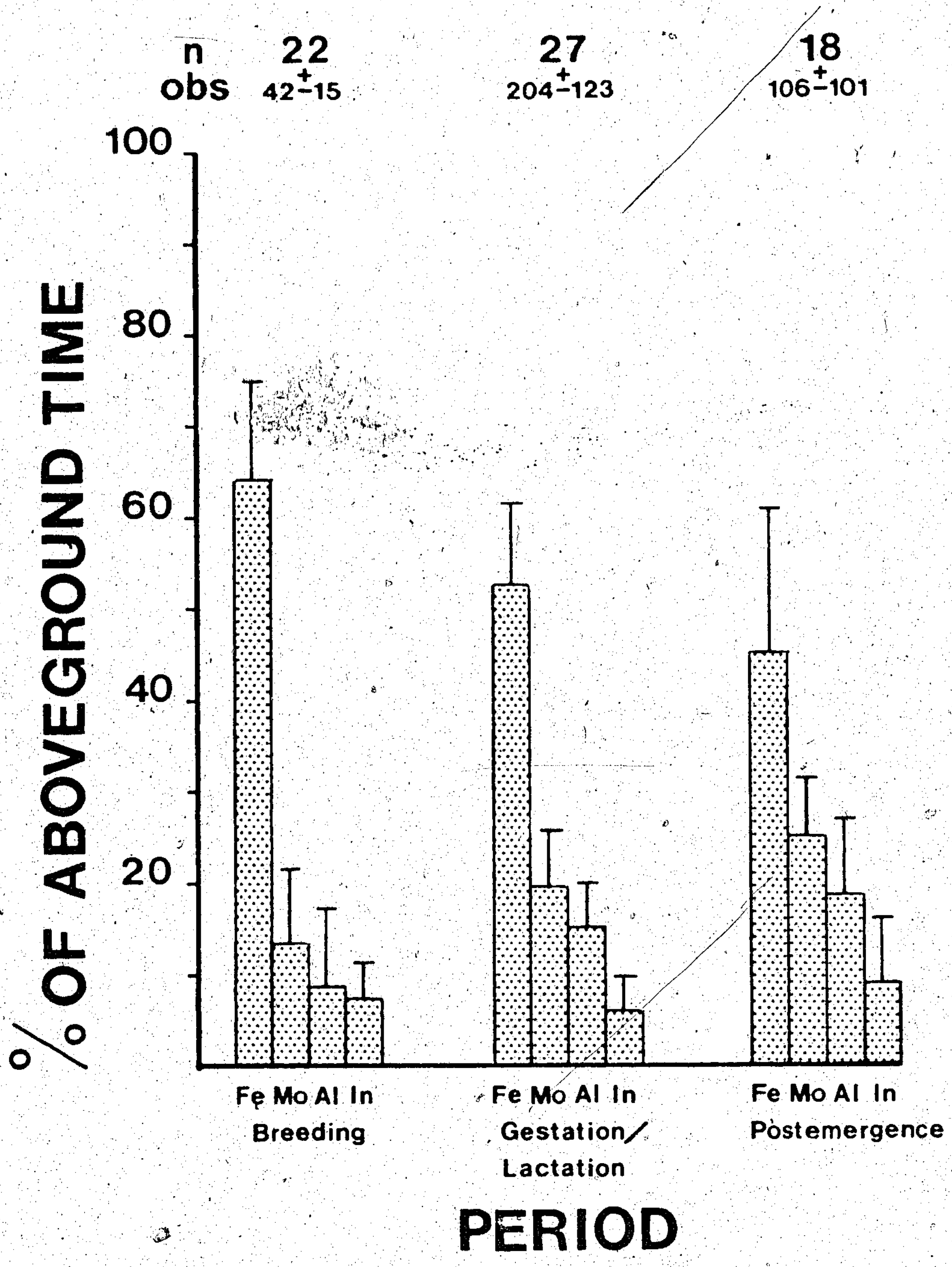

Fig. 3.6. Percentage of aboveground time spent feeding (Fe), moving about (Mo), Alert (Al), and Interacting (In) for adult female Richardson's ground squirrels during the breeding, gestation/lactation, and postemergence periods. Numbers of females and observations per female are given for each period.

3.4 Discussion

Adult female Richardson's ground squirrels upon emergence from hibernation spent most of their time feeding, moved about little, and consequently confined themselves to relatively small home ranges. When pregnant and suckling young adult females used larger areas and fed at a greater distance from the nest burrow. That was also a time of increased vigilance as females defended territories around their nest burrows that had been established following spring emergence. The decrease in adult female–female interaction rates in the postemergence period suggests that territorial defense is not as vigourous then.

Michener (1979:128) found home ranges of females (called "total ranges" by her) were smallest during the gestation/lactation period. Dunford (1977) found that in round-tailed ground squirrels size of home ranges of females decreased as the active season progressed. In a study of Columbian ground squirrels, home ranges of females were largest during late lactation and juvenile emergence (Festa–Bianchet and Boag, 1982). The differences apparent from these studies may in part be due to sampling differences. These studies provided home range estimates for short periods (8 – 14 days), while I chose periods that were directly related to significant biological events occurring in the population. Home range estimates are dependent upon sample size (Owings *et al* 1977, this study), and while the division of the active season into short periods of equal duration is useful for studying the relative amounts of space used per unit time, the home range estimates for the gestation/lactation period in this study (based on an average of over 200 observations per individual) illustrate that the actual area frequented by females when pregnant and lactating is larger than biweekly estimates would indicate (Michener 1979).

The demonstration in this study that adult female Richardson's ground squirrels exhibit territorial behaviour contradicts Michener's (1979) conclusion. My results agree with the impressions of Yeaton (1972), Quanstrom (1968), and Wehrell (1973), that female *S. richardsonii* defend territories. Territorial behaviour, as measured by the rate of agonistic interactions, was most pronounced in the latter part of the breeding period and the early part of the gestation/lactation period when boundaries were probably being established. Female territoriality has also been found in Belding's (Sherman 1980), Columbian (Festa-Bianchet and Boag 1982) and round-tailed (Dunford 1977) ground squirrels. The differences between this study and Michener's, are probably due to differences in definition and sampling technique.

For this study I define a territory as "any defended area" (Noble 1939), which is in essence, space related intolerance (Eibl-Eibesfeldt 1970), and is evidenced by site-related changes in dominance. Michener (1979), adhered more closely to Pitelka's (1959) definition that a territory is an area of exclusive use, and emphasized that Richardson's ground squirrels do not have exclusive use of any area. However, the latter definition supplies a function for territoriality without being based on the mechanism of spacing behaviour (Murie and Harris 1978), and the proximal importance of territorial behaviour to adult female relationships is not that territorial boundaries are sacrosanct, but that intruders are likely to be chased (Brown 1975). In female *S. richardsonii*, territoriality has been demonstrated, because within an individual's territory (approximated by 80% usage areas), the resident was much more likely to dominate and chase other females than be chased herself, whereas the reverse was true for areas outside the territory (after Murie and Harris 1978). By contrast, Michener (1979) did not observe interactions to completion, and classed both participants involved in a fight as behaving aggressively, even though most interactions between adult Richardson's ground squirrels result in displacement of one of the participants (see Chapter 5). Thus, by not measuring the outcome of interactions, Michener did not determine the likelihood of dominance and exclusion in relationship to space.

The form of territoriality observed in female Richardson's ground squirrels corresponds to Type A in Wilson's (1975) classification. That is, females defended large areas in which shelter, nesting, and most food gathering activities were located.

The observations that adult females exhibit site fidelity between years, and live near their natal area, agrees with the results from a trapping study of Richardson's ground squirrels (Michener and Michener 1973, 1977). There is a suggestion from the results of this study, albeit a very small sample, that uterine-kin may associate preferentially. Michener (1979) found that while kin were likely to be closer together than non-kin neighbours when simultaneously active, each maintained separate 50% usage areas. My results suggest that association between uterine-kin is greatest after the emergence of young. Association of adult female kin and their litters after emergence (clumping) occurs frequently in Arctic ground squirrels (McLean 1982). While clumping of litters does not appear to be a general phenomenon in *S. richardsonii*, I observed it once in 1979 (unpubl. data), between two females that were probably closely related because they exhibited extensive home range overlap (59% and 75%, respectively) and engaged in frequent "kiss" interactions, which are most common between kin (Davis 1982, see Chapter 5).

The finding that familiarity through length of association as adult neighbours, did not influence the propensity of neighbours to associate, agrees in substance with that of Sherman (1980) for *S. beldingi*. That does not, however, preclude familiarity from having an effect on the operation of sociality. There is evidence that familiar neighbours are treated preferentially to non-neighbours (Wehrell 1973, see Chapter 8).

Surprizingly, there has been little work on activity budgets in ground squirrels. Michener (1979) reported that time spent feeding increased throughout the active season and was highest during the postemergence phase. However, breeding success was extremely low in the year of Michener's study (Michener 1980b), and the feeding rate may have been affected by the high proportion of females not bringing up any young and those with only one young (56%). By contrast, Yeaton (1969) and Wehrell (1973) both found a decrease in the proportion of aboveground time spent feeding at the time of juvenile emergence. As in this study, Wehrell (1973) found that alert behaviour was most pronounced after juvenile emergence.

The picture that forms is that when females emerge in the breeding season they are reasonably sedentary, spending most of their time acquiring energy (feeding) in preparation for the energetically expensive processes of gestation and lactation. It is also the time when territorial boundaries begin to be established. The proportion of time spent feeding decreases during the gestation/lactation period as the result of time spent in territorial behaviour (alertness, interacting and moving about) and perhaps increased vigilance for predators. Similarly, low rates of feeding with relatively high percentages of time spent moving about and being alert, occur during the most territorial phase of male behaviour (see Chapter 2). After juvenile emergence, female–female interactions decrease, but time spent feeding is further depressed in those females with young, presumably because of an increased need for vigilance to protect the young. This is consistent with the behaviour of parous females of thirteen-lined ground squirrels, which are usually the only adults that will give alarm calls, and then only at the time of juvenile emergence (Schwagmeyer 1980).

There was no evidence that kin association or the presence of familiar neighbours affected activity budgets or reproductive success. However, sample sizes for uterine-kin neighbours were low, and a more direct experimental approach is warranted to investigate the effects of kin association (see Chapter 8).

3.5 Acknowlegements

I thank J.O. Murie for guidance and encouragement. I am grateful to F.T. McCaffrey for unswerving assistance during the summer of '79 and spring of '80, and J. Duncan for assisting during 6 weeks of 1980. G.R. Michener was most helpful in getting this study initiated, and provided much advice throughout. Mr and Mrs J. Bews of the Y-Cross Ranch provided me with access to their land. Financial support was provided by a NSERC grant (#A5865) to J.O. Murie and a Canadian Commonwealth Scholarship to the author.

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4. Socialization and Sex Differences in Juvenile Richardson's Ground Squirrels

(*Spermophilus richardsonii*)

4.1 Introduction

Due to their spatial proximity at birth, siblings have the potential to exhibit extremes of co-operation, mediated by kin selection, and competition (Alexander 1974). The development and expression of behavioural relationships early in the lives of juveniles, is an important part of the process of socialization that later shapes their behaviour as adults (Fedigan 1982). Yet, with few exceptions (e.g., Bekoff 1978, Berman 1982), there has been little attention given to the development of behavioural relationships amongst juveniles.

In ground squirrels, studies of juveniles have tended to concentrate on litter size (Murie *et al* 1980), growth rates (Koeppl and Hoffmann 1981), and the ontogeny of behavioural motor patterns (Ferron 1981). Recently it has been found that juvenile ground squirrels can differentiate their biological siblings from non-siblings even without postpartum experience of them (Davis 1982, Holmes and Sherman 1982), although in some species of rodent familiarity between juvenile conspecifics can override the effects of kin recognition (Kareem and Barnard 1982, Porter *et al* 1981). Since juvenile Richardson's ground squirrels (*Spermophilus richardsonii*) spend the first 30 days (Michener 1977) of their lives below ground in a nest with only their littermates and mother, they are more familiar with their siblings than with other juveniles, and hence could discriminate sibs from non-sibs whether the mechanism was based upon familiarity, a genetic recognition system, or both.

Studies in the field (Dunford 1977, Michener 1981, Yeaton 1972) and laboratory (Sheppard and Yoshida 1971), have shown that siblings treat each other less agonistically than do non-siblings. This is not, however, an universal phenomenon. Coyote siblings engage in serious fighting when 3 to 6 weeks old (Bekoff 1978), interactions between sibling Richardson's ground squirrels are as likely to include fighting behaviours as those between non-siblings (see Chapters 5 and 6), and in yellow-bellied marmots periods of extremely agonistic sibling interactions can precede dispersal by yearlings, with dominant sibs remaining in the colony and subordinates dispersing (Webb 1981). A similar process has been postulated to influence dispersal in Columbian ground squirrels (Boag and Murie 1981), and dominance relationships among siblings are common in other mammalian (e.g., Koyama 1967) and non-mammalian (e.g., Safriel 1981) species.

The link between juvenile behaviour and dispersal warrants exploration. In ground squirrels, as in most mammalian species, dispersal is male biased (Greenwood 1980). Although some authors have suggested that dispersal in *S. richardsonii* is accounted for mainly by spring dispersal of adult males (Michener and Michener 1977), others (Schmutz *et al* 1979) indicated that many male juveniles disperse in the summer of their first year. Despite the obvious sex bias in dispersal, behavioural sex differences among juveniles, which may correlate with dispersal tendency, have not been adequately investigated.

Socialization of juveniles was found to be a major determinant of later interactions in rhesus macaques (Berman 1982), but only in one study of ground squirrels has the ontogeny of juvenile relationships even been looked at. A preliminary study of juvenile relationships was made by Michener (1981) on 14 juvenile *S. richardsonii*, half of which were individually identifiable for the duration of the study.

In this study, I present results on the relationships between 134 juveniles, marked for individual identification from the time of emergence above ground at weaning, during four summer seasons at two localities. I examine use of space, activity budgets, and interactions for evidence of kin differential behaviour and sex differences, and relate the latter to data collected on dispersal by juveniles.

4.2 Methods

Juvenile Richardson's ground squirrels were studied during 1979 and 1980 at the Highwood River Study Area (HRSA) located 6 km northwest of Longview, Alberta, Canada (50°34'N, 114°18'W; elevation 1235 m), and during 1980 and 1981 at the Roi Lakes Study Area (RLSA), 12 km northwest of Stony Plain, Alberta (53°35'N, 114°05'W; elevation 730 m). Both areas were situated in grassland that was sometimes grazed by cattle. Each study site consisted of 1.3 ha divided into a grid of 10 x 10 m squares by using painted flags and stakes to mark the co-ordinates. All adults on and near the study areas were live-trapped and marked for individual identification when they emerged from hibernation in the spring (see Chapters 2 and 3). At the HRSA squirrels were trapped over a 10 ha region during the spring, that extended in all directions from the study area.

Adult female Richardson's ground squirrels copulate a few days after emergence from hibernation (Davis *in press*) and following a gestation period of 23–24 days, the young are born in a natal burrow from which they do not emerge above ground until the time of weaning when 30 days of age (Michener 1977). Dates of emergence for all litters on the study area were recorded. Young were live-trapped on the day of emergence or soon thereafter, when each juvenile was still associated with its natal burrow and mother, so that matrilineal kinship relationships could be determined. At capture, all juveniles were weighed (±5g) using a spring balance, and marked for individual identification with numbered metal ear tags in both ears, a coloured plastic disc or strip attached to one of the metal tags, and a letter or number painted on the pelage with "blue-black" human hair-dye. In all, 474 juveniles (HRSA: 126 [1979], 143 [1980]; RLSA: 137 [1980], 68 [1981]) were caught and marked on or in the vicinity of the study areas. Juveniles were usually only retrapped as necessary to renew dye marks. However, in 1981 juveniles at RLSA were trapped and weighed once per week (every Tuesday, weather permitting).

Squirrels on the study area were observed with 10 x 50 binoculars using instantaneous scan sampling (Altmann 1974) at 15 minute intervals on the quarter hour. Each animal's location and activity[2] at the instant it was seen in a systematic search of the area were recorded. Activities were classified into ten mutually exclusive and all inclusive categories. All occurrences of interactions were noted using sequence sampling (Slater 1978) in which the identities of participants, their locations, and the temporal sequence of behaviours were recorded (see Chapter 5). Juveniles were observed during 313.5 hours of observation, which included 166 and 488 scans at HRSA in 1979 and 1980, respectively, and 373 and 202 scans at RLSA in 1980 and 1981.

Home ranges were computed by fitting a minimum convex polygon (Mohr and Stumpf 1966) to an individual's locations. The most outlying 20% of locations from the individual's geometric centre of activity were excluded when calculating 80% usage areas (i.e., the minimum area in which the individual spent 80% of its time). Only juveniles that were sighted at least 20 times were used for area and activity budget calculations for the

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[2] activities were not recorded during 1979 at HRSA

postemergence period as a whole. A subsample of these individuals, with many sightings each, was used for the biweekly analysis of spatial relationships during the postemergence period. Unlike other studies that have divided time according to calender periods (e.g., Michener 1981), periods were allocated according to the age of the individuals being examined. Thus, home ranges and overlap between sibs were calculated for two week periods from the time of emergence of each litter. As juveniles emerge when 30 days old (Michener 1977), ages of juvenile within a period could be estimated (Table 4.1) and all juveniles included for a given period are approximately the same age.

Where data did not deviate from a normal distribution, parametric statistics were employed. The 0.05 probability of a Type I error is taken as the level of significance throughout this paper. Means are shown with one standard deviation.

4.3 Results

Overall, an average of 3 juveniles per adult female were weaned, except for 1980 at RLSA when breeding success was twice this high (Table 4.2). While the density of juveniles emergent upon the areas varied between years, there were consistent regional differences that were not affected by yearly variations in breeding success. Mean sizes of litters did not differ significantly between years on either area, but were significantly greater at RLSA than at HRSA (Student's *t*-test: $t = 3.24$, $P<0.005$). Weights of young at emergence were similar between RLSA in 1981 ($x = 105±20$ g, $n = 55$, minimum weight = 70 g) and HRSA in 1979 ($x = 97±21$ g, $n = 63$, minimum weight = 70 g). Weights did not vary between 1980 ($x = 111±23$ g, $n = 81$, minimum weight = 65 g) and 1981 at RLSA (Student's *t*-test: $t = 1.41$, $P>0.1$), but at HRSA juveniles emerged in significantly lighter condition in 1980 ($\bar{x} = 75±27$ g, $n = 90$, minimum weight = 30 g, 39 [43.3%] weighed less than 65g) than in 1979 (Student's *t*-test: $t = 5.72$, $P<<0.001$). Coupled with a doubling in the proportion of females failing to bring up a litter, the low weights in 1980 suggest the females may have been affected by the late snowfall (see Chapter 2) and/or disease. In fact, the density of young on the HRSA during 1980 was even lower than shown in Table 4.2, since many of the juveniles perished within the first few days following emergence, probably because of their apparently weakened condition.

Table 4.1. Ages of juveniles during weeks following emergence aboveground.

Post emergence (weeks)	1-2	3-4	5-6	7-8	9-10	11-12
Age (days)	30-43	44-57	58-71	72-85	86-99	100-113

Table 4.2. Variables related to the production of juveniles at HRSA and RLSA in the years of the study.

	HRSA		RLSA	
	1979	1980	1980	1981
# Adult females	29[1]	25[1]	20	19
% females without young	17	36	0	54[2]
Mean reproductive success (young/female)	3.1	2.8	6.1	3.0
Mean litter size at weaning	3.8±1.5	4.4±1.7	6.1±3.0	6.3±2.4
Range of litter size	1-6	1-8	2-13	2-10
# young on area	92	70	121	57
Density (young/ha)	71	54	93	44

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[1] not actual density of females, since many [illegible]d areas that extended beyond the 1.3 ha.

[2] adult females in 1981 had been subjected to an experimental removal, and reduced breeding success was probably in part related to the removal (see Chapter 8).

4.3.1 Postemergence Spatial Relationships Between Juveniles

Following emergence above ground at weaning, the family unit maintained its distinctiveness; juveniles continued to be active closer to their sibs than their non-sibs (Table 4.3), and within their mothers' territory (Fig. 4.1). Brothers were as likely to be near each other as were sisters (distances between activity centres of brothers averaged 7.7±5.7 m, n = 53, and those of sisters averaged 6.5±4.4 m, n = 50, t = 1.25, P>0.2), and where juveniles had both a brother or a sister present, they were no more likely to be nearer to a sib of the same sex than one of the opposite sex (distances between activity centres of nearest kin of the same sex, x = 6.3±5.1 m; between those of nearest kin of the opposite sex, x = 6.3±4.8 m, Paired t-test: t = 0.02, P>0.9, n = 78 pairs). Distances between centres of activity of nearest littermates were not greatly affected by density at either study area, however, activity centres of littermates were closer together at RLSA than at HRSA (Table 4.3).

Home range size of juveniles was significantly larger in the year of lowest density (1980) at HRSA, but that was not true at RLSA (Fig. 4.2). In all years, on both study areas, regardless of density, overlap of home ranges was greater between sibs than non-sibs (Fig. 4.3a), and juveniles spent more of their aboveground time in the areas of overlap with their littermates than in the areas of overlap with their non-littermates (Fig. 4.3b).

4.3.2 Activities

Juveniles apportioned their aboveground time in a relatively similar manner between years and study areas (Fig. 4.4), although some differences were apparent. During 1980 at RLSA, the year of highest density, proportion of time spent feeding was less than that at either RLSA (t = 7.00, P<<0.001) or HRSA (t = 7.12, P<<0.001) in years of low density. Play fighting between juveniles was more prevalent at RLSA than at HRSA (t = 6.81, P<<0.001), perhaps as a result of the closer association of juveniles at Roi Lakes compared to Highwood River (Table 4.3).

Overall, male and female juveniles spent similar proportions of their time engaged in moving about, vigilance, play fighting, and nest building (Fig. 4). However, on average females consistently tended to spend more of their aboveground time feeding than did males, and male juveniles usually spent more of their time engaging in agonistic

Table 4.3. Comparison of distances to activity centres of nearest littermate and nearest non-littermate (metres).

