

Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul

The Social Organization of the Cape Ground Squirrel (*Xerus inauris*; Rodentia: Sciuridae)

JANE M. WATERMAN

WATERMAN, J. M. 1995: The social organization of the Cape ground squirrel (*Xerus inauris*; Rodentia: Sciuridae). *Ethology* 101, 130–147.

Abstract

The Cape ground squirrel (*Xerus inauris*) of southern Africa is a tropical species that does not hibernate. Field observations using scan and all-occurrence sampling revealed that this species was highly social. Female Cape ground squirrels formed social units of related females and their subadult young, as is typical for other ground squirrels. Female social groups were usually composed of 2–3 adult females and 2–3 subadults of either sex. Members of these female social groups shared sleeping burrows and feeding ranges. Female social groups did not cooperatively defend their feeding ranges from adjacent groups in other burrow clusters. Interactions within female social groups were highly amicable, and no dominance hierarchy was evident. Males in this species also lived in groups. These all-male bands of up to 19 individuals lived almost independently from female groups. The entire male band shared one home range, although ephemeral sub-bands were formed daily. The composition and size of these sub-bands changed daily. Interactions among males, which were largely amicable, included allogrooming and sleeping together. Analysis of interactions within the band indicated a stable, linear, dominance hierarchy among males. Dispersal in this species appeared to be male biased as is typical of other ground-dwelling squirrels, with males dispersing at reproductive maturity. Males joining male bands were thus dispersers and were not likely to be closely related. Sociality in the Cape ground squirrel may be summarized as highly social female kin clusters and associated social non-kin bands of males.

Jane WATERMAN, Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, S7N 5E2.

Introduction

In mammals, social structure among females is thought to be most influenced by ecological pressures (such as resources), whereas social structure among males depends on the distribution and behaviour of females (EMLEN & ORING 1977; WRANGHAM 1980). Social structure in the ground-dwelling squirrels ranges from asocial to highly social species (ARMITAGE 1981; MICHENER 1983; TRAVIS &

SLOBODCHIKOFF 1993). Such a wide variety of social systems allows for comparative studies of social behaviour and the generation of predictive hypotheses of the underlying selective pressures leading to the evolution of sociality.

Many of the hypotheses about the evolution of sociality in the ground-dwelling sciurids have emphasized the importance of environmental constraints (BARASH 1974; ARMITAGE 1981; MICHENER 1983). The majority of North American ground squirrels hibernate for much of the year, resulting in limited breeding periods and short active seasons. The result of such short active seasons is that young of the year have only a short period of growth prior to hibernation. BARASH (1974) suggested that a shortened vegetative growing season in areas of increased environmental harshness (such as higher altitude or latitude) is correlated with delayed dispersal in marmots. Tolerance of subadults has evolved to allow the delayed dispersal of undersized young, and has ultimately led to sociality (BARASH 1974).

ARMITAGE (1981) suggested that delayed dispersal is a life-history tactic of social species. Species in which maturation and dispersal of offspring occurs in the first year tend to be asocial (ARMITAGE 1981). In species whose growing season is not long enough for offspring to mature before their first hibernation, parents tolerate offspring beyond weaning. This toleration is a form of direct parental investment as it allows offspring access to resources such as food and hibernacula, as well as better protection from predators (ARMITAGE 1981, 1988). Thus, species with higher levels of social organization have delayed dispersal and delayed reproductive maturity. Ground-dwelling sciurids that are not highly social usually breed as yearlings (ARMITAGE 1981, 1988).

The Cape ground squirrel, *Xerus inauris*, inhabits the arid regions of southern Africa. Unlike most North American ground-dwelling squirrels, individuals of this species do not hibernate and can breed throughout the year (HERZIG-STRASCHIL 1978; WATERMAN 1996). Adult weight and reproductive maturity are attained within the first year (WATERMAN 1996). In comparison with North American ground squirrels, Cape ground squirrels are considered a large-bodied species (approximately 550 g; HERZIG-STRASCHIL 1979). According to ARMITAGE's (1981) hypothesis, such life-history traits suggest that the Cape ground squirrel would not be highly social. Nonetheless, there is evidence that the Cape ground squirrel is a highly social species (HERZIG-STRASCHIL 1978), although few details about its social structure have been published.

The purpose of this paper is to describe the social structure of the Cape ground squirrel, to assess its degree of sociality compared to North American ground squirrels, and to discuss this sociality with respect to current hypotheses for the evolution of sociality in ground squirrels.