Area	Year	*n*	Sib	Non-sib	*t*	*P*
HRSA	1979	15	9.7±4.3	15.5±6.0	3.35	**
HRSA	1980	12	8.4±4.2	19.1±4.6	10.43	***
RLSA	1980	59	4.9±4.4	10.5±3.6	6.66	***
RLSA	1981	26	5.6±3.1	12.6±5.9	5.63	***

** $P<0.01$, paired *t*-test

*** $P<0.001$, paired *t*-test

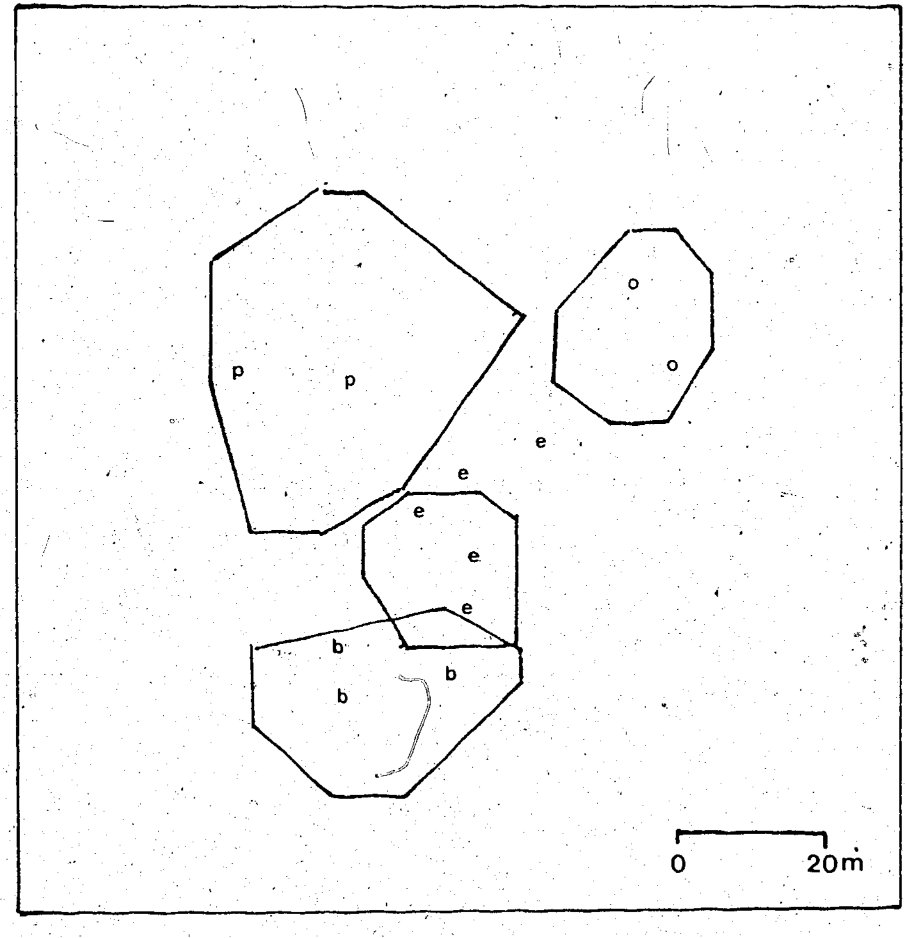

Fig. 4.1. Locations of juvenile activity centres during the postemergence period for four litters at HRSA in 1979 in relation to their mothers' 80% usage areas. Members of a litter are all designated by the same letter.

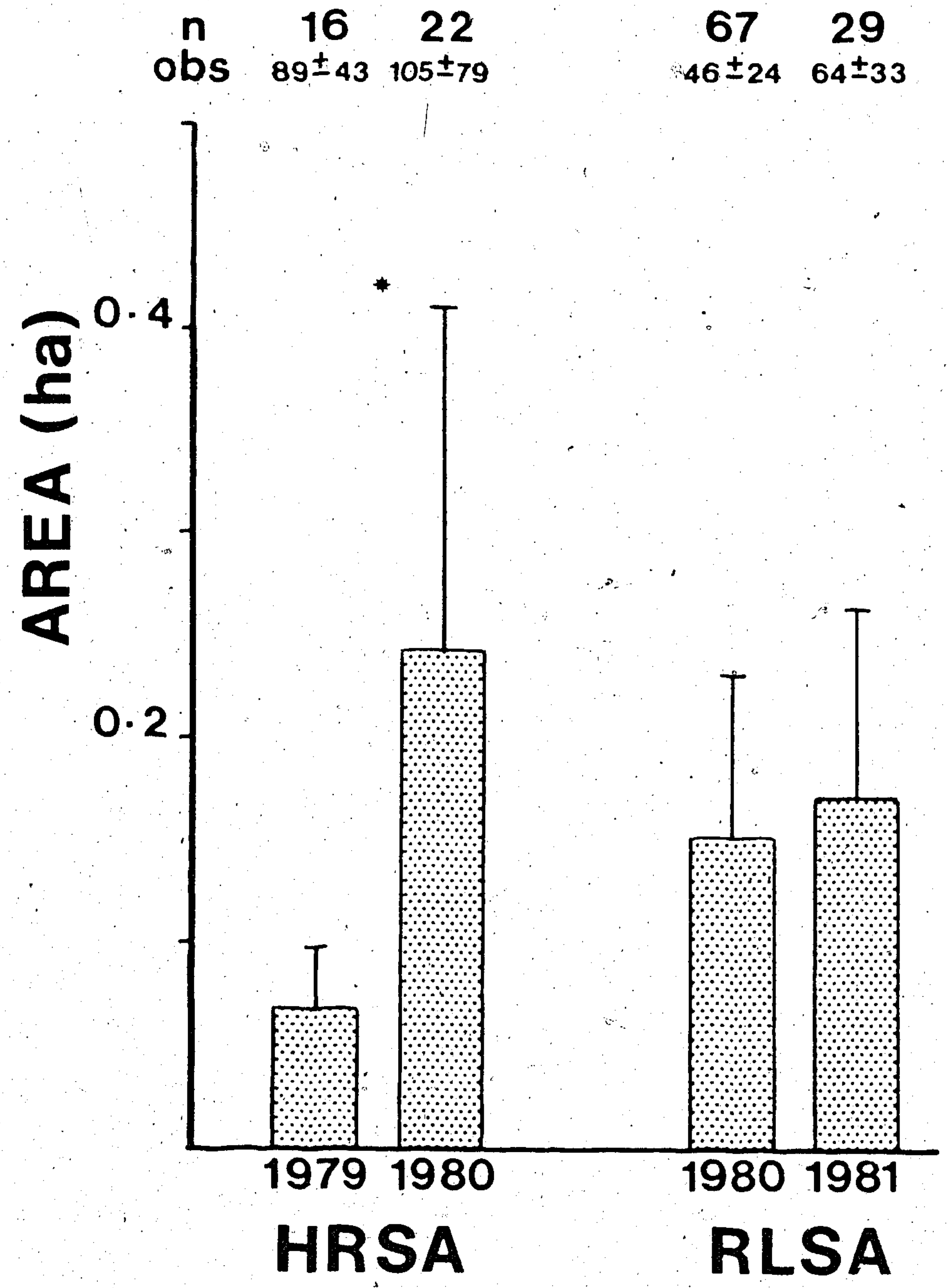

Fig. 4.2. Size of home ranges of juveniles during the postemergence period at the Highwood River study area (HRSA) in 1979 and 1980, and at the Roi Lakes study area (RLSA) in 1980 and 1981. The number of juveniles (n) and average number of observations per juvenile (obs) are given.
* $P<0.001$, Student's t-test $t = 4.03$.

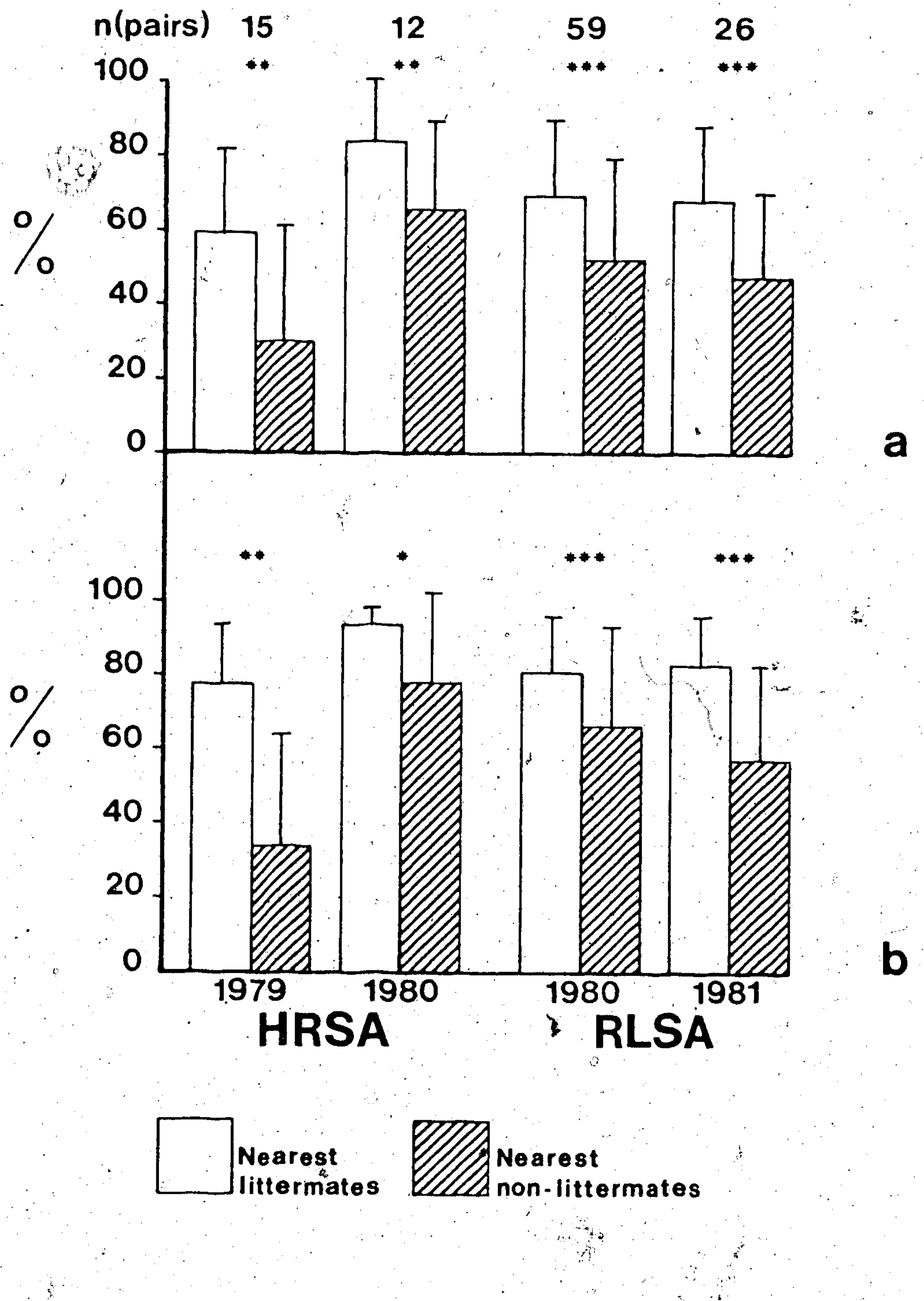

Fig. 4.3. a) Home range overlap of juvenile Richardson's ground squirrels during the postemergence period with their nearest littermate and their nearest non-littermate. b) Time spent in the area of overlap with nearest littermate and nearest non-littermate. * $P<0.05$, ** $P<0.01$, *** $P<0.001$, paired t-tests.

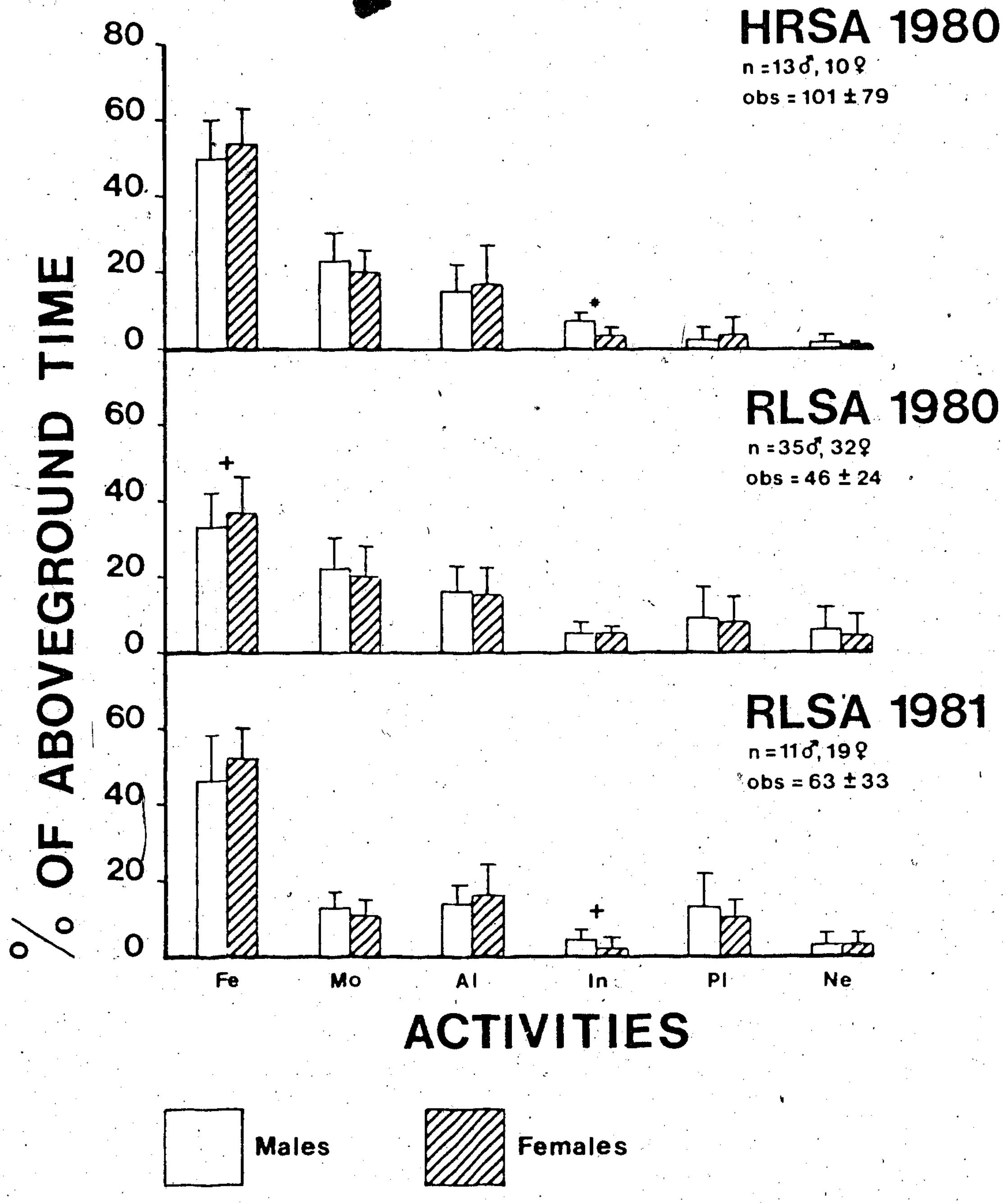

Fig. 4.4. Percentage of aboveground time of juveniles during the postemergence period devoted to feeding (Fe), moving about (Mo), being alert (Al), interacting (In), play fighting (Pl), and gathering nesting material or digging burrows (i.e. nest building) (Ne).
+ $0.05<P<0.1$, * $P<0.01$, Student's t-test (2 tailed). Numbers of males and females (n) and the average number of observations per individual (obs) are given.

interactions than did female juveniles (Fig. 4.4).

4.3.3 Ontogeny of Sibling Spatial Relationships

Home range size increased during the first two weeks above ground, reaching a peak in the 3rd and 4th week. Males consistently had larger home ranges than did females (Fig. 4.5). Similarly, mean distances from the nest burrow increased during weeks 1 and 2 above ground, and average distances from the nest burrow were somewhat greater for males than for females in nearly all periods (Fig. 4.5). Females tended to remain a constant distance from the nest burrow between weeks 3 and 10 (r = 0.47, P>0.5, slope = 0.25), while males increased their distance from the nest burrow during the same period (r = 0.93, P = 0.07, slope = 0.73). This implies that in some way the females had stabilized their movements as the season progressed, and in fact from weeks 3–4 to weeks 11–12 their home range size steadily decreased (r = −0.96, P<0.01) while that of the males remained more constant except for a decline in the 11th and 12th week period (r = −0.34, P>0.6, for weeks 3–4 to 9–10) (Fig. 4.5a). Overlap of core areas (80% usage areas) decreased throughout the season, but this decrease was much more dramatic between sisters than brothers, and from weeks 7–8 sisters showed significantly less overlap of core areas than did brothers (Fig. 4.6). This is consistent with the development of territorial behaviour between sisters about their 7th and 8th weeks above ground (unpubl. data). Distances between brothers when simultaneously active tended to be less than between sisters, further suggesting greater mutual avoidance on the part of juvenile sisters (Fig. 4.6).

4.3.4 Dispersal

Evidence for juvenile dispersal was examined in two ways. First, trapping records show a significantly greater loss of male juveniles from the population than female juveniles, between their emergence at weaning and emergence after their first hibernation (Table 4.4). Secondly, at RLSA in 1981, all juveniles born on the area were monitored each week until they disappeared, either because of death, dispersal, or entry into hibernation. Survival and hazard functions (Fig. 4.7) show that for both males and females a similar loss occurs during the first and second weeks aboveground, and that

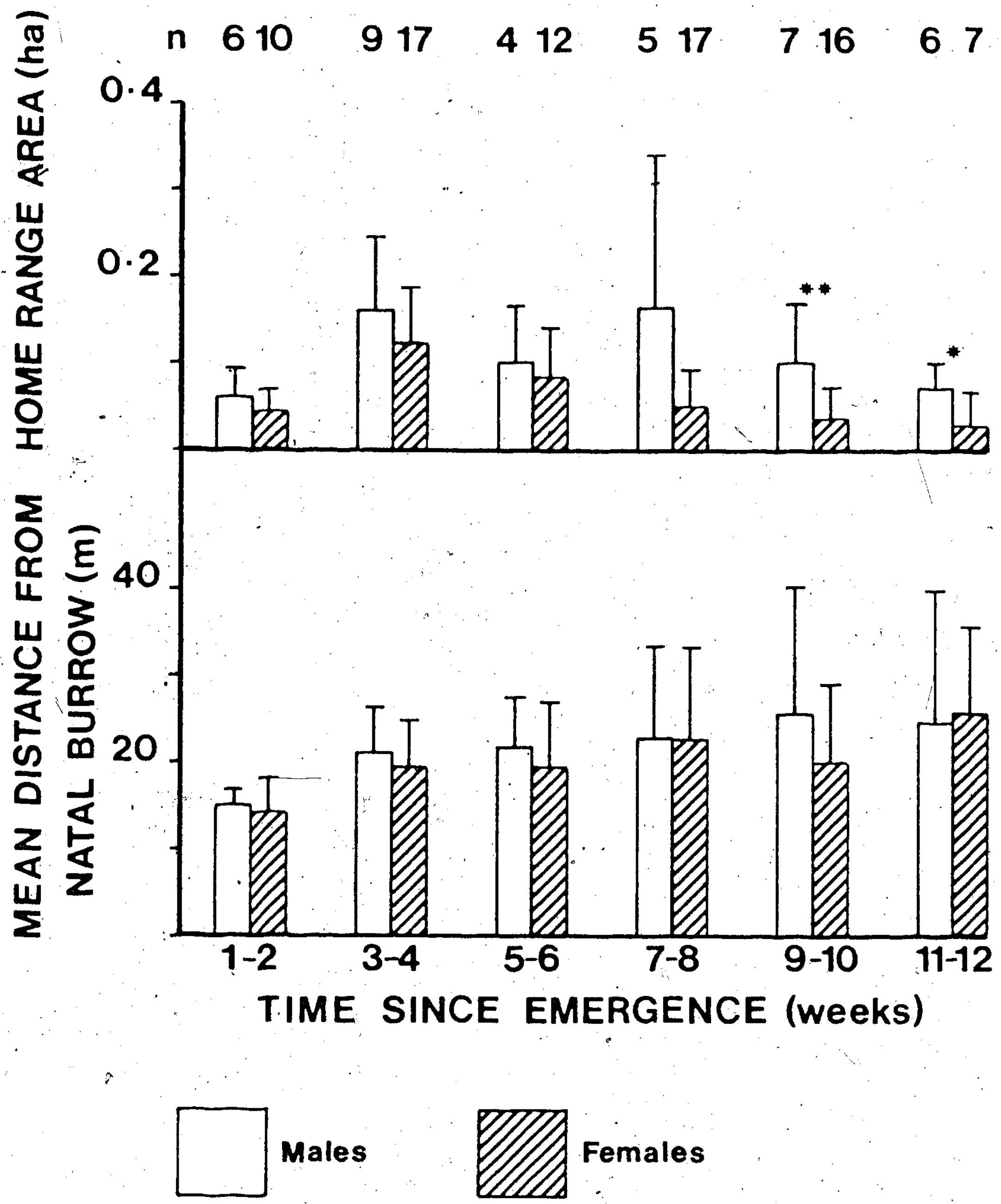

Fig. 4.5. Juvenile home ranges during two-week intervals (top) and distance from the natal burrow (bottom) since emergence at weaning.
* $P<0.05$, ** $P<0.01$, Mann-Whitney *U*-tests.

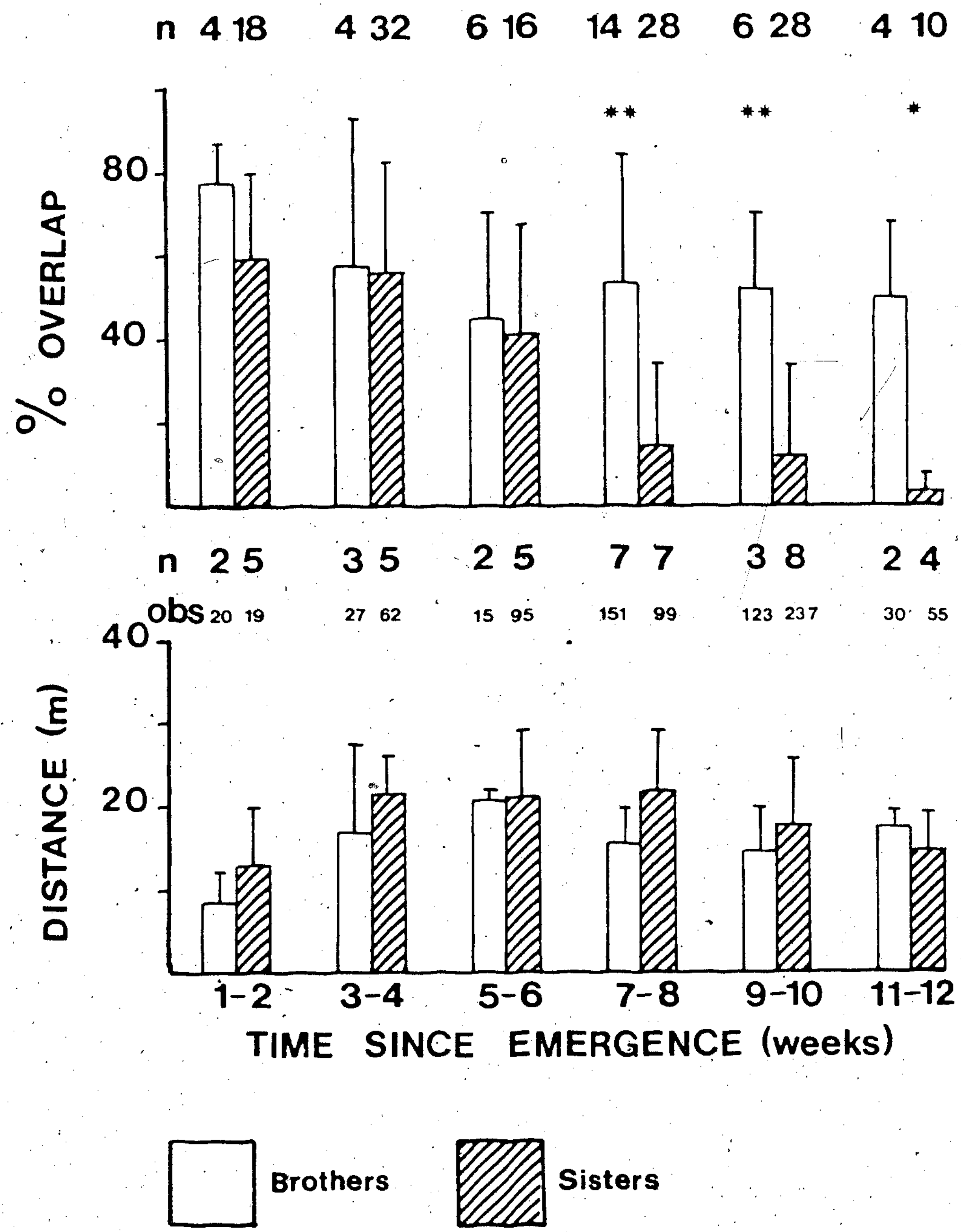

Fig. 4.6. Overlap of 80% usage areas between brothers and between sisters (top), and distances between brothers and between sisters when simultaneously aboveground (bottom).
* $P<0.01$, ** $P<0.001$, Mann–Whitney U–tests.

Table 4.4. Richardson's ground squirrels tagged as juveniles in 1979 (HRSA) and 1980 (RLSA), and recaptured in the spring following their first hibernation.

	# tagged	# recaptured	% recaptured	
HRSA				
Males	70	5	7	*
Females	56	12	21	
RLSA				
Males	66	7	11	**
Females	71	21	30	

* $X^2 = 4.28$, $P<0.05$

** $X^2 = 5.06$, $P<0.05$

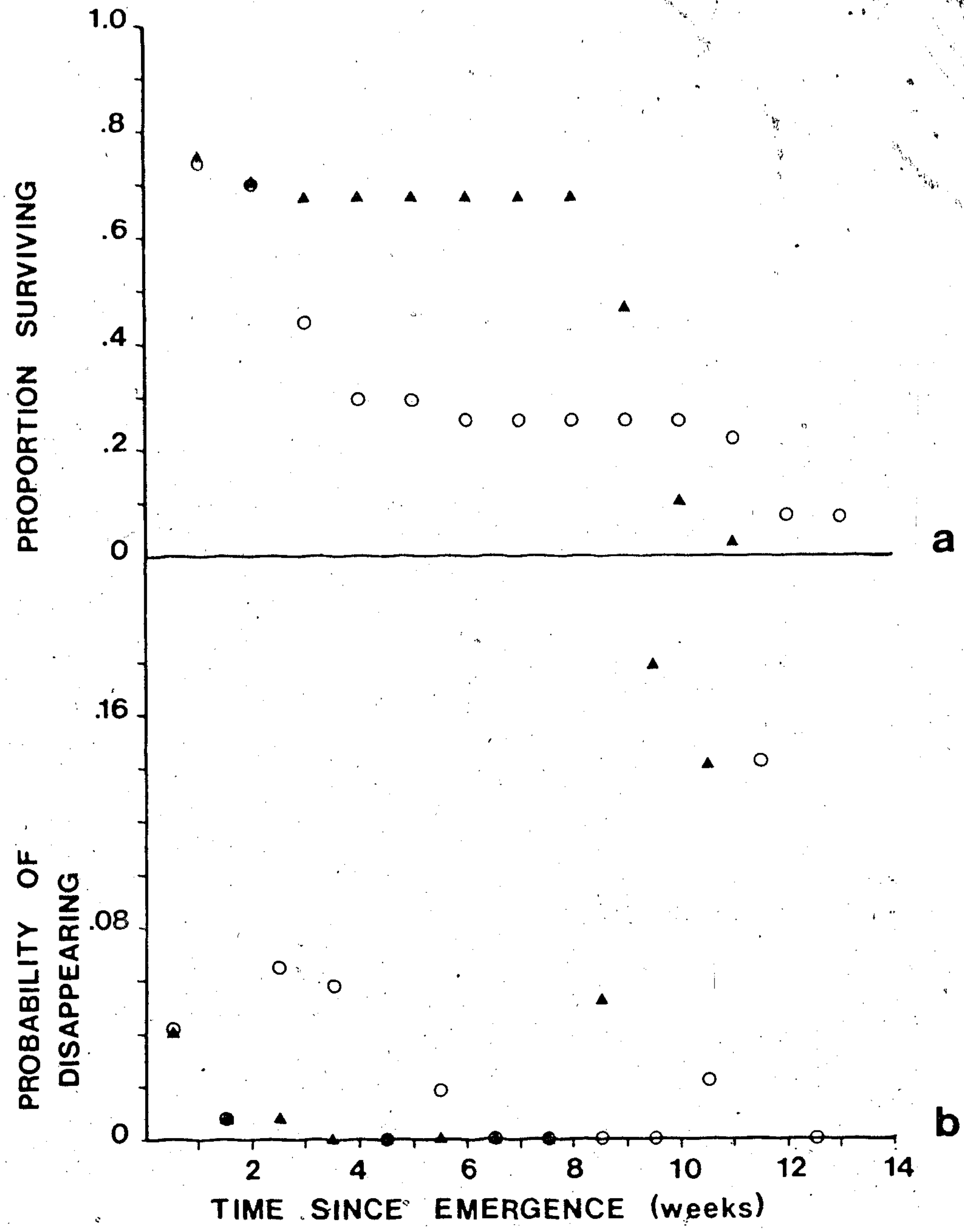

Fig. 4.7. a) Survival function of 27 male and 28 female juvenile at RLSA in 1981 at 1 week intervals following emergence at weaning. b) Hazard function of 27 male and 28 female juveniles, showing the probability per day that an individual that has remained on the area until the beginning of each week will disappear during that week. Triangles are females and open circles are males.

the risk of loss is very slight in the second week. This early loss can probably be attributed to the death of the weakest individuals during their first week aboveground. For females the likelihood of disappearing from the population remains near zero until the end of their eigtht week aboveground. During the ninth week the probability of disappearance increases and peaks during the tenth and eleventh weeks, after which all females have disappeared from the population. The disappearance of females during their 9th to 11th weeks aboveground was due to their going into hibernation, since during a limited amount of trapping on the area on 23 April 1982, the time of spring emergence from hibernation, six of these females were caught that had disappeared in their 9th (1), 10th (4), or 11th (1) week postweaning. By contrast, there was a high probability that males would disappear from the population during their 3rd and 4th weeks aboveground, and by the end of the fourth week, 70.4% of the males that emerged at weaning on the area had disappeared. This period of differential loss of males from the population compared to females can probably be attributed to dispersal by the male juveniles. In support of this conclusion, 8 of 9 (89%) juvenile immigrants onto the study area were males. Of those males born on the area that continued to remain there after their fourth week aboveground, the probability of disappearance was almost nil during the from the 5th until the end of their 11th week postweaning. The probability of disappearance was very high during their 12th week, by the end of which all males born on the area had gone. This loss of males from the population during their 12th week aboveground can probably be attributed to entering hibernation as their female contempories did during the preceding three weeks.

4.4 Discussion

Richardson's ground squirrels after emergence at weaning associate preferentially with their sibs compared to their non-sibs. The perseverance of close post-weaning relationships with both mother and littermates has also been noted in two other studies of juvenile ground squirrels (Dunford 1977, Michener 1981). Socialization in Richardson's ground squirrels appears to be a process that preserves and promotes affiliative bonds between members of matrilineal kinship groups (Michener 1981, Yeaton 1972, see Chapter 5), as occurs among primates (Berman 1982, Fedigan 1982, Kurland 1977). The preservation of natal–burrow associations into adulthood, together with an ability to distinguish biological kin from non–kin (Davis 1982, Holmes and Sherman 1982), would allow for the preferential treatment of closely related adult conspecifics (Dunford 1977, McLean 1982, Sherman 1980, see Chapters 3 and 8). Such associations could then form the basis for altruistic behaviour mediated by kin selection (Sherman 1977), and the degree of sociality characteristic of the species (Armitage 1981, Michener *in press*).

It is apparent from this study that while certain trends may characterize the species generally, there is still variability in reproductive output, spacing pattern, and behaviour, both between different localities and between different years. Similarly variability has been observed in Columbian ground squirrels at different elevations (F.S. Dobson *pers. comm.*, Murie *in press*, Murie *et al* 1980). Thus generalizations about the early socialization of Richardson's ground squirrels need to be approached with caution. Nevertheless, some general and consistent trends are elucidated by this study. While during the postemergence period litters continue to maintain their integrity, the ontogeny of spatial and social relationships demonstrate:

1. a process of differentiation, with juveniles becoming increasingly independent of their natal burrow and siblings, and
2. the early expression of sex differences.

During the initial four weeks above ground, juvenile males and females behave similarly, moving from the vicinity of the natal burrow, almost as if they are familiarizing themselves with their surroundings. Females then occupy increasingly disparate areas from those of their sisters and other juvenile females, and confine their movements to smaller and smaller areas. By contrast, males continue to roam over large areas, maintain considerable overlap in their movements with their brothers, spend a greater proportion of their time engaged in agonistic interactions and a smaller proportion in feeding than do females. The occurrence of such differences at an early age suggests that they might be precursors to the observed sex differences in dispersal.

The spatial and behavioural differences between the sexes are consistent with differences in the post–hibernation behaviour of males and females. Females are philopatric, continuing to spend their lives in the vicinity of their natal burrow (see Chapters 3 and 8). Males, on the other hand, disperse before breeding, either as juveniles

(Schmutz *et al* 1979, this study) or as yearlings (Michener and Michener 1977, see Chapter 2). Adult female Richardson's ground squirrels are territorial (see Chapter 3), and the prehibernation behaviour of juvenile females may be an early expression of their establishment of territories the next spring. Juvenile female Wyoming ground squirrels (*S. elegans*) are also thought to compete in the summer for areas they will use to breed the next year (Pfeifer 1980). Areas defended by yearling *S. richardsonii* females show great overlap with areas occupied as juveniles (see Chapter 3) On the other hand, there would seem to be little value for male juveniles to defend areas in the fall that they will not use the following year. Thus males might be expected to defend an area only so as to ensure the security of an hibernaculum and access to an adequate food supply. The larger home ranges of males may in part result from excursions that precede dispersal, since males were often seen to travel considerable distances and then return to their natal area (unpubl. data).

Juvenile sex differences are common in polygynous primate species (Fedigan 1982, Koyama 1967). They are expressed early and therefore may be under hormonal control. Perinatal gonadal hormones are known to be responsible for sex differences in behaviour of rodents and primates, including man (Quadagno *et al* 1977). Androgens produce greater aggressiveness in males (Brain 1972) and could account for the greater propensity of male Richardson's ground squirrel juveniles to engage in agonistic interactions. Female Belding's ground squirrel infants that were injected with testosterone soon after birth initiated more interactions than untreated females, and dispersed as juveniles (K.E. Holekamp, pers. comm.).

Aggressive behaviour has been suggested to influence male dispersal in yellow-bellied marmots (Webb 1981) and Columbian ground squirrels (Boag and Murie 1981), but was not found to be an important factor in the dispersal of round-tailed (Dunford 1977b), Belding's (Holekamp pers. comm.), or Wyoming (Pfeifer 1980) ground squirrels. Dispersal is characteristic of yearlings in marmots and Columbian ground squirrels, whereas juvenile dispersal appears to be the norm for the latter three species and Richardson's ground squirrels. Autumnal dispersal in spruce grouse is said to be under innate control whereas spring dispersal of yearlings is mediated by aggressive behaviour (Alway and Boag 1979). Richardson's ground squirrels may be similar, since while juvenile dispersal of males appears to occur irrespective of densities and proportion of time spent interacting, those males that hibernate on the area and emerge in spring as yearlings usually lose interactions with other males before disappearing (see Chapter 2).

In conclusion, the ontogeny of juvenile relationships resulting in the retention of sibling ties, female philopatry, and male dispersal, has important genetic consequences (Bekoff 1981) for the sociality of Richardson's ground squirrels. Due to their spatial and temporal proximity, differential behaviour mediated by kin selection is likely to occur in clusters of adult female uterine-kin (see Chapter 8).

4.5 Acknowledgements

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5. Behavioural Interactions of Richardson's Ground Squirrels: asymmetries based upon kinship

5.1 Introduction

If kin selection (Hamilton 1963, Maynard Smith 1964) is an important mediator of sociality in ground squirrels, as has been suggested (Armitage 1981, Barash 1974, Dunford 1977, Michener *in press*), then predictably, behavioural interactions should differ between kin and non-kin, as individuals should treat conspecifics according to their degree of relationship. Differential treatment of close relatives compared to distant and non-relatives has been well documented in insects (e.g., Hamilton 1972, Noonan 1981, Strassman 1981, West Eberhard 1975, Wilson 1971) and birds (e.g., Brown 1970, Craig 1980, Wolfenden 1975). Among mammalian species, behavioural asymmetries based upon kinship have been reported particularly in primates (e.g., Chagnon 1980, Kurland 1977) and ground-dwelling sciurids (e.g., Dunford 1977, Hoogland 1981, McLean 1982, Sherman 1977). However, not all behavioural asymmetries are related to kinship (Ligon and Ligon 1978, McCracken and Bradbury 1981). Also, when examining behavioural interactions, degrees of relatedness should not be the sole consideration, since sex, age, experience, dominance, and reproductive value of the participants will also differentially affect the costs and benefits associated with particular behaviours (Emlen 1981).

The aim of this study was to examine the behavioural interactions of Richardson's ground squirrels (*Spermophilus richardsonii*) in the field for any evidence that the degree of relatedness between participants may affect the nature of interactions. In both field (Michener 1973, 1981, Yeaton 1972) and laboratory (Michener 1974, Michener and Sheppard 1972, Sheppard and Yoshida 1971) situations, Richardson's ground squirrels that are uterine-kin (i.e., mother-offspring and sibling relationships, henceforth referred to as UK) have been found to treat each other more "amicably" than non-uterine-kin (NUK).

However, in these and other (e.g., Armitage 1974, Holmes and Sherman 1982, McLean 1981) studies of the ground-dwelling sciurids it has been common practice to subjectively interpret the motivational states of behaviours and assign interactions to "agonistic", "cohesive/amicable", or "neutral" categories. Comparisons of interactions between kin and non-kin using such categories leaves any differences that are apparent interpretable only within the limits of the observer's classification.

I chose to analyse all observed interactions in a field-study of Richardson's ground squirrels without any *a priori* attempt to categorize the "type" of interaction. Instead, the sequence of behaviours occurring in interactions were recorded. Groupings and associations between behaviours were determined objectively using factor analysis (Comrey 1973) and transitional analysis (Fagen and Young 1978), respectively. The pattern of behaviours occurring in interactions between UK and those between NUK were then compared in a multidimensional contingency table analysis (Colgan and Smith 1978), using the groupings obtained by the above method. Finally *post hoc* interpretation of the results of the analyses were made in light of the observed outcomes of the interactions.

5.2 Methods

5.2.1 Study area and subjects

Interactions of Richardson's ground squirrel were observed during 1979 and 1980 at the Highwood River Study Area, 6 km northwest of Longview, Alberta, Canada (50°34'N, 114°18'W; elevation 1235 m), and during 1981 at Roi Lakes Study Area, 12 km northwest of Stony Plain, Alberta (53°35'N, 114°05'W; elevation 730 m). Both study sites were 1.3 ha in area, divided into a grid of 10 x 10 m squares, and were sometimes grazed by cattle. Maximum densities of adult squirrels on the areas averaged 27/ha (range = 23-31), and the maximum densities of juveniles averaged 66/ha (range = 44-93).

All squirrels on the study areas were marked so that they were individually identifiable, by using numbered metal ear tags with a coloured plastic disc or strip attached to one tag, and by painting letters or numbers on their pelages with "blue-black" human hair-dye. Age class (juvenile/adult) and sex were known for all squirrels, and often matrilineal kinship relationships were known as well. The latter were determined by live-trapping litters when they emerged from their natal burrow at weaning.

5.2.2 Observations

Interactions were recorded using sequential sampling (Slater 1978). Observations were written on paper in a short-hand code, and later transcribed for computer analysis. Whenever possible, the identities of the initiator and responder, the starting location (this was defined as the location of the responder when the interaction was initiated), and the end location (the location of the responder when the interaction was terminated) were noted as well as the temporal sequence of behaviours in the interaction. Sequential sampling of interactions was conducted for 454 hours of observation. Observation periods usually lasted for 2 - 4 hours and were conducted between 0700 and 1900 hours (Mountain Daylight Time), with the majority occurring in the early morning (0700 - 1100) or late afternoon (1500 - 1800).

5.2.3 Analysis

The frequency of occurrence of 15 behaviours in 1774 interactions were arranged in a matrix and R-type factor analysis (Aspey 1977, Harris 1975) was used to determine underlying associations between the behaviours by reducing the data to a set of uncorrelated factors. Factor analysis was carried out using the SPSS program "Factor" (Nie *et al* 1975). A matrix of correlation coefficients between the 15 behaviours was computed, and the elements of the main diagonal replaced with communiality estimates, which were initially set as the squared multiple correlation between a given behaviour and the rest of the behaviours in the matrix. Factors were then extracted iteratively until the communiality estimates of one or more of the behaviours exceeded 1.0 (for the factor analysis performed here 5 iterations were needed. Only those factors with eigenvalues (measures of the variance accounted for by each factor) greater than 1.0 were then rotated using Kaiser's normal Varimax method which maximized the variance of the squared loadings of the behaviours on each factor. Factor loadings indicate the degree to which behaviours are associated with each factor. In this study, positive factor loadings of greater than 0.32 were considered to represent evidence of association of a behaviour with a factor, and according to Comrey (1973) values below 0.32 indicate very poor association (<10% of variance in common with the factor). Factors were considered interpretable only if they accounted for at least 10% of the total variance in the original data (in this study only the first four factors were considered therefore). For the sake of grouping the behaviours, any behaviours that did not load at greater than +0.32 onto any of these four factors was included with the factor onto which it loaded most highly, but was not used for interpretation of that factor.

Factor analysis has been criticized as being unsound for many practical situations (Chatfield and Collins 1980), but it remains a useful tool in behavioural research for seeking underlying structure in a set of observed variables (Aspey 1977, Chatfield and Collins 1980, Cooley and Lohnes 1971, Harris 1975).

Transitional analyses (Colgan and Smith 1978, Fagen and Mankovich 1980, Fagen and Young 1978) were carried out by arranging into contingency tables the frequency with which behaviours followed one another within an individual. Analyses were conducted using the BMDP program "P4F" (Brown 1981).

5.3 Results and Discussion

Fifteen readily recognizable, mutually exclusive, and virtually all-inclusive, behaviours were initially described (Table 5.1). All behaviours were described in strictly physical, operational terms, without any attempt to imply a motivational state or allocate them to a functional grouping. Other behaviours (e.g., ano-genital sniffing, allogrooming) occurred at such extremely low frequencies that the ethogram could be treated as complete without them (Fagen and Goldman 1977). As well, the inclusion of such rare acts in the behavioural catalogue would have seriously undermined the robustness of any contingency table analyses by introducing too many cells with small expected values (Colgan and Smith 1978). The behaviours recognized in this study were in many instances similar to those described elsewhere (Table 5.1), and the basic behavioural postures of Richardson's ground squirrels (Clark and Deniston 1970, Michener and Sheppard 1972, Quanstrom 1971, Sheppard and Yoshida 1971, this study) are similar in form to those of other ground squirrels (Betts 1976, Owings *et al* 1977, Steiner 1970, Watton and Keenleyside 1974).

R-type factor analysis (Aspey 1977, Harris 1975) was used to determine whether there were any underlying associations between the behaviours that could be used to group them in a non-arbitrary manner. The varimax rotated factor matrix of the

Table 5.1. Ethogram of behaviours of Richardson's ground squirrels used in social interactions. Names given by other authors to equivalent behaviours in ground squirrels are also shown.