Methods

The study area was a 3500-ha farm 185 km southeast of Windhoek, Namibia, in the Kalahari-bushveld region (23°25' S, 18°00' E). The vegetation of the area was dominated by *Acacia* bush and trees, including *Acacia erioloba*, *A. hebeclada*, *A. karoo*, and *A. mellifera*. *Catophractes alexandri* and *Boscia albitunes* were also common. Common grasses include *Schmidtia kalarensis*, *Rhynchelytrum*

Table 1: Operational definitions of behaviour of Cape ground squirrels used in social interactions

Behaviour	Description
Chase	running after a moving individual
Mild fight	two individuals facing each other, strike each other with forepaws
Fight	similar to mild fight, but with escalated striking and individuals jumping into the air and kicking with hindlegs
Attack	one individual leaps at another individual and strikes with forepaws
Run at	running within 10 cm of another individual, with the other individual not moving away
Approach	walking to within 10 cm of another individual
Follow	walking in pursuit of another individual
'Greet'	mutual contact with naso-oral areas
Allogroom	one individual grooms another
Play	play behaviour
Jump back	one individual leaps away from another
Group Defense	two or more members of a social group simultaneously attacking, chasing or fighting with a member(s) of an adjacent social group
No reaction	although in contact with or near another individual, no response to the behaviour of the other individual is perceivable

repens, *Anthephora pubescens*, *Chloris virgata*, *Eragrostis superba*, *Enneapogon cenchroides* and *Aristida stipitata*.

Since the spatial dynamics of the Cape ground squirrel do not easily fit the conventional terms used to describe ground squirrels, I have attempted to avoid confusion by using the following terms: a burrow cluster is defined as an aggregation of burrow openings clearly separated from adjacent clusters by areas without burrows that are larger than the cluster area (HERZIG-STRASCHIL 1978). Burrow clusters were composed of a number of burrow systems (a system being a series of connecting burrows); a social group is defined as a group of animals living together in the same burrow system (HERZIG-STRASCHIL 1978).

Two sites located 5 km apart were chosen for trapping and observations, one site of 14 ha (area 1) and one of 6 ha (area 2). All individuals in 12 burrow clusters were live-trapped and detailed observations were made at eight of these burrow clusters. The habitat structure of six additional burrow clusters in the study area was also examined. Locations of squirrels were recorded using a grid that was marked by coloured flags placed at 10-m intervals within burrow clusters and at 20-m intervals in adjacent areas.

All squirrels were captured using Tomahawk (15 × 15 × 50 cm) and Havahart (21 × 21 × 90 cm) live traps baited with peanut butter and oats. Individuals were marked for identification using numbered metal tags in their ears (National Band and Tag Co., Monel No. 1) and dye marks on the body (Lady Clairol Nice N'Easy and Nyanzol). As ear tags were frequently removed by squirrels, permanent identification was ensured by freeze branding (ROOD & NELLIS 1980). Individuals were weighed and examined for sex, age, reproductive condition, and external parasites. Testis size and the degree of vaginal swelling (indicative of the onset of oestrus) were also recorded to determine reproductive condition. Adult and subadult animals could be distinguished. Subadult males were either non-scrotal or partly scrotal, whereas adult males are scrotal all year round. Adult females had swollen nipples that remained permanently swollen after first pregnancy, whereas subadults had inconspicuous nipples. By the second year of the study, male age could be further distinguished by fur condition. Males that were older than 2 years had a reduction of fur to the face area, and the fur on the body was sparser than younger males or females of any age.

I made behavioural observations from June 1989 to Apr. 1990, Jun. 1990 to Feb. 1991, and Jul. 1991 to Dec. 1991. I observed squirrels from trees, windpumps and a vehicle, using 10 × 50 binoculars

and a 15–45 × 60 spotting scope. In total, I made 2000 h of behavioural observations. Observations focussed on the times when these squirrels interacted most, i.e. in the early morning and upon their return from feeding in the late afternoon. Periodically, observations of squirrels were also made throughout the day. Squirrels were still observed well into the time in which they had scattered from the burrow cluster to feed. Squirrels were considered to be grouped if the distance between a pair of individuals was 10 m or less. Squirrels move over relatively large home ranges (see below), and during their daily feeding, they often disperse quite widely. Thus, 10 m was considered to be a conservative estimate of grouping. During observation periods, the identity, location, and activities of all squirrels were recorded every 5 min using scan sampling, and interactions were recorded using all-occurrences sampling (ALTMANN 1974). The behaviours recorded during observations were based on descriptions by STEINER (1970a, b) for *Spermophilus columbianus* and EWER (1966) for *Xerus erythropus*. Overall time-budget analysis pooled an individual's behaviour from scan data into six categories: 1. Social (all interactions); 2. Alert (all postures in which the squirrels were in a vertical stance, either with only two feet and the hind end on the ground or on tip-toe); 3. Sitting (all times at which the squirrels were resting with four feet on the ground); 4. Locomotion (included running, loping and walking); 5. Maintenance behaviour (grooming, and sandbathing); and 6. Feeding. Behaviours used to analyse social interactions are described in Table 1. All-occurrence data on male–male interactions were used to determine the dominance hierarchy, which was analysed using Landau's index of linearity (LEHNER 1979). The behaviour of individuals on days when females were in oestrus was excluded from analysis in this paper, as that behaviour differs from days of non-oestrus and the scope of reproductive behaviour was too broad to be covered thoroughly within the context of overall social behaviour. It is described in detail elsewhere (WATERMAN 1994).

Six males in one band were fitted with radio-transmitter collars (148 MHz) and monitored for 40–60 days to track movement patterns. Sizes of feeding ranges and core areas were calculated for all individuals using the minimum-polygon method (MOHR 1947) using RANGES IV (KENWARD 1990). The core areas, within which an animal's locations were concentrated (KENWARD 1990), were determined by sequentially dropping the outermost points, which initially reduced the area considered. Little decrease in this 'utilization distribution' occurred, however, when more than 50 % of the points were dropped, indicating that only core fixes remain (KENWARD 1990). Thus, core areas were calculated from the innermost 50 % of the observation points. Females from adjacent social groups sometimes fed in the same area. Therefore, feeding ranges were estimated using all observation points. Overlap of an individual's feeding range (or core area) was calculated as the percentage of its feeding range (or core area) that was shared with another individual's feeding range (or core area). The activity centre is the arithmetic mean position of all location points (KENWARD 1990). As the third yr of the study concentrated only on morning and evening observations, with few all-day sessions, data for the first 2 yr of the study were used to calculate range sizes.

When data were found to be normal and homoscedastic, parametric statistics were used (SOKAL & ROHLF 1981; SNEDECOR & COCHRAN 1989); otherwise non-parametric statistics were employed (CONOVER 1980). A 0.05 probability of a Type I error was considered significant. Results are expressed as mean ± 1 SE, unless otherwise stated.

Results

Habitat Description

The average area encompassed by a burrow cluster was $692.8 \pm 100.0 \text{ m}^2$ (range 120–1500, $n = 18$), with 59.3 ± 7.1 (20–149, $n = 18$) burrow openings. Adjacent burrow clusters were separated by $194.6 \pm 31.6 \text{ m}$ ($n = 18$). In study area 1, there were 11 burrow clusters. The nearest aggregation of burrow clusters to area 1 was 2 km away. Similarly, the nearest aggregation of burrow clusters to area 2 (seven burrow clusters) was 1 km away. During any year, 1–3 burrow clusters were vacant (not occupied continuously by squirrels). All burrow clusters were located in areas predominated by the annual grass *Schmidtia kalahariensis*, a species that is highly nutritious and usually grows to a maximum height of 90 cm

Table 2: Densities of Cape ground squirrels in all study years (both study sites)

	1989		1990		1991		All years /ha
	total	/ha	total	/ha	total	/ha	
Adults							
Female	23	1.2	21	1.1	28	1.4	1.2
Male	24	1.2	23	1.2	28	1.4	1.3
Total	47	2.4	44	2.2	56	2.8	2.5
Subadults							
Female	16	0.8	15	0.8	9	0.5	0.7
Male	16	0.8	20	1.0	3	0.2	0.7
Total	32	1.6	35	1.8	12	0.6	1.3
All individuals	79	4.0	79	4.0	68	3.4	3.8

(MULLER 1984). A taller, perennial grass, *Aristida stipitata*, covered 10 % of the area of one burrow cluster. This grass is densely tufted and non-nutritious, growing up to 150 cm (MULLER 1984). *Acacia erolobia* trees occurred in 47 % of the burrow clusters, whereas 37 % contained *A. karoo* bushes. However, most burrows within a cluster were located away from bushes. Any small plants that appeared after the rains were consumed by squirrels, so burrow areas were bare most of the year.