Behaviour	Description	Equivalent
Chase	– pursue an opponent by running after it	*chase*[1247]
Flee	– rapidly run from an opponent	*flee*[1]
Run towards	– rapidly approach an opponent	*running approach*[2]
Move towards	– approach an opponent by walking towards it	*walking approach*[2]
Move away	– withdrawal by orientating the body away from an opponent, without leaving the vicinity of the interaction	
Side	– the back is arched, with the animal turned sideways, presenting its flank to an opponent. There is piloerection of the hairs on the back and tail, and the mouth is often held open	*arching*[5]*,back arched*[2]*,flank to flank*[7]*,lateral approach*[4]
Rise	– the anterior of the body is raised so that the front paws are lifted from the ground. The animal is facing its opponent, one paw is often extended towards the opponent, and the mouth is usually open	*warding*[5]
Box	– standing upon hindlegs facing [illegible]onent with forepaws extended, the animal strikes at its opponent with adductions of the foreleg. The mouth is usually open.	*sparring*[5]*, standup fight*[2]
Forward	– the animal is crouched facing its opponent. There is some piloerection, the mouth is usually open, and sometimes a single forepaw may be extended towards the opponent.	*threat*[5]
Lunge	– the animal leaps at its opponent, forequarters first. May sometimes be accompanied by biting.	*attack*[5]*, lunge*[12]
Standover	– standing upon its hindlegs, the animals has its forepaws resting on its opponent. Frequently this posture is held for several seconds.	
Supine	– the animal is lying upon its back, with legs raised upwards and the head and neck tilted forwards.	*full submission*[3]
Roll fight	– the animal tumbles over with its opponent, striking at it with adductions of the legs	*fight*[57]*, rolling fight*[2]
Kiss	– the neck is extended towards an opponent and the head tilted slightly to one side. The mouth is open and contact is made with the naso-oral area	*greeting*[6]*, kissing*[1]*, nasal-nasal*[7]*, nose-nose*[25]*, nose-to-cheek*[4]
No reaction	– although in contact with or beside an opponent, no reaction is discernible in response to behaviour of the opponent	

[1]Betts 1976, [2]Dunford 1977, [3]Michener and Sheppard 1972, [4]Owings *et al* 1977, [5]Sheppard and Yoshida 1971, [6]Steiner 1975, [7]Watton and Keenleyside 1974.

frequency of occurrence of the 15 behaviours in 1774 interactions produced four factors that together accounted for 93.4% of the total variance (Table 5.2). Twelve of the behaviours had positive factor loadings on one of the four factors that exceeded 0.32.

The groupings were interpreted, *post hoc*, as:

1. Factor 1: Chase–flee behaviours. These often occurred in interactions in which dominance was obvious from the outset, being dependent largely upon the location of the participants. Such behaviours were common in territorial disputes (see Chapter 2), intrusions by non–neighbouring conspecifics (see Chapter 8), and interactions between unrelated adult females and juveniles (see Chapter 3).
2. Factor 2: Appeasement situation behaviours. These tended to bring about a cessation of the interaction, and often stemmed from the following group of behaviours.
3. Factor 3: Fighting behaviours. These behaviours frequently occurred in interactions where dominance was not immediately obvious and was determined in the course of the interaction. They are similar to the behaviours used to assess social rank in other species of rodents (Davis 1979).
4. Factor 4: Identification behaviours. Naso–oral contacts, which were often preceded by passive approach and resulted in no further interaction, have been interpreted as most likely having an identification function (Steiner 1975).

The frequencies with which behaviours followed one another within an individual were organized into a contingency table (Appendix 5.1) of two–act transitions occurring during 1774 interactions. In all, there were 5420 such transitions, which far exceeded the recommended sample size of at least $10R^2$ (R = repertoire size) acts ($10R^2 = 2250$ in this study) that is desirable when conducting transitional analysis (Fagen and Young 1978). Expected values for each two–act transition if the occurrence of a behaviour was independent of the nature of the preceding behaviour, were calculated in the same manner as for cells in a X^2 test for independence.

Those transitions that occurred significantly more often than expected by chance were determined following the method of Ainley (1974), so that the magnitudes of the positive standardized residuals (observed – expected/square root of expected) were used to identify the most important transitions. The standardized residuals were regarded

Table 5.2. Varimax rotated factor matrix based on the frequency of occurrence of 15 behaviours during 1774 interactions of Richardson's ground squirrels.

	FACTORS			
Behaviour	F1	F2	F3	F4
Chase	0.84			
Flee	0.95			
Run towards	0.61			
Move towards				0.58
Move away			0.41	
Side			0.53	
Rise			0.49	
Box			0.40	
Forward			0.16	
Lunge	0.31			
Standover		0.78		
Supine		0.80		
Roll fight			0.25	
Kiss				0.53
No reaction				0.39
% Total Variance	40.9	26.7	15.8	10.0
% Cumulative Variance	40.9	67.6	83.4	93.4

as approximate standard normal variates. However, when using a relatively large behavioural catalogue, the observed frequencies of some cells will differ significantly from chance expectation ($P<0.05$) through random sampling error. Hence I adjusted the probability level at which a behavioural transition was considered to occur at a frequency significantly wayward from chance expectation by dividing the 0.05 probability level by the repertoire size ($0.05/15 = 0.003$) (Aspey pers. comm.). Transitions were considered significant then, if the magnitude of the standardized residual was +3.0 or greater ($P<0.003$, since +2.96 gives $P = 0.003$).

Several relationships are apparent from a flow diagram of significant transitions in interactions of Richardson's ground squirrels (Fig. 5.1). The "chase–flee" (Factor 1) behaviours were linked in a pattern of "run to" – "chase" – "lunge" – "flee" – "run to"[3] that is consistent with a pattern that would result from reversals of dominance as seen in reverse chases over territorial boundaries. The "appeasement situation" behaviours (Factor 2) were preceded by a "fighting" behaviour ("boxing", Factor 3) involving physical contact, and led to passive withdrawal or no response on the part of a "standing over" animal. This suggests that "standover" is the dominant posture, and that "supine" is the appeasement, submissive posture of the two (Grant and Chance 1958). Apart from "rise" and "roll fight", "fighting" behaviours often tended to be followed by "moving away", while none were significantly likely to lead to fleeing. Hence, "fighting" behaviours need not result in a displacement of the participants, if both terminate the interaction by orienting away ("moving away") from the other. Also, "fighting" behaviours are often followed by more of the same or other "fighting" behaviours. The "side" posture precedes other "fighting" behaviours, and because it is often followed by withdrawal without leading to other "fighting" behaviours that involve physical combat (i.e., "box" and "roll fight"), it may be reasonable to interpret this as a threat behaviour (Sheppard and Yoshida 1971). However, it also anticipates the contact "fighting" behaviours, so cannot be said to always prevent aggression as is generally supposed to be the adaptive advantage of threat postures (Alcock 1976, Davis 1979).

Ainley's (1974) method of assessing significant behavioural transitions is relatively insensitive to significant transitions occurring between rare acts (Fagen and Young 1978).

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[3] N.B. this is not necessarily the sequence of behaviours as they occur in any given interaction, since it is derived from two-act transition probabilities only.

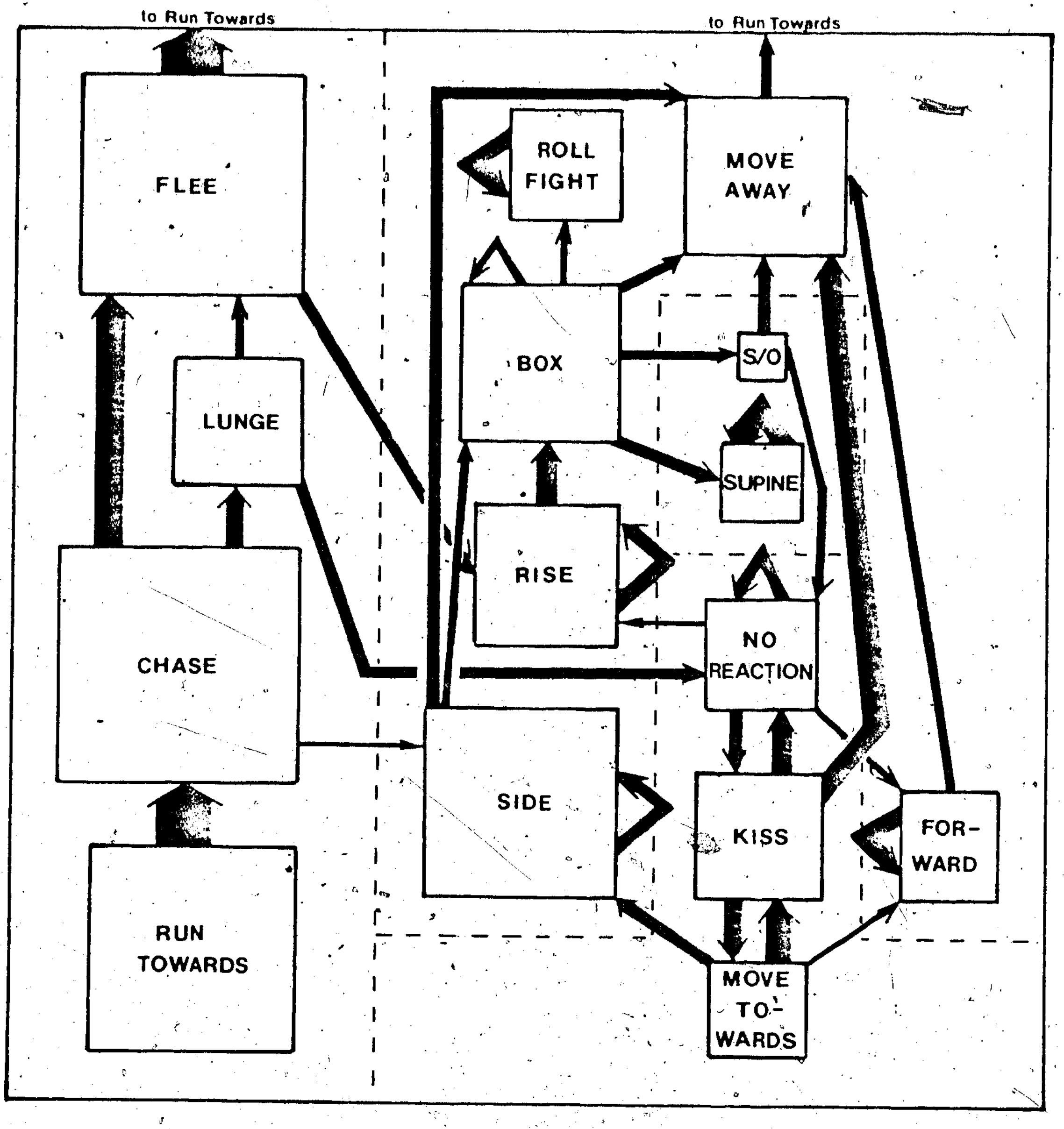

Fig. 5.1. Flow diagram of intra-individual significant transitions between behaviours used in 1774 interactions of Richardson's ground squirrels. The area of the square is proportional to the frequency of the behaviour, and the width of the arrows showing direction of significant transitions is proportional to the magnitude of the standardized residual. Dashed lines enclose factor groupings. (S/O = Standover)

Fagen and Mankovich (1980) recommend a method based upon an algorithm of Brown (1974), that calculates significant transitions in a stepwise manner by sequentially identifying those cells in a contingency table that contribute most heavily to the X^2 statistic. This method picks up many more significant transitions (Appendix 5.2) involving the rarer acts (59 versus 34 for the above method). However, its heuristic value for interpreting the patterns of behaviour when the behavioural repertoire is relatively large, as in this study, is limited as so many transitions appear as significant. Since rarely occurring transitions are probably not so important for understanding the general patterns of behaviour, the method of Ainley (1974) and others like it (Andrew 1956, Aspey 1977, this study) would appear to be more useful for interpretation, precisely because of the conservativeness of the test. However, the method of Fagen and Mankovich (1980) is useful for illustrating the complexity and variability present in the patterns of behaviour of Richardson's ground squirrels.

To examine whether the interactions between uterine-kin and non-uterine-kin differed in complexity, transitional analysis was repeated separately for interactions between UK and interactions between NUK. "Complexity" was measured by the number of behaviours that were followed significantly by more than one behaviour. The rationale for this was that when behavioural patterns were completely stereotyped, and hence least "complex", a given behaviour would always be followed by only one other. Twenty-two transitions in interactions between UK were significant, and 28 among interactions of NUK. Only 12 significant transitions were common to both groups, so that 68.4% (26/38) were uniquely significant in either UK or NUK interactions. Six of the 15 behaviours in interactions of UK had significant transitions leading to two or more behaviours, compared to 10 of the 15 in interactions of NUK ($X^2 = 1.21$, $P = 0.27$). Thus interactions between UK are not more complex than those between NUK, and there is even a suggestion that there is a trend towards greater complexity in interactions involving non-uterine-kin.

5.3.1 Asymmetries based upon kinship

Behaviours were grouped according to the factor groupings obtained above, and the frequencies with which the categories of behaviour followed each other within the same individual during 1161 (271[UK], 890[NUK]) interactions were arranged in a 4x4x2 three-dimensional contingency table, with the degree of relatedness as the third dimension (Table 5.3). The hypothesis tested was whether the sequence of behaviours (P and F) was independent of the relatedness (R) of the participants. Hypotheses are most easily tested in three-dimensional contingency tables by fitting a hierarchical set of log-linear models to the data. The fit of a particular model is tested by comparing estimated expected cell frequencies with the observed cell frequencies using a chi-square statistic (Colgan and Smith 1978). The fits of all models are shown in Table 5.4. Since all sub-models of the saturated model (i.e., the complete model, which has a perfect fit as it incorporates effects of all variables at all levels) have significant X^2 values, none of the models adequately explain the data. This means that there are extremely complex interactions incorporating 1st, 2nd, and 3rd order effects between the variables (preceding behaviour, following behaviour, and relationship) in the agonistic interactions of Richardson's ground squirrels.

The particular model of interest (R,PF) has a highly significant X^2 value ($X^2 = 452.85$, df = 15, $P<<0.001$), indicating relatedness of the participants is *not* independent of the sequence of behaviours in interactions of Richardson's ground squirrels. The likelihood ratio statistic can be further partitioned into components to evaluate the conditional significance of individual terms in the models. Thus, the significance of the interaction effect between preceding behaviour and relatedness (PR) is examined by taking the difference in the Chi-square statistic for models (FR,PF) and (PF,PR,FR) ($X^2 = 33.63$, df = 3, $P<0.001$). Similarly, the significance of the FR term ($X^2 = 265.60$, df = 3, $P<<0.001$) and R term ($X^2 = 595.81$, df = 1, $P<<0.001$) are evaluated. Thus, relatedness has a highly significant effect in terms of the sequence of behaviours exhibited during interactions. Richardson's ground squirrels act differently in how they behave and how they continue to respond, depending upon whether they are closely related (UK) or not (NUK) to the other participant in an interaction.

Table 5.3. Three dimensional contingency table of Preceding by Following Behaviours within an individual during interactions between Uterine-kin (UK) and Non-Uterine-kin (NUK). Behaviours are grouped according to the factor groups: "Chase-Flee", "Identification", "Fighting", and "Appeasement".

		PRECEDING				
RELATION	FOLLOWING	Ch.-fl.	Ident.	Fight.	Appease.	Total
UK	Ch.-fl.	33	4	32	2	71
	Ident.	53	85	20	3	161
	Fight.	75	56	80	13	224
	Appease.	5	5	7	2	19
	Total	166	150	139	20	475
NUK	Ch.fl.	629	24	155	2	810
	Ident.	21	29	14	2	66
	Fight.	274	108	267	9	658
	Appease.	4	1	11	0	16
	Total	928	162	447	13	1550

Table 5.4. Hierarchical set of all models of the varaibles Preceding behaviour (P), Following behaviour (F), and Relationship (R), and their fit to the data in Table 5.3 using the likelihood-ratio chi-square.

Model	df	X^2	*P*
P	28	2898.41	0.0000
F	28	2869.82	0.0000
R	30	3659.84	0.0000
P,F	25	1512.57	0.0000
F,R	27	2274.00	0.0000
R,P	27	2302.59	0.0000
P,F,R	24	916.74	0.0000
PF	16	1048.66	0.0000
PR	24	2145.08	0.0000
FR	24	1884.52	0.0000
P,FR	21	527.28	0.0000
F,PR	21	759.24	0.0000
R,PF	15	452.85	0.0000
PF,PR	12	295.34	0.0000
PR,FR	18	369.76	0.0000
FR,PF	12	63.37	0.0000
PF,PR,FR	9	29.74	0.0005

These differences in interactions between UK and NUK had marked effects on the outcome of interactions. Whereas 81.2% (723/890) of interactions between NUK resulted in the displacement of one of the participants (i.e., one fled the area, usually chased by the other), only 31.7% (86/271) of interactions between UK ended in displacement of one of the participants (Fig 5.2). This difference was highly significant (X^2 = 240.96, df = 1, $P<<0.001$), and was independent of the age or sex of the participants (Fig 5.3).

The differences in outcomes cannot be attributed to less agonism or "fighting" behaviour between UK than NUK, as has been traditionally held (e.g., Michener 1981), since "fighting" behaviours (Factor 3) were as likely to occur in interactions between UK as those between NUK (Table 5.5). However, "appeasement situation" behaviours (Factor 2) and "identification" behaviours (Factor 4) were more common in interactions of UK compared to NUK. Naso-oral contacts ("kissing"), which perhaps is used to reinforce the bond between two squirrels, and appeasement postures ("supine") served to minimize the consequences of agonism between uterine-kin. By contrast, the paucity of such behaviours in interactions involving non-uterine-kin, meant that agonism was often escalated, resulting in a greater preponderance of "chase-flee" behaviours (Factor 1).

The resultant effect of the differential treatment accorded close kin compared to less-related conspecifics, is that UK tolerate more spatial overlap and greater proximity with each other than do NUK (see Chapters 3, 4, and 8). Such space-sharing behaviour can be viewed as nepotistic, and advantages may accrue from a sharing of resources within the overlap area (i.e., food and burrows). However, the advantage of sharing a boundary or overlap area with a close relative may simply lie in reducing the costs of aggression. Not only can fighting result in wounding (Davis *in press*, McLean 1981), it is also energetically very expensive. Heart rates of free-living Uinta ground squirrels (*S. armatus*) frequently exceed 400 beats/minute during combat, compared to a basal level of 284 beats/minute, and this increase in energy output occurs irrespective of whether the animal initiates the encounter or is the responder (Ruff 1971).

Behavioural mechanisms that reduce the level of aggression between UK, would also reduce the physiological costs for both participants. Hence, behavioural asymmetries observed in this study cannot be regarded as altruistic, since it is likely that both

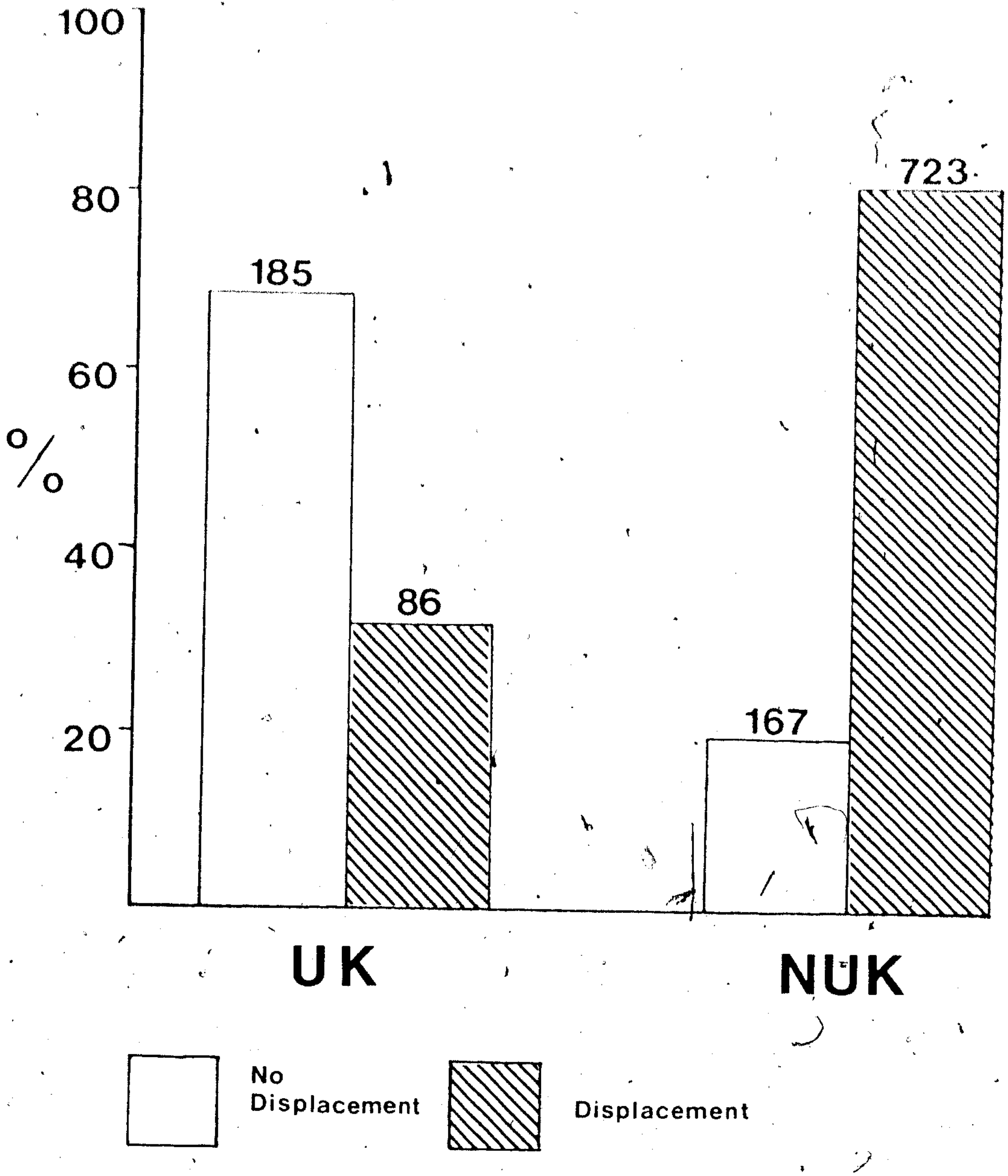

Fig. 5.2. Percentage of interactions between uterine-kin (UK) and non-uterine-kin (NUK) that resulted in displacement or no displacement of the participants. Numbers above the bars indicate the number of interactions involved.

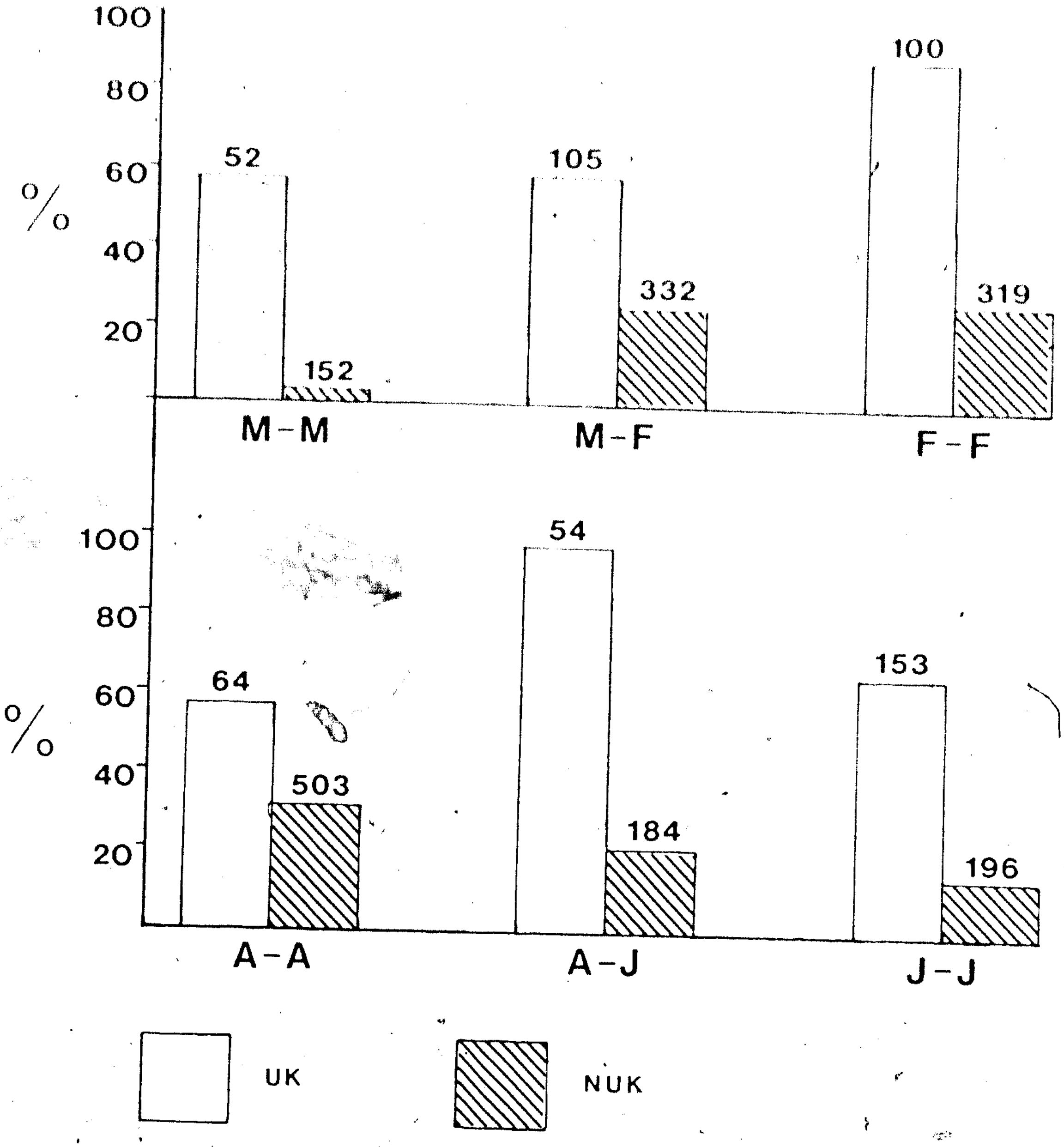

Fig. 5.3. Percentage of interactions that result in no displacement of the participants in interactions between uterine-kin (UK) and between non-uterine-kin (NUK) grouped by sex class (top) and age class (bottom). (M = male, F = female, A = adult, J = juvenile). Sample sizes are given atop the bars.

Table 5.5. Absolute frequencies (f) and relative frequencies (rel. f) of behaviours in 271 and 890 interactions between uterine kin and non-uterine kin respectively

Behaviour	UK f	rel. f	NUK f	rel. f
Chase	100	7.4	823	17.8
Flee	106	7.8	1019	22.1
Run towards	120	8.8	684	14.8
Move towards	102	7.5	155	3.4
Move away	144	10.6	328	7.1
Side	105	7.7	378	8.2
Rise	104	7.7	220	4.8
Box	70	5.2	236	5.1
Forward	42	3.1	176	3.8
Lunge	25	1.8	171	3.7
Standover	19	1.4	18	0.4
Supine	38	2.8	53	1.1
Roll fight	14	1.0	135	2.9
Kiss	247	18.2	77	1.7
No reaction	121	8.9	144	3.1

participants in an interaction between close kin would benefit from a de-escalation in the level of agonism. Richardson's ground squirrels are territorial (see Chapters 2, 3 and 4) and kin tend to live in greater proximity than do non-kin neighbours (see Chapters 3, 4 and 8). Territorial disputes between neighbouring ground squirrels often involve "reverse chases", where individuals alternatively displace each other across a territorial boundary (e.g. Murie and Harris 1978). Territorial conflicts of that nature accounted for 13.1% (117/890) of all interactions between NdK, whereas they made up only [illegible] of interactions between CK ($\chi^2 = 37.14$, df = 1, $P < 0.001$). Thus, kin are less often involved in energetically expensive territorial disputes, and this may ultimately lead to greater reproductive success (see Chapter 8).

5.4 Concluding Discussion

The use of multivariate analyses has become more commonplace in behavioural studies since Wiepkema (1961) applied factor analysis to the analysis of fish behaviour. In studies of ground-dwelling sciurids, multivariate techniques have been used to analyse responses of marmots (Svendsen and Armitage 1973) and ground squirrels (Balfour 1979) to mirror-image stimulation, to analyse factors correlated with sociality (Armitage 1981), and to analyse differences in acoustical behaviour between species (Koeppl *et al.* 1978). Data gathered in behavioural studies rarely satisfies all the underlying assumptions of most multivariate techniques, but fortunately the techniques are robust enough to often withstand departures from the assumptions (Harris 1975). Even so, care needs to be exercised in interpreting the results of multivariate analyses.

The advantages of the objective approach used here are:

1. It avoids subjective *a priori* classifications of what constitute "agonistic" or "amicable" behaviours. For example, "alert" (Armitage 1974, 1977, Johns and Armitage 1979) and "avoidance behaviour" (Holmes and Sherman 1982, Johns and Armitage 1979, Michener 1973) have been classified as "agonistic" behaviours; but is an animal that is watching another or moving away from another really behaving agonistically?
2. It avoids classifying interactions as a whole, which are often composed of elements of more than one category, and represent paths to resolving the opposing

tendencies of aggressiveness and submissiveness. Yeaton (1972) recognized the problem, and scored an interaction as 'agonistic' if it contained any agonistic component at all within its sequence of behaviours. Definitional differences between individual researchers make comparisons of their data difficult. That is, are any differences in their data representative of actual differences between the populations under study, or are they in part or whole the result of inconsistencies among the observers' observational criteria? For example, interactions between adult female Richardson's ground squirrels have been variously reported as being mainly amicable between related females but almost entirely agonistic between unrelated females (Michener 1981), as mainly agonistic between female kin but less than for non-kin (Yeaton 1972), and as involving equal amounts of agonism in interactions of related and unrelated females (Wehrell 1973).

3. It takes into account subtle differences in quality and intensity of interactions. Use of inclusive categories such as 'agonistic' and 'amicable' to analyse interactions can obscure subtle differences in behaviour and motivation (Durand 1977).

Whatever the technique employed, it is imperative not to lose sight of the animal for the numbers. Just as the analyses are abstractions of the data, so the data are abstractions of the animal and its behaviour. The results of any analysis must be interpretable in a manner that explains the behaviour of the actual animal, and not the change in a given variable. Judicious application of multivariate techniques to the study of animal behaviour (e.g. Aspey 1977, Bekoff 1978) can result in an understanding of behavioural patterns that would otherwise be too complex to interpret accurately.

From the analyses used in this study, it can be concluded that interactions between uterine-kin differ from those involving usually less closely related conspecifics (non-uterine-kin). These differences were due to a greater preponderance of behaviours interpreted, in light of the analyses, as appeasement and identification behaviours in interactions of UK, that resulted in less chasing and fleeing behaviour, and ultimately in less displacement of the participants in interactions of UK. The outcome of the behavioural asymmetries based upon kinship was the same irrespective of age class or sex class. Hence the results are consistent with the occurrence of favouritism of relatives (nepotism) in Richardson's ground squirrels that is mediated by kin selection.

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Appendix 5.1. Frequencies of observed intra-individual behavioural transitions during 1774 interactions of Richardson's ground squirrels. Behaviours are: Chase (A); Flee (B), Run towards (C), Move towards (D), Move away (E), Side (F), Rise (G), Box (H), Forward (I), Lunge (J), Standover (K), Supine (L), Roll fight (M), Kiss (N), and No reaction (O). FOLL = Following, TOT = Total.

	PRECEDING															
FOLL.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	TOT.
A	78	28	704	13	3	109	11	36	16	20	3	4	38	5	11	1079
B	276	95	20	8	10	37	61	48	40	53	1	17	43	7	42	758
C	1	310	26	0	18	4	4	1	2	0	0	3	1	0	8	378
D	0	0	3	6	2	6	1	1	5	1	0	1	0	15	0	41
E	25	1	30	29	5	143	40	88	57	39	30	15	35	96	16	649
F	106	81	84	72	17	114	9	32	10	30	1	2	12	2	19	591
G	20	73	21	20	6	20	46	23	9	4	0	5	14	6	23	290
H	35	34	25	7	2	84	99	53	24	18	1	1	10	8	10	411
I	22	40	31	21	4	8	2	7	40	8	2	2	1	0	18	206
J	99	9	47	8	7	42	11	5	18	2	0	0	0	0	4	252
K	5	0	1	0	1	8	2	15	0	2	2	1	5	1	1	44
L	1	10	2	4	1	4	11	29	1	2	0	21	8	2	10	106
M	33	34	11	4	4	15	10	24	4	15	0	0	31	0	1	186
N	2	1	58	86	0	12	40	2	13	0	1	3	0	23	41	282
O	19	10	12	8	6	4	4	4	1	17	6	1	1	31	23	147
TOT.	722	726	1075	286	86	610	351	368	240	211	47	76	199	196	227	5420

Appendix 5.2. Ranked list of significant positive intra-individual behavioural transitions in 1774 interactions of Richardson's ground squirrels, using the method of Fagen and Mankovich (1980).

Transition	X^2	*P*	*d.f*
Flee-Run to	4356.33	0.00000	195
Run to-Chase	2967.56	0.00000	194
Move to-Kiss	2796.21	0.00000	193
Supine-Supine	2723.00	0.00000	192
Move away-Run to	2658.23	0.00000	191
Chase-flee	2438.21	0.00000	190
Chase-Lunge	2309.38	0.00000	189
Kiss-Move away	2186.50	0.00000	188
Kiss-No reaction	2103.98	0.00000	187
Kiss-Move to	2037.91	0.00000	186
Kiss-Kiss	1979.19	0.00000	185
Rise-Box	1883.30	0.00000	184
No reaction-Kiss	1824.82	0.00000	183
Run to-Kiss	1738.96	0.00000	182
Rise-Kiss	1640.49	0.00000	181
Standover-Move away	1530.89	0.00000	179
Forward-Forward	1304.43	0.00000	176
No reaction-No reaction	1272.60	0.00000	175
Standover-No reaction	1252.65	0.00000	174
Box-Supine	1216.70	0.00000	173
Move to-Side	1170.15	0.00000	172
Roll fight-Roll fight	1138.84	0.00000	171
Forward-Kiss	1114.31	0.00000	170
Rise-Rise	1016.20	0.00000	168
Move to-Forward	847.85	0.00000	164
Flee-Rise	811.66	0.00000	163
Flee-Forward	766.44	0.00000	161
No reaction-Forward	740.37	0.00000	160
Move to-Move to	727.21	0.00000	159
Box-Standover	707.84	0.00000	158
Standover-Standover	700.24	0.00000	157
Lunge-No reaction	682.90	0.00000	156
No reaction-Rise	663.96	0.00000	155
Move to-Rise	643.47	0.00000	154
No reaction-Supine	628.10	0.00000	153
Rise-Supine	605.59	0.00000	151
Roll fight-Supine	571.60	0.00000	148
Move to-No reaction	534.60	0.00000	145
Move away-No reaction	524.36	0.00000	144
Box-Box	510.09	0.00000	143
Forward-Lunge	499.09	0.00000	142
Forward-Move to	491.02	0.00000	141
Standover-Forward	465.76	0.00000	139
Roll fight-Standover	438.17	0.00000	136
Move away-Lunge	431.31	0.00000	135
Move away-Move to	426.69	0.00000	134
No reaction-Flee	398.79	0.00000	132
Roll fight-Rise	383.81	0.00000	130
Box-Rise	373.78	0.00000	129
Move away-Rise	352.04	0.00000	126

Move away–Side	342.01	0.00000	125
Move away–Forward	335.81	0.00000	124
Box–Move away	290.27	0.00000	118
Supine–Rise	269.44	0.00000	116
Flee–Side	237.59	0.00000	113
Flee–Roll fight	228.72	0.00000	112
Box–Roll fight	218.97	0.00000	111
Forward–Move away	197.93	0.00000	109
Roll fight–Move away	162.42	0.00028	105
Supine–Move away	156.27	0.00070	104
Supine–Move to	153.86	0.00087	103
Forward–Box	142.20	0.00435	101

6. Sibling Recognition in Richardson's Ground Squirrels (*Spermophilus richardsonii*)

6.1 Introduction

For kin selection (Hamilton 1963, 1964, Maynard Smith 1964) to operate, individuals must be able to distinguish, on average, between kin and non-kin if there is to be any asymmetry in behaviour directed towards them. Where animals are predictably more likely to associate spatially and/or temporally with kin, or more likely to be familiar with kin than non-kin, such a mechanism need not involve an ability to recognize genetic relatives, *per se* (Sherman 1980, Bekoff 1981).

Behavioural asymmetries based on kinship have been found in field studies of Richardson's ground squirrels *Spermophilus richardsonii* (Michener 1981, see Chapter 5) and other ground-dwelling sciurids (Barash 1975, Dunford 1977a, 1977b, Sherman 1977, 1980, 1981, Hoogland 1981, McLean 1982). Sherman (1980) concluded that discrimination between kin and non-kin in *S. beldingi* took place by singling out kin from among other conspecifics, rather than through a mechanism based on spatial proximity or length of association of individuals.

In ground squirrels discrimination between conspecifics seems to occur about (Sherman 1980, Holmes and Sherman 1982) or just before (Michener 1974) the time of weaning, coincident with the development of olfactory investigation of littermates (Ferron 1981) and emergence from the nest, when encounters can first occur among non-nestmates. Recognition in ground squirrels, then, could be based on preweaning familiarity (i.e., experiential influences of sharing a nest burrow) and/or an ability to recognize genetically related conspecifics even without prior experience of them.

Holmes and Sherman (1982) concluded that the mechanism for discrimination of relatives in *S. beldingi* and *S. parryi* was largely through preweaning familiarity, although recognition was demonstrable between sisters even when they had been reared apart from soon after birth, and between full- and maternal half-sibs reared in a common nest. Evidence for recognition between unfamiliar siblings has been found in sweat bees, *Lasioglossum zephyrum* (Greenberg 1979), Cascades frog tadpoles, *Rana cascadae* (Blaustein and O'Hara 1981), pigtail macaques, *Macaca nemestrina* (Wu et al. 1980), and white-footed mice, *Peromyscus leucopus* (Grau 1982).

The purpose of this study was to distinguish the contribution to sibling recognition in Richardson's ground squirrels, if any, of association before and about the time of weaning ("familiarity component"), and of an ability to distinguish genetically related individuals from non-sibs irrespective of postpartum rearing experience (termed "prenatal component" in this paper, although immediate postpartum effects cannot be excluded).

6.2 Materials and Methods

6.2.1 Crossfostering

During early April 1981 18 pregnant adult female *S. richardsonii* were live-trapped on a grassy clearing approximately 12 km northwest of Stony Plain, Alberta, and brought into the laboratory. They were kept individually in large cages (48 x 38 x 21 cm) provided with nesting material (wood shavings). Young were crossfostered within 24 hours of birth, and only between litters born less than 24 hours apart. In all, 30 young were crossfostered between 5 pairs of litters. Dams of reciprocally crossfostered young were trapped at a mean distance of 115m apart (range = 82 – 157m). It was unlikely that pairs of fostered litters were sired by the same male, or that dams were closely related, because the average male home range during the breeding period was only 0.33 ha (SD = ± 0.18), and closely related females had overlapping and adjacent areas (see Chapter 8). Mean litter size was 7.2 (SD = ± 1.5, range = 5–10).

The crossfostering procedure took about 10 minutes per pair of litters and was as follows: Mothers were put in holding cages, and a like number of young was removed from each nest (this number ranged from 2–4 and was always less than half of the smaller litter size). These young had their left-front index toe clipped and were then transferred to their foster nest. Thus, litter sizes remained the same and were now composed of uterine sibs (unclipped) and foster sibs (clipped). [All young were handled with surgical gloves.] Dams were then returned to their original nests, and appeared to treat the fostered young similarly to their own young in all cases. Hence, there were four possible "pair-types" based upon genetic relatedness and post-partum experience: sibs reared together (SRT), sibs reared apart (SRA), non-sibs reared together (NSRT), and non-sibs reared apart (NSRA).

Litters were weaned at 30 days of age by removing the adult female from the cage. Litters remained caged together until 37 days of age, when all individuals were eartagged and placed in separate cages (46 x 24 x 20 cm). Cages were kept on racks in a room (3.8 x 3.7 m) which was maintained on a 12:12 LD cycle and at 21°C. Food ("Wayne mouse/rat diet" and "Wayne dog food" in a 3:1 mixture) and water were provided ad libitum.

6.2.2 Test Conditions

Testing took place within an arena (1.6 x 1.6 m) that had a moveable partition dividing it in half. Three walls of the arena (51 cm high) were constructed from 1.8 cm plywood and the front wall from 0.6 cm plexiglass. Floor tiles divided the floor of the arena into a grid of 100 individually numbered squares (each 16 x 16 cm). Between trials the floor was swept of faeces, and the walls and floor were wiped with vinegar (acetic acid).

At the beginning of each trial, a pair of ground squirrels was placed in the arena on either side of the partition by an assistant. After 2 minutes the partition was raised via a pulley system operated by the observer from outside the testing room. The behaviour of the dyad was then recorded for 10 minutes. For most trials observations were recorded directly through one-way glass windows. I recorded all behaviours, while an assistant observer noted the positions of the squirrels at 15 second intervals given by an electronic metronome. When an assistant observer was not available, encounters were recorded by a video camera mounted on a stand beside the arena at approximately the same height and angle as that when observations were being made through the one-way glass. Operation and monitoring of the video equipment was done outside the testing room, so that during trials squirrels were alone in the room. After testing, the video tapes were played through twice (at normal speed, without stops). I recorded locations using the electronic metronome on the first run, and behaviours on the second run. Hence, data were recorded in the same manner as for trials for which there were two observers. Identical results were obtained when both the assistant and I recorded locations on a test run. Approaches and contact between the animals were used to classify behaviours, and these were clearly discernible on the video tapes as well as through the one-way glass. The video tapes also provide a permanent record of representative arena trials.

6.2.3 Test Procedures

Based on field (see Chapter 5) and laboratory (Sheppard and Yoshida 1971) studies of interactions between sibling and non-sibling Richardson's ground squirrels, as well as preliminary testing in the arena of field-trapped ground squirrels of known relationship (unpubl. data), five *a priori* predictions were made concerning recognition. In both the field and laboratory, siblings tend to associate more closely than do non-siblings, and engage in more contact, including naso-oral contacts. Hence, it was predicted that squirrels recognizing each other as sibs, compared to those that did not, would: a) be closer together on average, b) make more approaches to each other, c) engage in more "kiss" interactions (naso-oral contact, see Betts 1976), d) contact each other more often, and e) spend more time in contact.

Locations were recorded every 15 seconds using instantaneous sampling (Altmann 1974) by noting the grid square each squirrel was in. I carried out all-occurrences sampling (Altmann 1974) of "approaches" (an approach was defined as one squirrel moving directly towards the other and coming within one grid square of it), "kisses", "contacts" (any contact between the two squirrels involving the head or forepaws of at least one of them), and cumulatively recorded the length of all such contacts using a stopwatch.

Agonistic behaviours, defined as "arching", "warding", "sparring", "attack", and "fight" by Sheppard and Yoshida (1971), were also recorded. Holmes and Sherman (1982) had found agonistic behaviours provided the only measurement that varied consistently during arena tests and was asymmetrical between sibs and non-sibs of *S. beldingi* and *S. parryi*. However, in this experiment no *a priori* predictions were made concerning the effect of recognition on agonistic behaviour between Richardson's ground squirrels, and it was deemed an unlikely assay for recognition, because field observations of interactions between uterine-kin and non uterine-kin of *S. richardsonii* showed that the proportion of agonistic behaviours did not differ markedly (see Chapter 5).

A "blind" experimental method was employed. Prior to testing, a list of pairs to be used was given to an assistant. The assistant was ignorant of the "pair type" to which each test pair belonged, being given only the squirrel eartag numbers, and pairs of at least two different "pair-types" were tested on any given day. The assistant randomly assigned the order in which pairs were to be presented, assigned dye marks to individuals (a redundant system of dye marks, usually an O, X, or J, made with Lady Clairol blue-black hair-dye was used so squirrels could be distinguished during trials by the observer), and randomly assigned the individuals of each pair to either side of the arena, all without my knowledge. Trials were numbered consecutively and corresponded with records kept by the assistant in which the identities of the test squirrels were noted. Individual identities of the participants were not matched to each trial until after data from all trials had been collected.

A paired-experiment design was used so that one individual (the "test subject") was always tested in separate trials with two others (the "test objects") of differing "pair-types", and the results of the two trials compared. For example, within a particular set of paired trials "test subjects" were tested with uterine-sibs with which they were familiar (SRT) and, at another time, with uterine-sibs with which they were unfamiliar (SRA). "Test objects" were always matched for sex and age. "Test subjects" were used as subjects only once within each set of paired trials, but could be used again in other combinations of "pair-types". Each squirrel was tested in the arena for an average of 3.5 trials (range = 1-7), and while squirrels could be tested only once on any given day, testing usually took place on consecutive days where squirrels were used in more than one trial. However, there were no significant correlations between the measured variables and the number of times a squirrel was used in the arena (*P*>0.2 in all cases). As well, the order of trials was randomized, so that had there been any effect from prior experience of the arena it would have been distributed evenly across all "pair-types". Sample sizes varied for each set of paired trials as the number of possible "test subjects" was limited by the availability of "test objects" of the appropriate relatedness and rearing experience. The mean age of squirrels when tested was 110 days (SD = ± 21 days). In all, 83 trials were conducted using 47 individuals, 27 females and 20 males. In each set of paired trials the ratio of male-male, female-female, and male-female trials was about the same.