Densities

The overall density of squirrels did not differ between area 1 ($\bar{X} = 3.81 \pm 0.11$ per ha) and area 2 ($\bar{X} = 3.66 \pm 0.44$; Friedman's test, $F = 0.33$, $p = 0.56$). Densities also remained fairly constant across years (Table 2; Friedman's test, $F = 3.0$, $p = 0.22$) in both study sites. Sex ratios did not differ significantly from 1:1 in either subadults or adults (Adults: $\chi^2 = 0.06$, $df = 2$, $p = 0.97$; subadults $\chi^2 = 3.70$, $df = 2$, $p = 0.16$).

Female Social Organization

Females lived in social groups composed of 2.2 ± 0.2 adult females (range 1–4; $n = 31$) and 2.5 ± 0.4 subadults of either sex (0–9; $n = 32$). Group sizes did not differ between study years (Kruskal-Wallis, $K = 0.22$, $p = 0.89$). A burrow cluster was usually inhabited by only a single female social group.

Formation of groups: Natal females were usually recruited into their natal social group. Prior to 5 mo of age, there were no sex differences in the disappearance of emerged juveniles (27.8 % of 36 females vs. 26.9 % of 26 males; $\chi^2 = 0.01$, $p = 0.94$). Males older than 5 mo disappeared at much higher rates than females of comparable age (SAS (LIFETEST), Wilcoxon $\chi^2 = 11.82$, $p = 0.0006$). This disappearance seemed to be most frequent between 8 and 10 mo (Fig. 1). By 18 mo of age, 13 of 15 males had disappeared, whereas, at the same age, only two

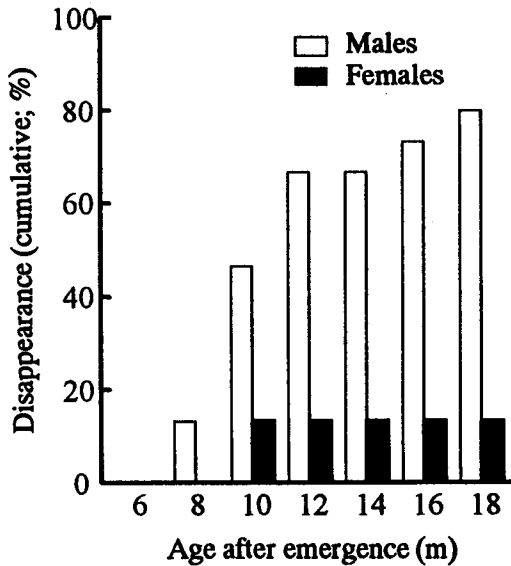


Fig. 1: Cumulative percentage of the subadult Cape ground squirrels that disappeared during the 6-18 mo after first emergence (males, $n = 15$; females, $n = 15$)

of 15 females had disappeared. Of the 13 remaining females, 10 were documented breeding in their natal burrow area, and the other three lived in burrow clusters that were trapped but not observed. In 1991, all seven social groups whose relationships were known contained at least one mother-daughter pair. Additionally, three of these contained at least one mother with two daughters from different litters.

Use of space: Members of these social groups shared sleeping burrows with the exception of lactating females, which isolated themselves from the social group (either in a different burrow system within the burrow cluster or in a different burrow cluster). After the emergence of their young at weaning, these females returned with their litters.

Adult-female feeding ranges covered 4.0 ± 0.25 ha ($n = 17$ individuals), and core-area size was 0.25 ± 0.07 ha ($n = 17$), usually encompassing the area of the burrow cluster. Range sizes did not differ between years (Mann-Whitney $U = 30$, $p = 0.55$, $n = 17$). Within a social group, all individuals shared a common range and core area. Overlap of adult feeding ranges among females within a social group was $88.8 \pm 1.5\%$ in 1989 ($n = 29$) and $72.6 \pm 5.7\%$ in 1990 ($n = 24$). Core areas overlapped by $66.3 \pm 4.9\%$ ($n = 53$, no difference in core area overlap between years, Mann-Whitney $U = 253$, $p = 0.16$). Between social groups, there was some overlap of female feeding ranges ($26.0 \pm 5.4\%$, $n = 18$ females in 5 groups, no difference between years, Mann-Whitney $U = 22$, $p = 0.11$), but no overlap of core areas (0%; Fig. 2).