6.2.4 Analysis

In experiments such as this it is often necessary for individuals to be common to more than one treatment (i.e., "pair-type"). In several studies analyses of variance have been used to test for differences between treatments, even though ANOVA assumes residuals are of equal variance and independent (Choi 1978). By contrast, the "randomized pair design" (Finney 1980) employed in this experiment permits the use of paired-difference tests (paired *t*-tests) which do not assume independence between the pairings (i.e., paired trials) or equality of variances (Choi 1978). Hence, in this case, comparisons are valid within any set of paired trials, but would be invalid between sets of paired trials because some squirrels are common to more than one "pair-type". As *a priori* predictions were made concerning the nature and direction of the measurements should recognition occur, significance levels for one-tailed tests were used.

6.3 Results

6.3.1 Control

If the five variables chosen *a priori* are valid measures of recognition, they must differ between arena encounters in which the "test subject" is with a related, familiar "test object" (SRT) and those in which it is with an unrelated, unfamiliar "test object" (NSRA), since in the latter case there is no possibility for recognition. For all five variables the differences were significant and in the direction predicted (Table 6.1). Therefore, the variables represent valid measures of the abilities of Richardson's ground squirrels to discriminate between conspecifics based on recognition. By contrast, the number of agonistic behaviours was highly variable between trials, and did not differ significantly in trials between SRT and NSRA (P(two-tailed)=0.20). Hence, agonistic behaviours were not used as a measure of recognition in subsequent analyses.

Table 6.1 Comparison of behaviour in paired 10 min trials between sibs reared together (SRT) and non-sibs reared apart (NSRA) ($n = 21$ pairs of trials)

Variable	SRT		NSRA			
	$\bar{x}$	SD	$\bar{x}$	SD	t	
Mean distance apart (x 16cm)	4.8	1.5	5.9	1.3	2.8	**
Approaches	21.4	8.2	14.0	8.2	2.8	**
Kisses	6.9	3.9	4.9	4.1	1.9	*
Contacts	18.6	10.0	12.6	9.7	2.6	**
Contact time (s)	68.7	55.9	43.2	36.9	2.3	*
Agonistic behaviours	4.6	7.2	2.2	3.0	1.3	ns

* $P<0.05$ paired t-test (one-tail)

** $P<0.01$ paired t-test (one-tail)

6.3.2 Is there a "prenatal component" to recognition?

In paired trials of squirrels that were reared apart, where test objects differed in their genetic relatedness to the test subject, the differences between trials involving sibs and those involving non-sibs were highly significant for three of the five variables (Table 6.2). Hence, *S. richardsonii* can recognize their sibs in the absence of postpartum familiarity gained from rearing experience.

6.3.3 Does "familiarity" affect recognition of sibs?

Richardson's ground squirrels, for the most part, treated sibs alike irrespective of whether they were reared together (SRT) or reared apart (SRA) (Table 6.3). The number of approaches was significantly higher for SRT, indicating that familiarity may influence discrimination between sibs, if only slightly.

6.3.4 Is there a "familiarity component" to recognition?

In paired trials between non-sibs differing only in rearing experience, squirrels displayed no overwhelming ability to distinguish those squirrels with which they were familiar (NSRT) from those that were unfamiliar (NSRA) (Table 6.4). The number of contacts was the only variable that differed significantly, suggesting that discrimination, albeit mild, can occur when based solely on familiarity.

6.3.5 Does "genetic relatedness" affect recognition between familiar juveniles?

Even when Richardson's ground squirrels were reared together they showed a degree of differentiation between uterine-sibs and non-sibs (Table 6.5). The numbers of approaches and kisses were significantly greater in trials between uterine-sibs (SRT) compared to those between non-sibs (NSRT).

Table 6.2. Comparison of behaviour in paired 10–min trials between sibs reared apart (SRA) and non–sibs reared apart (NSRA). (*n* = 16 pairs of trials).

Variable	SRA		NSRA			
	x	SD	x	SD	*t*	
Mean distance apart (x 16cm)	4.8	1.5	6.1	1.2	3.6	**
Approaches	19.2	8.7	14.8	~~8.3~~	1.5	ns
Kisses	5.4	3.1	5.1	3.9	0.3	ns
Contacts	22.1	9.0	10.9	7.2	3.7	**
Contact time (s)	82.2	62.8	34.8	22.8	2.7	**

**$P<0.01$ paired *t*–test (one–tail)

Table 6.3. Comparison of behaviour in paired 10–min trials between sibs reared together (SRT) and sibs reared apart (SRA). (*n* = 13 pairs of trials).

Variable	SRT		SRA			
	$\bar{x}$	SD	$\bar{x}$	SD	*t*	
Mean distance apart (x 16cm)	4.9	1.7	5.0	1.5	0.2	ns
Approaches	22.8	6.8	17.5	9.2	2.1	*
Kisses	5.8	2.4	4.8	2.2	1.2	ns
Contacts	18.9	10.7	21.2	9.4	0.6	ns
Contact time (s)	66.6	69.7	72.7	54.8	0.2	ns

* $P<0.05$ paired *t*–test (one–tail)

Table 6.4. Comparison of behaviour in paired 10-min trials between non-sibs reared together (NSRT) and non-sibs reared apart (NSRA). (*n* = 17 pairs of trials).

Variable	NSRT		NSRA			
	$\bar{x}$	SD	$\bar{x}$	SD	*t*	
Mean distance apart (x16cm)	5.3	2.3	5.8	1.5	0.7	ns
Approaches	18.5	9.7	13.6	7.8	1.6	ns
Kisses	3.9	2.4	4.6	3.1	0.6	ns
Contacts	20.6	10.7	12.1	10.2	2.1	*
Contact time (s)	70.2	50.9	47.1	39.7	1.3	ns

* $P \leq 0.05$ paired *t*-test (one-tail)

Table 6.5. Comparison of behaviour in paired 10–min trials between sibs reared together (SRT) and non–sibs reared together (NSRT). (*n* = 15 pairs of trials).

Variable	SRT		NSRT			
	x	SD	x	SD	*t*	
Mean distance apart (x 16cm)	4.6	1.4	5.2	2.3	1.2	ns
Approaches	23.1	8.3	18.2	7.7	2.4	*
Kisses	6.8	4.1	4.1	2.3	2.3	*
Contacts	17.1	8.7	21.2	10.2	1.5	ns
Contact time (s)	63.6	51.3	74.4	52.6	0.9	ns

* $P<0.05$ paired *t*–test (one–tail)

6.4 Discussion

The results are consistent with the existence of a genetic recognition system for sibling recognition in Richardson's ground squirrels. However, the possibility of intra-uterine epigenetic effects or immediate postpartum imprinting cannot be ruled out either. That is, juvenile *S. richardsonii* displayed an ability, determined prenatally or soon after birth, to recognize their biological siblings. Familiarity, based upon association before and at the time of weaning, also affected discrimination between conspecifics, although less strongly.

By contrast, Holmes and Sherman (1982) found familiarity to be the primary component of recognition in arena tests with *S. beldingi* and *S. parryi*. This difference in the relative importance of the two components between the two studies may be due to differences in experimental design. In their study, *S. parryi* juveniles in the "reared together" groups were kept together with their dam until 20 to 30 minutes before testing when the mean age was 51 days, and *S. beldingi* juveniles were kept together until they went into hibernation at 3 months of age, and were tested soon after emergence from hibernation when about 8 months of age (Holmes and Sherman 1982). Thus, the pre-trial familiarity being measured included much post-weaning familiarity, whereas in this study only the effect of association up to about the time of weaning was measured.

Familiarity has been demonstrated to be the major component of recognition in spiny mice *Acomys cahirinus* (Porter et al. 1981). However, recognition ability is lost if the animals are separated for 8 days (Porter and Wyrick 1979, Porter et al. 1981). Hence, to be effective as a means of discrimination, familiarity may need to be continually reinforced.

In the field, familiarity between littermate juvenile Richardson's ground squirrels would continue to be reinforced after weaning, as siblings associate much more than non-siblings (Michener 1981, see Chapter 4). No conclusions can be drawn here, therefore, concerning the relative contributions of familiarity or prenatal components to sibling recognition of Richardson's ground squirrels in the wild.

The importance of this study lies in its demonstration that, in the absence of familiarity, Richardson's ground squirrels can still recognize their sibs. The existence of a genetic recognition system has important implications for the operation of kin selection within the social system of *S. richardsonii*. If close kin can be discriminated without prior experience of them, there is the potential for behaving differentially towards them in a manner that benefits the behaver's inclusive fitness (Hamilton 1964). Among Richardson's ground squirrels, classes of such close relatives that do not share any pre-weaning experiences include: father-offspring relationships, non-littermate siblings, paternal half-sibs, aunt-neice relationships, and grandmother-granddaughter relationships. Recognition in the absence of familiarity has been demonstrated for non-littermate siblings in white-footed mice *Peromyscus leucopus* (Grau 1982), and discrimination has been shown between littermate full- and maternal half-sibs of Belding's ground squirrels reared together in the field that cannot be accounted for by simple differences in familiarity (Holmes and Sherman 1982).

An ability to recognize biological relatives without prior experience of them could occur most plausibly via a system of phenotypic matching (Barash et al. 1978, Greenberg 1979, Blaustein and O'Hara 1981, Buckle and Greenberg 1981, Holmes and Sherman 1982). Evidence indicates that pheromones are important for individual identification in some mammals (Brown 1979), and possibly in ground squirrels (Harris and Murie 1982). Perhaps closely related ground squirrels produce similar odours, and if an animal could detect odours similar to its own, the potential would exist for differentiating those animals that smell similar to it from those that do not. In essence, such a phenotypic matching would be a good predictor of genetic relatedness. Such a system appears to operate in sweat bees (Greenberg 1979, Buckle and Greenberg 1981) and tadpoles (Blaustein and O'Hara 1981).

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7. Alarm calling in Richardson's Ground Squirrels (*Spermophilus richardsonii*)

7.1 Introduction

An advantage of sociality in many animal species is the increased detection of predators that it affords (Bertram 1978). Individuals within a social group can benefit from the vigilance of other group members, so that earlier detection of predators is enhanced and predator success is diminished (e.g., Kenward 1978). However, for group members to profit from the perceptions of their companions, a group requires some system by which the detection of a predator by one individual can be transmitted to others. Among the North American ground-dwelling sciurids this is most frequently accomplished by the detector emitting a call which alerts its conspecifics to the presence of danger.

Intuitively, there is a problem in explaining the evolution of alarm calling behaviour and the selective advantage that calling might be to the caller. Why should an animal that has detected a predator invest time and energy into giving alarm calls that seemingly benefit only its conspecifics, and therefore potential competitors, and may even jeopardize its own safety? There is evidence that in *Spermophilus beldingi*, at least, callers are at greater risk of being preyed upon than are non-callers (Sherman 1977). Ostensibly, then, it should pay an animal that has detected a predator to be quiet and not indulge in what appears to be altruistic behaviour.

Hypotheses for the evolution and maintenance of alarm-calling have been summarized (Harvey and Greenwood 1978, Sherman 1977), and fall into two categories. The first maintains that alarm calling is, in fact, selfish behaviour that reduces a caller's chances of being preyed upon immediately or in the future (Trivers 1971, Charnov and Krebs 1975). The second group of hypotheses (Hamilton 1963, 1964, Maynard Smith 1965) argue that alarm calling functions to warn genetically related conspecifics of danger, thereby increasing the caller's inclusive fitness. Although the latter hypotheses can account for the evolution of alarm calling even when there is danger to the caller in calling, they need not invoke risk to the caller (Harvey and Greenwood 1978), for kin selection will favour alarm calling as long as it improves the survival of conspecifics where there is a likelihood that some of the conspecifics are related to the caller (Barash

1975). Indeed, for round-tailed ground squirrels (Dunford 1977a) and marmots (Barash 1975; Noyes and Holmes 1979) there is no evidence to suggest callers are in greater danger of being preyed upon than non-callers.

The prediction from these kin selection hypotheses is that those animals most likely to have close kin within their vocal range will be most inclined to alarm call. In *S. tereticaudus* (Dunford 1977a), *S. beldingi* (Sherman 1977), and *S. tridecemlineatus* (Schwagmeyer 1980) adult males call less often than do adult females; and in the latter two species, as well as *S. beecheyi* (Owings and Leger 1980), females with post-emergent young are more likely to call than non-parous females. Since male ground squirrels tend to disperse before and after breeding (Armitage 1981) they are less likely to be resident near closely related kin than are the more philopatric females, and females with young clearly have close kin nearby whereas females without young may not. Thus for those species of *Spermophilus* studied so far, the results are in accordance with the kin selection hypotheses.

It was the aim of this study to examine Richardson's ground squirrels for evidence of asymmetries in the likelihood of alarm calling based upon the probability of having close kin nearby, to assess the relevance of calls and the responses to them with regard to the context in which they were given, and to evaluate whether callers place themeselves in jeopardy by calling.

The acoustical repertoire of *S. richardsonii* has been described as consisting of chirps, whistles, and churrs, any of which may be given in alarm (Koeppl *et al* 1978).

7.2 Methods

7.2.1 Observations of naturally elicited alarm calls

Responses of Richardson's ground squirrels to naturally occurring encounters with potential predators were observed during 1979 and 1980 at the Highwood River Study Area (HRSA: 50°34'N, 114°18'W; elevation 1235 m), and during 1981 at Roi Lakes Study Area (RLSA: 53°35'N, 114°05'W; elevation 730 m), in Alberta, Canada. Both study sites were 1.3 ha and situated in open grasslands that were sometimes grazed by cattle. All squirrels on the study area were marked so that they were individually identifiable, by using numbered metal ear tags with a coloured plastic disc or strip attached to one tag, and by painting letters or numbers on their pelages with "blue-black" human hair-dye. Age class (juvenile/adult) and sex were known for all squirrels. In this paper, a "non-parous female" is one that failed to bring up a litter.

Instantaneous scan sampling (Altmann 1974) of the squirrels present on the area was conducted at 15 minute intervals, so that the number and composition of squirrels aboveground was known for each quarter hour period. When a potential predator was observed on or near the study area the species of the predator, its behaviour, the reaction of the squirrels, the type of alarm call given, if any, and the outcome of the attack, were recorded. In the case of a terrestrial predator, a quick scan of the area was made to locate callers, who could be identified by the pumping of the thorax and opening and closing of the mouth. In encounters with aerial predators, callers could be identified only if they were being observed at the instant the bird appeared, or if they happened to be the only squirrel aboveground in the direction of the call (calls to aerial predators were quite localizable, see below). I seldom found it possible to identify the first squirrel to give an alarm call, since calls were often given simultaneously, or very close together, from several different sources. In all, 139 natural encounters with predators were observed during 454 hours of observation, and the identities of 136 squirrels giving alarm calls were noted during 64 of these encounters.

7.2.2 Experimentally elicited alarm calls

Alarm calling was experimentally studied at RLSA in the postemergence period (i.e., the period following the emergence of juveniles aboveground at the time of weaning). An assistant and I approached to an average distance of 20.3 m (SD = 7.5, *n* = 73) from a squirrel. The squirrels were accustomed to our presence and did not alarm call at our approach, nor remain alert once we stopped. When the squirrel had begun feeding, my assistant flicked an orange frisbee so that it passed 2.2 m (SD = 1.9, *n* = 73) over the subject squirrel, while I observed the subject through 10 power binoculars. I noted whether or not the squirrel alarm called, when it called, whether it ran to a burrow, and if so, how far the burrow was from the subject's position at the beginning of the trial. The frisbee was silent, could be thrown inconspicuously, its flight path could be directed accurately, and it elicited responses from the squirrels that did not differ qualitatively from those observed during natural encounters with aerial predators Seventy-three trials were conducted on 35 individuals (2 adult males, 6 parous and 4 non-parous adult females, 7 juvenile males, and 16 juvenile females) Each squirrel was tested in an average of 2 trials (range = 1-4), and the mean time between trials was 11 days (SD = 9, *n* = 35). All trials were conducted between 23 June and 4 August

7.2.3 Sonograms

Recordings of some alarm calls were made using a Nagra IV tape recorder and directional microphone, at a tape speed of 10 cm/s. Sonagrams of recordings were produced with a Kay "Sona-Graph" model 661A. Sonograms were made of calls considered to be representative of the types of alarm call given by Richarson's ground squirrels. Inter- and intra-individual variation were not measured.

7.3 Results

7.3.1 Natural Encounters with Predators

Potential predators (including non-predators that elicited alarm calls) and their rates of appearance on or near the study areas during 454 hours of observation are shown in Table 7.1. Observed rates almost certainly underestimate the rate of natural encounters, since the presence of an unconcealed observer probably discouraged several predators from frequenting the area during the hours of observation. Even so, the ground squirrels encountered situations involving a potential predator approximately once every three hours.

There were at least two types of alarm call, and possibly three, employed by the squirrels. These calls were readily distinguishable to the human ear. A short chirp (duration = 75 ms) of relatively low pitch and highly frequency modulated (8 kHz to 3.5 kHz) was given in response to an aerial predator (Fig. 1a). For terrestrial predators the alarm call was a long whistle (duration = 0.40 s) of high frequency (10 kHz) and with little frequency modulation (Fig. 1b). Although the call given to badgers was similar to other whistles, it could be distinguished by the human ear. A sonogram revealed it to be a high pitched

Table 7.1. Incidence of potential predators (including non-predators that elicited alarm calls) on or near a 1.3 ha study area during 454 hours of observation. Shown are the number of encounters (#) and the number of encounters per 100 hours (rate).

Predator		#	Rate
Aerial			
Swainson's hawk	*Buteo swainsoni*	17	3.7
Common raven	*Corvus corax*	9	2.0
Red-tailed hawk	*Buteo jamaicensis*	6	1.3
Goshawk	*Accipiter gentilis*	6	1.3
Marsh hawk	*Circus cyaneus*	5	1.1
Bald eagle	*Haliaeetus leucocephalus*	5	1.1
Golden eagle	*Aquila chrysaetos*	3	0.7
Sparrow hawk	*Falco sparverius*	1	0.2
Prairie falcon	*Falco mexicanus*	1	0.2
Turkey vulture	*Cathartes aura*	1	0.2
Barn swallow	*Hirundo rustica*	1	0.2
Unidentified raptor		1	0.2
Terrestrial			
Long-tailed weasel	*Mustela frenata*	66	14.5
Badger	*Taxidea taxus*	11	2.4
Coyote	*Canis latrans*	4	0.9
White-tailed deer	*Odocoileus virginianus*	2	0.4
		139	30.6

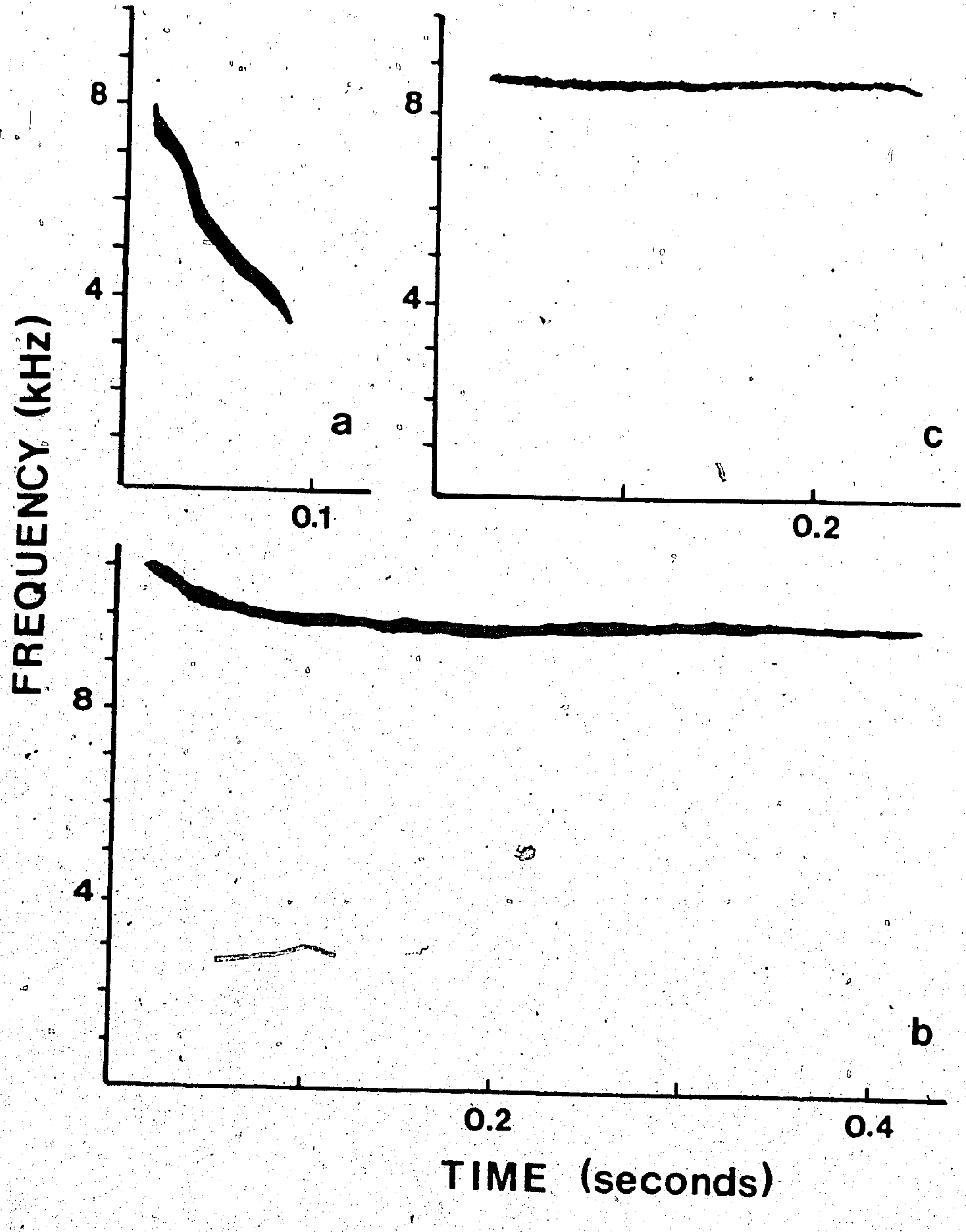

Fig. 7.1. Tracings of sonograms of alarm calls given by *Spermophilus richardsonii*: a) chirp ("aerial") alarm call, elicited by a frisbee; b) whistle ("terrestrial") alarm call, elicited by a dog; c) whistle alarm call, elicited by a badger.

whistle of 8.5 kHz and 0.22 s duration, with virtually no frequency modulation (Fig. 1c). Alarm calls given in the presence of badgers elicited a more intense response from conspecifics than did those given to weasels. Squirrels would stand erect and look in the direction of the predator for up to 75 – 150 m from a badger, compared to only 40 – 70 m from a weasel.

Calls appeared to contain information about the type of predator and the context of the danger. Firstly, of 88 instances in which alarm calls were given and were classified by the type of call, only chirps were given to aerial predators (25/25), while only whistles were given when the predator was a terrestrial one (63/63). Furthermore, in five cases where a bird landed on or near the study area (two Swainson's hawks, three common ravens), ground squirrels continued to give chirps while the bird was on the ground. Secondly, the responses of squirrels in 86 situations in which alarm calls were given, were also different depending upon the type of call and situation (Table 7.2).

One hundred and thirty–six callers were identified and classified according to age and sex class. The numbers of each age/sex class present on the area during encounters with potential predators were obtained from the scan sample taken immediately prior to the appearance of the predator. Expected numbers of observed callers for each age/sex class were calculated upon the basis of the null hypothesis that the likelihood of calling was equally probable for each class, so that the numbers of observed callers should have been in direct proportion to their relative abundance in the aboveground population at the time of the encounter (Table 7.3). The overall likelihood of calling was not the same for all age/sex classes ($X^2 = 8.27$, 3df, $P<0.05$). Due to the early immergence of adult males into hibernation, they were not present during most of the postemergence period, and no instances of an adult male giving an alarm call after all litters of young had emerged on the area were recorded. During the gestation/lactation period however, adult males were significantly much more likely to give alarm calls than were adult females ($X^2 = 7.26$, 1df, $P<0.01$) (Table 7.3). Adult males were also more likely to chase weasels than were adult females ($X^2 = 6.89$, 1df, $P<0.01$) (Table 7.4). All adult males that alarm called and/or chased weasels during the gestation/lactation period had either been present during the breeding period on the study area and had continued to reside in the area they had occupied during the breeding period, or were yearling males that had not dispersed from

Table 7.2. Responses of Richardson's ground squirrels to chirp ("aerial") and whistle ("terrestrial") alarm calls given by conspecifics to aerial and terrestrial predators, respectively.

Response	Type of Alarm Call	
	Chirp	Whistle
Ran immediately to burrow	13	
Ran immediately to burrow then stood erect	1	
Ran immediately to and into burrow	4	
Stood erect	2	58
Stood erect and fled from predator when approached		8

Table 7.3. Incidence of alarm calling by age/sex class for Richarson's ground squirrels during the overall study, gestation/lactation period, and postemergence period. See text for method of calculation of expected values.

Age/Sex Class	# Present	# Call	# Expected	% Call
Overall				
Adult male	61	16	12.0	26.2
Adult female	336	59	65.7	17.6
Juvenile male	163	24	32.0	14.7
Juvenile female	135	37	36.4	27.4
Gestation/lactation				
Adult male	38	14	7.4	36.8
Adult female	163	25	31.6	15.3
Postemergence				
Parous adult female	99	24	23.0	24.2
Non-parous adult female	39	8	9.0	20.5
Juvenile male	163	24	33.4	14.7
[illegible]nile female	135	37	27.6	27.4

Table 7.4. Sex of adult Richardson's ground squirrels observed chasing long-tailed weasels during the gestation/lactation period.

Sex	# Present	# Chase	# Expected	% Chase
Male	14	4	1.3	28.6
Female	63	3	5.7	4.8

their natal area and shared overlapping ranges with their mothers.

In the postemergence period, the probability of giving an alarm call was not statistically different for females of different ages or reproductive condition (Table 7.3), although the proportion of non-parous females that called was slightly lower than for other females. (As well, while parous females were seen chasing weasels on 8 occasions, no non-parous female was ever observed to chase a weasel.) Juvenile males, however, called significantly less often than did juvenile females ($X^2 = 5.85$, 1df, $P<0.025$). Some juvenile males disperse, and the number of juvenile males present included several immigrants that were unlikely to have been related to any of their neighbouring conspecifics. These immigrants were never observed to give alarm calls, although an immigrant was present 27 times during encounters with predators. If such males are excluded from consideration, there was no significant difference between the likelihood of juvenile males and juvenile females born on the area to give alarm calls ($X^2 = 2.86$, 1df, $P>0.05$).

In 9 instances predators were observed to be successful. A golden eagle, Swainson's hawks, and a red-tailed hawk killed one adult, two adults, and one juvenile respectively. Long-tailed weasels entered the nest burrows of four females and carried their infants to another burrow after killing the infants. A badger dug up a nest burrow and emerged chewing the contents of the nest. Successful badger predation was also inferred from badger diggings at the site of two females' nest burrows and an adult male's hibernaculum.

7.3.2 Experimental Observations

"Aerial" alarm calling to a thrown frisbee was not equally probable for all age/sex classes (Table 7.5). All testing was carried out during the postemergence period, and adult males never called, although males were tested on only three occasions. No adult females without young called, whereas adult females with young gave alarm calls in 55% of the trials; this difference was statistically significant ($X^2 = 5.73$, 1df, $P<0.05$). The proportion of juvenile males calling (35%) was not different from the proportion of juvenile females calling (34%) ($X^2 = 0.01$, 1df, $P>0.9$).

Squirrels reacted to the stimulus in a manner appropriate to an aerial attack, and ran to a burrow in 78% (57/73) of the trials. The lack of calling in non-parous females did not result from a lack of a response to the stimulus object as a source of danger, since non-parous females always ran to a burrow when tested. Nor could lack of calling by non-parous females be attributed to their being more exposed or vulnerable, since on average non-parous females tended to be closer to a burrow than other age/sex classes (Table 7.5).

It appears unlikely that calling would increase the danger of an individual being caught by a predator. In 11 of 22 cases (50%) the squirrel did not call until it had reached the safety of a burrow, and on a further 6 occasions (27%) the squirrel called as it was running to a burrow. Only 5 times (23%) did a squirrel call either without running, or before running, to a burrow. In all 5 instances the distance of the frisbee from the squirrel ($\bar{x}$ = 6.1 m, SD = 3.1) was significantly greater than in the other trials in which the squirrels called as or after they had run for a burrow ($\bar{x}$ = 1.6 m, SD = 1.4) (Mann-Whitney *U*-test: *U* = 81.5, $P<0.01$), and probably represented a less intense stimulus.

7.4 Discussion

Although *S. tridecemlineatus* (Matocha 1977), *S. tereticaudus* (Dunford 1977a, pers. comm.) and possibly *S. columbianus* (Betts 1976, Murie and Harris *pers. comm.*) appear to have no specific avian alarm call, distinct calls for terrestrial and aerial predators have been noted in *S. armatus* (Balph and Balph 1966), *S. beecheyi* (Leger and Owings 1978), *S. beldingi* (Robinson 1981, Sherman 1977, Turner 1973), and *S. parryi* (Melchoir 1971). In contrast to this study, Koeppl *et al* (1978) did not note any differential use of the whistle and chirp calls, although they recorded mainly calls of squirrels caught in live-traps (Koeppl, pers. comm.). As well, they stated that the principal alarm call of *S. richardsonii* was the churr call. During this study, I found that squirrels churred most frequently to an approach by humans, and then usually when they were in their burrows (personal observation).

Hypotheses for the evolution of alarm call types in birds (e.g., Marler 1955), suggest that calls for aerial predators should be difficult to locate, since they are of high

Table 7.5. Responses of Richardson's ground squirrels by age/sex class to 73 trials in which a frisbee was thrown so that it passed above them.

Age/sex	No call	Call	Run to burrow	Distance to burrow (m)	a[1]	b[2]	c[3]
Adult male	3	0	1	0.5			
Parous adult female	5	6	9	0.9±0.7		4	2
Non-parous adult female	7	0	7	0.4±0.6			
Juvenile male	11	6	14	1.8±1.5	2	1	3
Juvenile female	23	12	26	1.2±1.5	3	1	6

a[1] – called before running to burrow

b[2] – called as running to burrow

c[3] – called after reaching burrow

frequency and have little frequency modulation. Such calls have been reported for *S. beecheyi* (Leger *et al* 1980), *S. beldingi* (Turner 1973), and *S. tereticaudus* (Dunford 1977a). In contrast, sonograms of "aerial" alarm calls in *S. armatus* (Balph and Balph 1966) and *S. richardsonii* (this study) show that the calls are highly frequency modulated, making them easily localizable. Avian predators probably hunt by using visual cues, and a diving raptor has probably already selected its target. Unlike birds, ground squirrels can escape into burrows, so that selection has favoured, instead of a non-localizable call, a short, loud, and piercing chirp (Koeppl *et al* 1978), which unambiguously alerts nearby conspecifics of the imminent danger, yet requires little investment of time by the caller.

That Richardson's ground squirrels, and indeed, many ground squirrel species, have different calls that vary consistently with the situations in which they are emitted, and hence provide information to conspecifics about the situation (Owings and Leger 1980), speaks against one of the "selfish" hypotheses for the maintenance of alarm calling, i.e. manipulation of conspecifics (e.g., Charnov & Krebs 1975, Dawkins and Krebs 1978). Dawkins and Krebs (1978) suggest that any information shared is likely to be false, but the differential and appropriate reactions of Richardson's ground squirrels to the aerial and terrestrial alarm situations, indicates conspecifics can extract correct information concerning the context of these calls. Playbacks of alarm calls to thirteen-lined (Schwagmeyer and Brown 1981) and Columbian (Harris *et al in press*) ground squirrels also indicated the transmission of true information, since responses were more appropriate for the detection and evasion of predators than were responses to other calls or sounds.

The differential responses were appropriate to the context. When danger was from an aerial predator, there was often no time to ascertain the direction or position of the bird, and instead the best evasive action was to run immediately to the safety of a burrow. By contrast, the threat from terrestrial predators was less immediate. There was time to stand up, look around and locate the predator, and then react further if necessary. Terrestrial predators could either enter burrows (weasel) or dig them up (badger, and possibly coyote), so that burrows did not represent a haven of safety as in the case of an attack by a raptor. Therefore, the appropriate response to the close proximity of a terrestrial predator was to flee from the predator without going into a burrow (Table

7.2).

The finding that during the gestation/lactation period adult male Richardson's ground squirrels are the most likely to give alarm calls is opposite to the situation observed in Belding's (Sherman 1977), round-tailed (Dunford 1977a), and thirteen-lined (Schwagmeyer 1980) ground squirrels. However, in *S. beldingi* (Sherman 1976), *S. tereticaudus* (Dunford 1977b) and *S. tridecemlineatus* (McCarley 1966, Schwagmeyer pers. comm.), males do not defend territories during the breeding period, and disperse after breeding. In contrast, some *S. richardsonii* males defend territories during the breeding period, and continue to reside there during the gestation/lactation period (see Chapter 2). Such males had probably sired young within their range. Also, some males do not disperse from their natal area and remain in an area that overlaps their mother's territory as yearlings (see Chapter 2).

Trivers (1972) predicted that the parent which invests least in the offspring (in this case, the male), should be tempted to desert and not give parental care. However, parental behaviour should be optimized to maximize reproductive success (Maynard Smith 1978). Paternal care in Richardson's ground squirrels would be favoured if the female alone could not ensure the survival of the offspring, and the male could act in a way to contribute to the survival of the young that gained him more than through desertion. Selection for the evolution of male protective care could occur without the male being assured of paternity, so long as there is a high probability he is the father (Grafen 1980).

Because female ground squirrels breed only once per year following emergence from hibernation in the spring (Davis in press), a male cannot increase his investment by inseminating more females after the breeding period, so that the main advantage to desertion is the avoidance of inbreeding in subsequent seasons (Wade 1979, see Chapter 2). In this study, weasels were the most frequent predator present, and the largest known cause of infant mortality during lactation when the infants were below ground. Females plug their nest burrows at this time (Davis unpubl. data), and this may well be in part a defense against interspecific predation rather than intraspecific predation as suggested by McLean (1978) for Columbian ground squirrels. Males could contribute to the survival of young within their range through alarm calling (warning the females, and perhaps informing the weasel that it has been seen), and chasing weasels. Females are much lighter than males at this time (unpubl. data) and probably would be at greater risk if they were to confront a weasel. After the juveniles are weaned, females increase in weight, and the likelihood that they will chase weasels also increases. Thus adult males may be able to invest in the survival of offspring or half-sibs by remaining in the area where they bred or remaining within their mother's area, respectively.

Paternal care has been demonstrated in Arctic ground squirrels (*S. parryii*) where some males defend their likely offspring against intraspecific infanticide (McLean in press). During the period when the infants are below ground, adult males also spend a greater proportion of their aboveground time vocalizing than do adult females (McLean in press).

Further evidence that alarm calling is most pronounced when it can warn relatives comes from the experimental trials. My results agree with those of Sherman (1977) and Dunford (1977a) since adult females with young were the most likely to call, non-parous females did not call, and juvenile males and females called equally frequently. That immigrant juvenile males did not call under natural conditions also supports the predictions based on kin selection, as immigrants were probably unrelated to any of their neighbouring conspecifics. Calling by non-parous females under natural conditions does not necessarily contradict the kin selection hypothesis, since non-parous females may well have had adult sisters, daughters, or mothers near to them. In the experimental trials, non-parous females did not have any close adult female relatives as neighbours (see Chapter 8).

In conclusion, alarm calling in Richardson's ground squirrels is consistent with the prediction of kin selection theory, that animals will be most likely to call when they have close relatives nearby. Calling appears to be nepotistic but not altruistic behaviour, because there is no evidence that it involves a cost to the caller.

7.5 Acknowledgements

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8. Is Kin Clustering Advantageous for Adult Female Richardson's Ground Squrrels?: an experimental study

8.1 Introduction

A substantial body of theory (Barash 1982, Dawkins 1976, Hamilton 1963, 1964, 1972, Wilson 1975) elucidated the possibility, indeed the inevitability (Dawkins 1979), that 'kin selection' (Maynard Smith 1964) is a consequence of natural selection. The principles of kin selection provided a novel perspective for the study of animal behaviour: instead of seeing adaptive advantage only in how behaviour influenced the individual's reproductive success, behaviour could be viewed in terms of its effect on the survival and reproductive success of kin, and hence, the individual's 'inclusive fitness' (Hamilton 1963). A bandwagon resulted (Dawkins 1979), and a rash of studies soon documented the occurrence of kin-preferential behaviour in wild populations (e.g., Bertram 1976, Dunford 1977a, Hoogland 1981, Kurland 1977, Sherman 1977, Wilson 1971). More recently studies have attempted to identify mechanisms for kin-differential behaviour, i.e., how animals distinguish their kin from non-kin (Blaustein and O'Hara 1981, Davis 1982, Greenberg 1979, Holmes and Sherman 1982, Waldman and Adler 1979).

In the rush to quantify *where* and *how* kin preferential behaviour occurs, *why* it occurs has most often been overlooked. Hamilton's (1963) formula for the evolution of altruistic behaviour, predicts that nepotism will occur only when the ratio of the benefit to the recipient over the cost to the actor exceeds the reciprocal of the coefficient of genetic relatedness between the two. Yet while considerable effort has gone into deriving relatedness between conspecifics (e.g., Hanken and Sherman 1981), little attention has been paid to establishing costs and benefits of behaviours. Notable exceptions have been attempts to measure the effect of behaviour on inclusive fitness directly (Packer and Pusey 1982), or indirectly through experimental manipulation (Barash 1980, Brown and Brown 1981). An advantage of current sociobiological theory is that it is predictive (Barash 1980), and while many of its predictions may be difficult to test (Pulliam 1981), experiments should be designed to test the hypothesis that kin-preferential behaviour is indeed beneficial to the recipient and may therefore influence inclusive fitness.

In many ground-dwelling sciurids, adult females live in kin clusters and behave differently towards their kin than their non-kin (see Armitage 1981 and Michener *in press* for reviews). As adults, female Richardson's ground squirrels reside near kin (Michener 1979, 1981), and it has been proposed that kin clustering improves survival and reproductive success through increased likelihood of predator detection and a sharing of resources (Michener *in press*). To test the predicted advantages of kin clustering, I experimentally manipulated a field population of *S. richardsonii*, so that on one half of the area all females were members of kin clusters while on the other half females did not have close relatives as neighbours. It was predicted *a priori* that on the area with kin clusters:

1. females should share more space with their kin than females on the other area shared with their neighbours,
2. females should spend less time alert for predators, and hence, be able to devote more time to feeding,
3. interactions between kin should be less severe than those between non-kin, and
4. there should be a higher survival of young to weaning (reproductive success).

8.2 Methods

The study site was situated at Roi Lakes (53°35'N, 114°05'W; elevation 730 m), 12 km north-west of Stony Plain, Alberta, Canada. The study area was 1.3 ha of rolling grasslands amid a clearing surrounded by aspen forest. A grid of painted stakes marked the area into 10 x 10m squares, and the area was sometimes grazed by cattle.

This study was initiated in May 1980, at which time all adult ground squirrels on or near the study area were live-trapped, eartagged, and dye-marked with human hair dye for individual identification. At the time of weaning, young of all litters on the area were live-trapped and similarly marked, on or soon after emergence while the young were still associated with their natal burrow and mother. Hence, matrilineal kinship was determined. In all, 168 squirrels were tagged in 1980, including 137 juveniles, 71 of which were females.

In the spring of 1981, squirrels were re-dyed as they emerged from hibernation. The study area was divided in half, and following the end of the breeding period on 7

April (by which time 98% of females had emerged [see Chapter 2]), females were removed from one half of the area so that all those remaining had at least one uterine–kin female (i.e., a mother, daughter, or sister) as a contiguous neighbour. This was called the Kin Cluster Group (KC), and in fact each female had on average 2.8 uterine–kin females (SD = 0.5, range = 2–3, *n* = 8) as near neighbours, representing all or part of three matrilineal kin clusters. (At the outset of the experiment another female from another kin cluster was included in the KC group, but as her two daughters, although both neighbours, resided off the study area, they were seldom seen and insufficient data were available to make valid estimates of amount of space shared. Hence, the mother was not included in the subsequent analysis of the experiment's results.) On the other half of the study area, females were removed so that those remaining had no uterine–kin as contiguous neighbours (the No Kin Cluster Group, NKC). Eight females were removed, four from each half of the study area, and densities remained approximately equal at 15 females/ha (KC) and 14 females/ha (NKC).

Squirrels were observed using instantaneous scan sampling (Altmann 1974) at 15 minute intervals. The location and activity at the instant each squirrel was seen in a systematic scanning search of the study area were recorded. As well all–occurrences sampling (Altmann 1974) was conducted for interactions, from which the identity of the participants, the location of the interaction, and the outcome of the interaction were noted. During the two years 239 hours of observation were made of the squirrels on the study area (1980: 100.75 hours, 1981: 138.25 hours). The active season was divided into the phases recognized by Michener (1982), and during 1981 adult females were seen in 83 scans during the breeding period, 206 scans during the gestation–lactation period, and 127 scans during the post–emergence period.

8.3 Results

8.3.1 Control

In 1980 breeding success, as measured by the number of young successfully weaned per female, was not significantly different for the two halves of the study area (x = 5.8, SD = 3.1, *n* = 12; x = 6.5, SD = 2.9, *n* = 8; Student's *t*-test: *t* = 0.54, *P*>0.5). All females on the study area brought up young. During the breeding period in 1981, no significant differences existed in the behaviour of females on the two halves (Fig. 8.1a). Therefore, there was no *a priori* reason to suspect that the two halves of the area were different before the experimental treatment.

8.3.2 Gestation-Lactation Period (8 April - 27 May)

This is the period following breeding until the emergence of all young above ground at the time of weaning. During this period females in the NKC group tended to be alert more often, and spend less time feeding than their counterparts in the KC group (Fig. 8.1b). The amount of time spent alert increased significantly for NKC females after the removal (paired *t*-test: *t* = 3.14, *P*<0.05, *n* = 6), whereas KC females spent similar amounts of time alert during the gestation-lactation period as during the breeding period (*t* = 0.10, *P*>0.9, *n* = 6).

Geometric centres of activity were calculated for all females during the gestation-lactation period. The mean distance between activity centres of females and their nearest neighbour in the NKC group was 17.6 m (SD = 4.7, *n* = 10). Distances between activity centres of KC females and their nearest uterine-kin neighbour averaged 15.9 m (SD = 6.5, *n* = 8). However, for only four of these females was their nearest kin also their nearest neighbour, and in these cases the distance between their activity centres (x = 12.5 m, SD = 2.0, *n* = 4), was significantly less than that between nearest neighbours in the NKC group (Mann-Whitney *U*-test: *U* = 4, *P*<0.05).