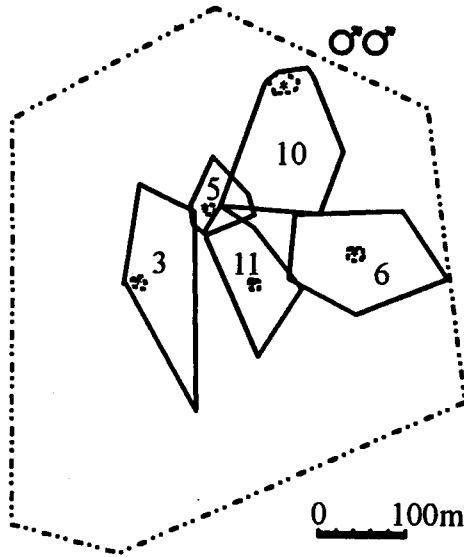


Fig. 2: The feeding ranges (solid lines) and core areas (dotted lines) of five female social groups and a male band (dotted and dashed line) in 1990. Asterisks indicate the site of the burrow cluster. The numbers within each feeding range refer to the number of individuals in the female social group

Females' activity centres reflect not only the stability of range use but also the cohesiveness of groups. Overall, the distance between activity centres of individuals in the same social group averaged 3.3 ± 0.48 m ($n = 72$). Shifts in the activity centres of individuals between years were also relatively small (36.9 ± 9.3 m, $n = 18$).

Behaviour: Adult females spent 42.6 ± 0.02 % ($n = 17$) of their above-ground time alone, 49.6 ± 0.01 % within 10 m of a member of their social group, and 7.8 ± 0.03 % within 10 m of a squirrel outside of their social group (usually an adult male). Most of their time was spent in feeding and locomotion (Fig. 3).

Although females spend nearly 50 % of their time near another social-group member, less than 10 % of their overall time was spent in social interactions (Fig. 3). The types of social interactions that establish dominance relationships in males, such as jumping back and running away, occurred rarely among females (average number of such interactions in female-female dyads was 0.8 ± 0.2 , $n = 71$; average number of such interactions in male-male dyads was 3.4 ± 0.2 , $n = 446$; Mann-Whitney $U = 139.1$, $p < 0.0001$). Interactions within the social group were usually amicable, with frequent approaching, greeting and allogrooming behaviour (Fig. 4). The frequency and type of interaction between juveniles (<4 mo) and their mothers did not differ significantly from interactions between juveniles and other females in their social group (Fig. 5).

Members of adjacent social groups rarely interacted with each other. In only

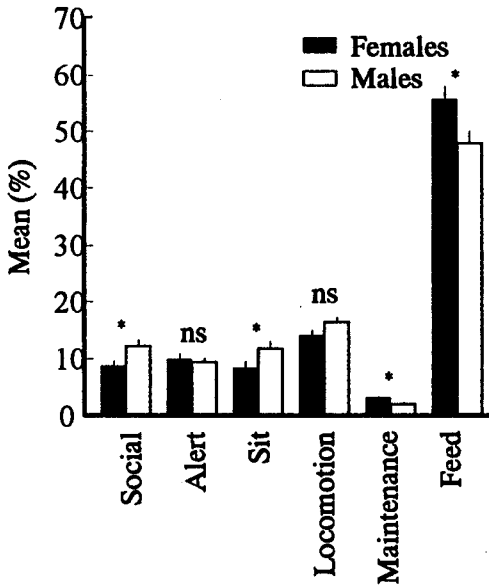


Fig. 3: Time budget of adult Cape ground squirrels, using behavioural categories: social, alert, sitting, locomotion, maintenance (grooming), and feeding. The time budgets of individuals (25 males and 17 females) were averaged to produce the overall time budget for each sex. Asterisks indicate significant differences (Mann-Whitney U, $p < 0.05$) between male and female behaviours

2.3 % ($n = 9016$) of observations of adult females was a member of another social group within 10 m. Additionally, in only 10.6 % ($n = 208$) of these cases were females seen to interact; most females continued in non-social behaviour such as feeding and walking. However, when interactions occurred they were usually agonistic (Fig. 4). Members of a social group were never seen to cooperatively approach, defend against, or interact agonistically with a member of an adjacent social group (Fig. 4).