Home range sizes were similar for KC (x = 0.15 ha, SD = 0.07) and NKC (x = 0.11 ha, SD = 0.06) females during the gestation-lactation period (*U* = 25, *P*>0.2). Average overlap of home ranges between KC females and their nearest uterine-kin (47.1%) was only slightly higher than overlap between nearest neighbours in the NKC group (39.4%),

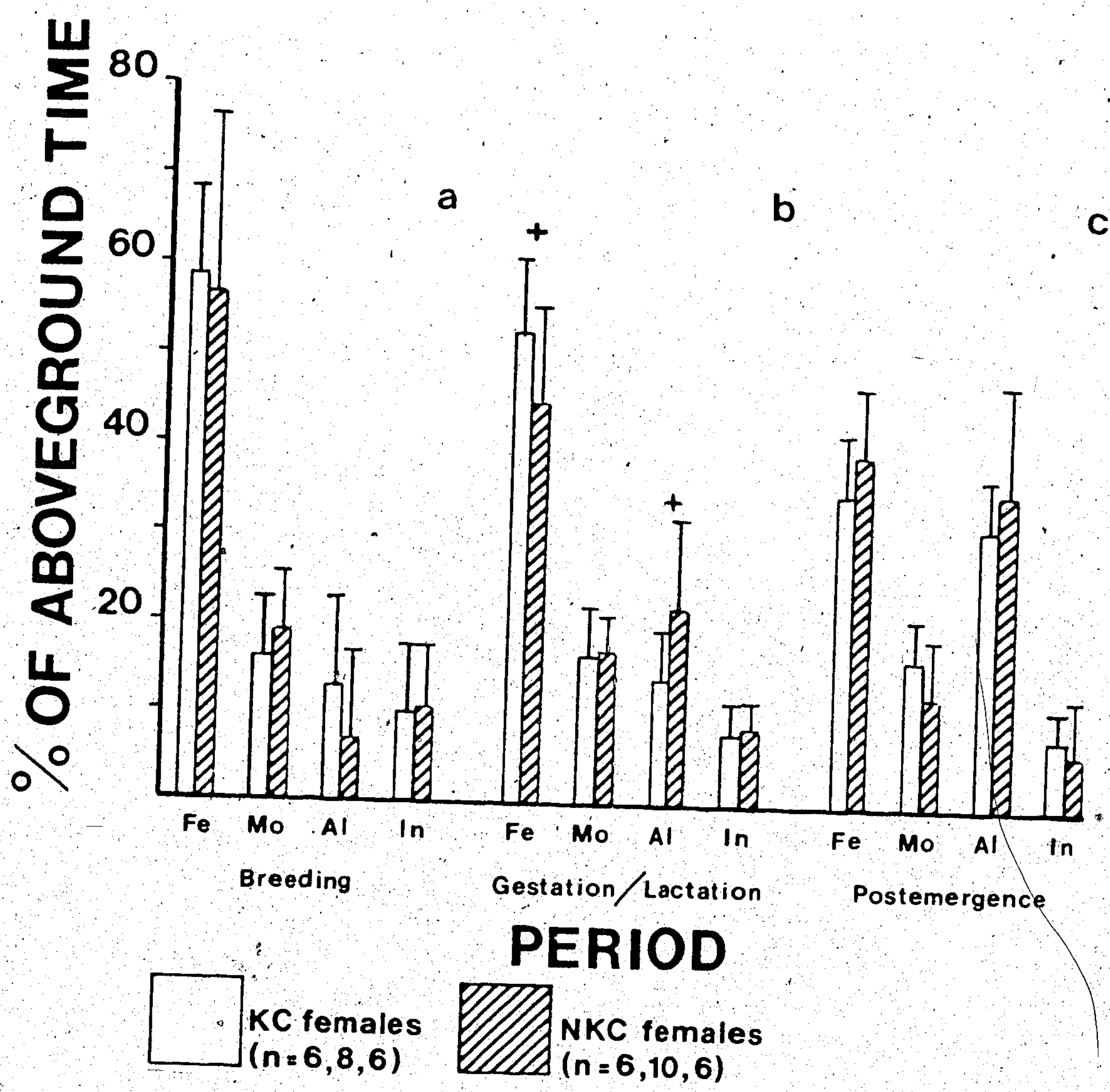

Fig. 8.1. Percentage of aboveground time spent feeding (Fe), moving about (Mo), alert (Al), and interacting with conspecifics (In) for adult female Richardson's ground squirrels on the No Kin Cluster (NKC) area and the Kin Cluster (KC) area during the breeding (a), gestation/lactation [8 April – 27 May] (b), and postemergence (c) periods. Each female was seen on average 35±12 times during 83 scans (a), 99±39 times during 206 scans (b), and 48±20 times during 127 scans (c).
+ $0.05 < P < 0.1$, Mann-Whitney *U*-test.

but considerably higher if only kin that were also nearest neighbours were used (63.0%), albeit non-significant due to the large variances (Fig. 8.2). The same pattern held for the amount of time each female spent in the overlap zones (Fig. 8.2). These differences were accentuated if core areas (the minimum area in which a female spent 80% of her time) were considered. Overlap of the core areas of uterine-kin that were also nearest neighbours in the KC group (x = 45.0%, SD = 35.7, n = 4) was significantly greater (U = 5, $P<0.05$) than the overlap between the core area of NKC nearest neighbours (x = 15.6%, SD = 8.9, n = 10).

Thus, uterine-kin appeared to share more space than did females whose neighbours were not closely related. However, the average distance between KC females and their nearest neighbouring kin when both were simultaneously present above ground (x = 21.6 m, SD = 5.0) was not different (U = 32, $P>0.5$) from the mean distance between NKC females and their nearest neighbour (x = 20.2 m, SD = 6.8). Overlap of space between kin need not imply mutual attraction then, but rather mutual tolerance, since there was not a concommitant temporal overlap in the use of the shared space.

As uterine-kin did not spend more time in close spatial proximity than did non-uterine-kin, the potential to interact with conspecifics should have been the same for KC and NKC females and, indeed, the groups did not differ in proportion of time spent interacting (Fig. 8.1b). But proportion of time spent interacting with conspecifics was a gross measure that did not take into account differences in the quality or type of interaction. Mean female-female interaction rates (# interactions per hour that each female was seen above ground) did not differ (U = 35, $P>0.6$) between KC (x = 0.30 interactions/hour, SD = 0.15) and NKC (x = 0.32 interactions/hour, SD = 0.17) females. However, interactions between uterine-kin seldom resulted in displacement (i.e., one squirrel fleeing the area of the interaction, usually chased by the other) of the participants, whereas one female was usually displaced in interactions involving other females (Fig. 8.3). But in those interactions where the participants were not closely related, non-neighbouring females (i.e., females with core areas that were not contiguous) were always (19/19) chased away, while neighbouring females were only displaced 73% (37/51) of the time (X^2 = 6.5, P = 0.01, with Yate's correction for continuity). As well, when chases did occur, non-neighbours were chased further (x = 13.8 m, SD = 6.4, n =

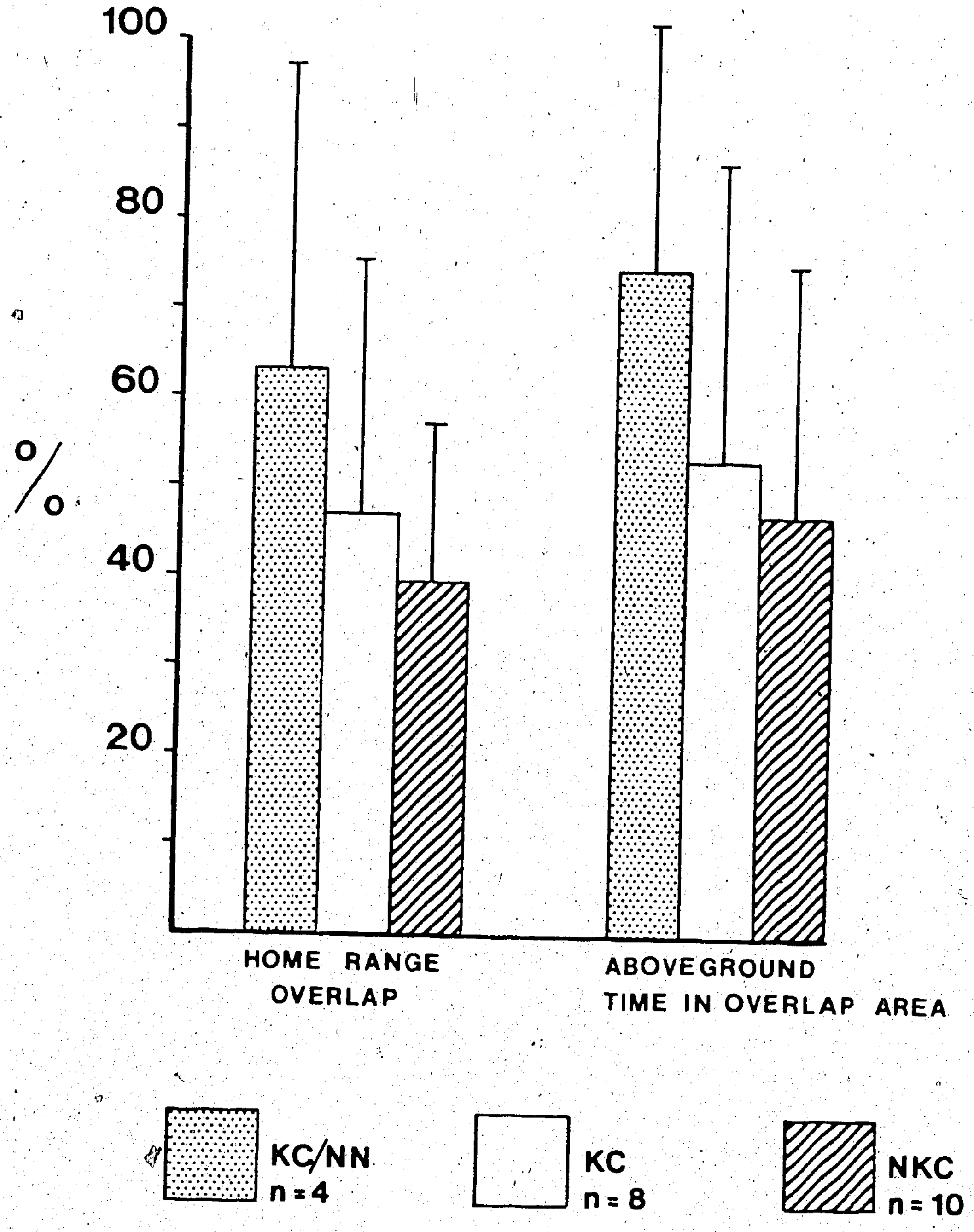

Fig. 8.2. Overlap of home ranges during the gestation/lactation period, and time spent in the overlap area for NKC females and their nearest neighbours, KC females and their nearest uterine-kin, and KC females and their nearest uterine-kin which were also nearest neighbours (KC/NN).

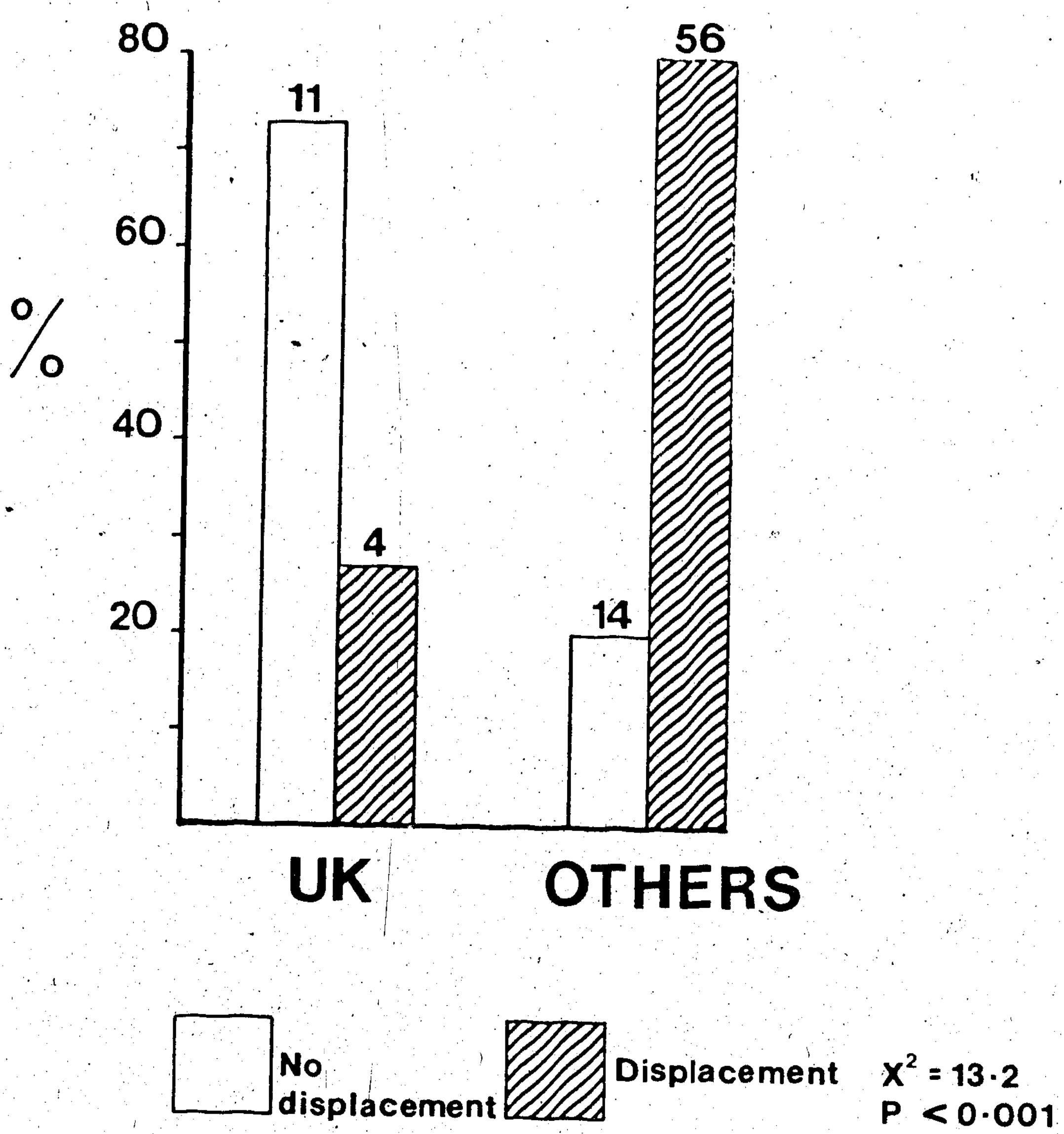

Fig. 8.3. Proportion of adult female–female interactions, with uterine–kin and others, initiated by the 18 study animals during the gestation/lactation period that resulted in displacement or no displacement. Numbers of interactions are given atop the bars.

16) than were neighbours ($\bar{x}$ = 8.4 m, SD = 5.2, n = 29) (U = 117.5, $P<0.01$). Thus, while uterine-kin seldom chased each other, proximal association affected interactions among non-uterine-kin, such that non-uterine-kin neighbours were chased less often and for shorter distances than were non-neighbours.

Breeding success, measured as the mean number of young weaned per female, was much greater for KC females (5.3 young/female) than for NKC females (0.2 young/female). Whereas only 2 KC females failed to bring up a litter, 9 NKC females failed to wean any young, and the other one brought up only two. It seems unreasonable to attribute such a disparity in breeding success entirely to the effects of the experimental manipulation, especially given the relatively small behavioural differences between the groups. Predation probably contributed in large part to the differential success between the two areas. For 4 NKC females the cause of their litters' demise was known. In one case a weasel entered a female's nest burrow and removed 10 young, and on another occasion a weasel was observed in the nest burrow of a female. Badgers dug up the nest burrows of two other NKC females. By contrast, no KC litters were lost to badgers. It seems unlikely that the presence or absence of relatives could do much to avert predation by badgers, and the effect of such predation on breeding success in this experiment should probably be viewed as random sampling error.

8.3.3 Post-Emergence

Following emergence of the juveniles on the area, KC and NKC females spent their time similarly, despite the absence of young on the NKC area (Fig. 8.1c). Most females without young disappeared early in the postemergence period (presumably they had gone into hibernation as several of these disappearing females were recovered on the area the following spring), and detailed examination of their behaviour was not possible.

8.4 Discussion

The close association of adult female uterine-kin has been documented in several species of ground-dwelling sciurids (*S. beldingi*: Sherman 1981a, *S. columbianus*: W.J. King pers. comm., *S. parryii*: McLean 1982, *S. richardsonii*: Michener 1979, *S. tereticaudus*: Dunford 1977b, *Marmota flaviventris*: Johns and Armitage 1979). Differences in alarm calling (Dunford 1977a, Schwagmeyer 1980, Sherman 1977), home range overlap (McLean 1982), interactions (McLean 1982, Sherman 1981a), and use of burrows (Dunford 1977b, M.A. Harris and J.O. Murie pers. comm., Johns and Armitage 1979, McLean 1982) between uterine-kin and non-uterine-kin has led to the assertion that kin clustering improves survival and reproductive success through increasing the likelihood of predator detection and a sharing of resources (Michener *in press*). With the exception of McLean's (*in press*) experiment to measure the effects of the presence of presumptive fathers on the incidence of infanticide in Arctic ground squirrels, there have been no attempts to measure the actual costs/benefits of these behavioural asymmetries in the Marmotini.

In this experiment the *a priori* predictions were generally upheld, although not always strongly. Female kin did share an area of greater extent than that shared between non-kin, particularly when the related females were also nearest neighbours. Females without closely related neighbours spent more time being vigilant, while females in kin clusters were possibly able to devote more time to feeding as a result of a reduced need for vigilance. Although both groups of females interacted with conspecifics to the same extent, and female-female interaction rates were the same, interactions between kin most often resulted in no displacement, while the majority of interactions between non-uterine-kin ended in chases. Finally, reproductive success was greater for females in kin clusters.

The difference in the outcome of interactions between uterine-kin and non-uterine-kin may have accounted for the greater space sharing by kin. Overlap was not the result of active attraction, since uterine-kin were no more likely at any instant in time to be closer together than any neighbouring conspecifics. Spatial overlap may have occurred through passive mutual tolerance between close kin, such that females were less likely to be chased away *when* detected by the resident if they were related to the resident, and hence females *learned* that they could trespass with impunity.

There is probably a high cost in terms of energy expenditure involved with fighting and chasing (Ruff 1971). This cost is often reduced to near zero in interactions between uterine-kin, and this reduction together with the greater amount of time devoted to energy aquisition (feeding) in the KC group, may have positively influenced the females' abilities to provide nourishment for their embryos and young.

The greater vigilance on the NKC area may have been due to a reduced likelihood that surrounding conspecifics would emit alarm calls (see Chapter 7), requiring more alertness by individuals to detect predators, or it may have been due to a greater need for attentiveness against intrusions by conspecifics. Without a common border shared with a close relative, all sides of a female's territory would have to be actively defended. Known instances of predation were higher on the NKC area, and predation was the single most important, identifiable feature responsible for the differences in breeding success between the two areas, suggesting the vigilance was a response to their litters' greater vulnerabilty to predators. The increased vigilance and poor reproductive success of females in the group without close kin, would also be consistent with the hypothesis that infanticide will occur between unrelated sciurids (Sherman 1981b), although there were no observations nor evidence of infanticide in this study.

The variability apparent among the uterine-kin in how they behave, may in part be due to the different types of relationship represented. In defining the limits of ground squirrel nepotism, the cutoff has generally been made so as to include mother-daughther and sister relationships in the favoured group (Sherman 1980, 1981a, McLean 1982). Since the likelihood of a particular gene being present in a daughter or sister is 0.5 for both, kin selection would seem to predict that daughters and sisters should be favoured equally (Hamilton 1964). Yet there are good theoretical arguments for investment being greater in offspring than in siblings (Charlesworth 1978, Rubenstein and Wrangham 1980), and this would especially be true if multiple paternity occurred, thereby reducing the certainty of relatedness between littermates. Evidence of multiple paternity has been found for *S. beldingi* (Hanken and Sherman 1981), although current electrophoretic research on *S. richardsonii* has not produced any similar evidence, to date (G.R. Michener pers. comm.). In addition to the arguments of Charlesworth (1978) and Rubenstein and

Wrangham (1980), I believe investment in offspring rather than siblings should be favoured for the following reason: Natural selection, the differential survival of genes (Dawkins 1976), is based upon the *relative* frequencies of genes in the gene pool. In diploid individuals, production of two nieces or nephews while contributing the same amount of a particular gene to the gene pool as if the individual had produced one offspring of its own, promotes the survival of a greater proportion of genes not shared with the individual. Thus, the *relative* frequencies of the individual's gene in the gene pool would be less than if it produced only its own offspring.

In this experiment, where uterine-kin were also nearest neighbours they were usually mothers and daughters, whereas sisters most often had a non-uterine-kin as a nearest neighbour.

Finally, this experiment indicates that social interactions are controlled by factors other than just kinship. Among females that were not closely related familiarity appears to reduce the likelihood and severity of chases in agonistic encounters. Sherman (1981a) denied that length of association affected the outcome of interactions within his various classes of relatedness, but some of his correlations were very close to being statistically significant (e.g., $P = 0.07$), and perhaps indicated evidence of a relationship between length of association and the probability of fights or chases. As well Sherman's results (Table 1, 1981a) show that in two of four groups of unrelated conspecifics, neighbours were treated preferentially compared to non-neighbours.

In conclusion, the results of this study suggest that clustering of adult female kin in Richardson's ground squirrels can have measureable effects upon the females' behaviour and breeding success. The results are a preliminary indication only, and there is a pressing need for more studies to investigate the adaptive advantage, if any, of behavioural asymmetries based upon kinship.

8.5 Acknowledgements

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9. Conclusion

Sociality in Richardson's ground squirrels is characterized by the prominent role of familial bonds. Conspecifics treat each other differently depending on their level of relatedness (Chapter 5). The persistance of natal burrow associations (uterine-kin), either through a mechanism of familiarity and/or an ability to distinguish biological kin (Chapter 6), after weaning (Chapter 4) and into adulthood (Chapter 3) shape the behavioural predilections of *S. richardsonii*. Uterine-kin are likely to overlap in space, and are unlikely to displace each other during encounters. Squirrels are most likely to give alarm calls when they have offspring or siblings nearby (Chapter 7). This includes some adult males, which because of the territorial nature of the mating system (Chapter 2), have probably sired some offspring within their post-breeding ranges. The proximal advantages of kin association and kin preferential behaviour in Richardson's ground squirrels appear to include:

1. reduced costs of aggression through de-escalation of conflicts,
2. reduced chances of predation, and
3. increased time available for food acquisition through reduction in the amount of time needed to be devoted to vigilance,

which may ultimately increase reproductive success (Chapter 8).

Thus the findings of this study are consistent with predictions of kin selection in as much as differential treatment of kin occurs in Richardson's ground squirrels in a manner that appears to be adaptive. To put this conclusion in perspective, however, it should be qualified by the following two points:

1. The family unit is a key aspect of group living in *S. richardsonii*, but that is not to say that group living would not be selected for in the absence of the proximity of close relatives. The advantages of group living (Alexander 1974, Bertram 1978) may still apply to unrelated groups of conspecifics, as occurs in the bat *Phyllostomus hastatus* (McCracken and Bradbury 1981). Kin selection alone is unlikely to be responsible for the evolution of sociality in Richardson's ground squirrels, but rather has mediated the form it has taken.
2. While selection has favoured preferential treatment of related conspecifics in *S. richardsonii*, there is no evidence to suggest there is a cost involved. Nepotism in

this species appears not to represent altruistic behaviour, but rather beneficent behaviour (West Eberhard 1975) from which both the animal performing the behaviour and the recipient probably profit.

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