Male Social Organization

Similar to adult females, males also lived together in groups that shared sleeping burrows. Male bands were observed in both study sites, although sufficient data on behaviour and use of space was only available for study area 1. Male bands, of up to 19 males, persisted throughout the year, and for the most part lived independently of female social groups. Temporary sub-bands formed among these individuals and the composition and size of these sub-bands changed daily. Due to the size of the male home range (see below) not all the male sub-bands could be observed on any single day. On only 12 occasions was male sub-band composition observed to persist for more than 1 d (range: 2–10 d). Average group size of males observed to enter and/or leave a sleeping burrow was 4.75 ± 0.14 ($\bar{X} = 4$, $n = 443$, Fig. 6).

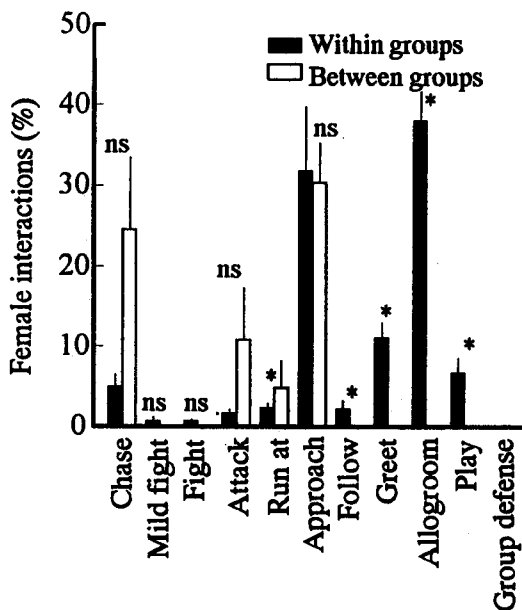


Fig. 4: Comparison of social interactions that adult female Cape ground squirrels had with members of their own social group (bars) and the interactions they had with members of different social groups (open bars). These interactions were divided into 10 categories for each female and then averaged for all females ($n = 17$). Asterisks indicate significant differences (Mann-Whitney U, $p < 0.05$) between the frequency of behaviours between the social interactions within social groups and between social groups

Formation of groups: Each year, 3–4 (21 % in 1990 and 16 % in 1991, $n = 19$ each year) of the members of the male band that appeared from outside the study area were young. One male disperser settled 5 km from his point of initial trapping, where he also had not been a natal resident. Fur condition indicated that most new males were young, although, in one case, a new male was definitely an older individual. Another 19 % ($n = 19$ in both 1990 and 1991) of the males in the band were from local natal groups. In six of the 12 burrow clusters that were censused, at least one natal male did not disperse from his natal social group. Instead, these males remained with their natal group long after reaching sexual maturity. The ages of these males were estimated by several means. Three were young non-scrotal males when the study started, and, assuming the age of becoming scrotal is 8 mo (WATERMAN 1996), these males were at least 3 yr old when the study ended. The ages of another two males were estimated by applying their weight at first capture to a regression equation of the weights of individuals of known ages (WATERMAN 1996). These males were at least 28 mo old at the end of the study. Finally, two adult males of known age (16 and 19 mo, respectively) were still living with their natal social groups when the study ended. No males older than 3 yr were observed living amicably with female social groups, suggesting that such males do eventually disperse. While resident in their natal groups, these

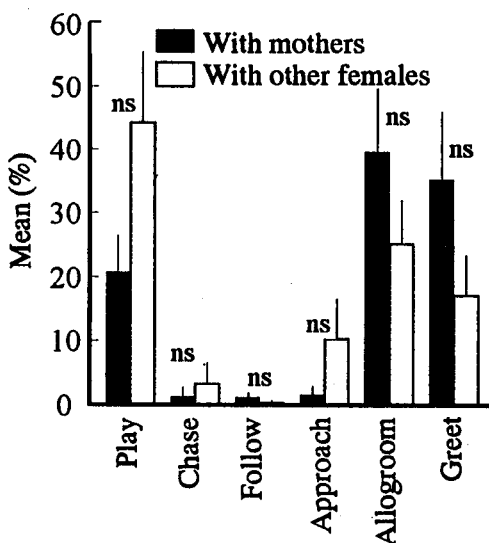


Fig. 5: Comparison of social interactions that juvenile Cape ground squirrels had with their mother (black bars) and other adult females in their social group (open bars). These interactions were divided into six categories for each juvenile and then averaged for all juveniles ($n = 10$). Juveniles were observed for an average of 236.6 ± 42 h. Asterisks indicate significant differences between the interactions of juveniles with their mothers and the interactions of juveniles with other females in their social group

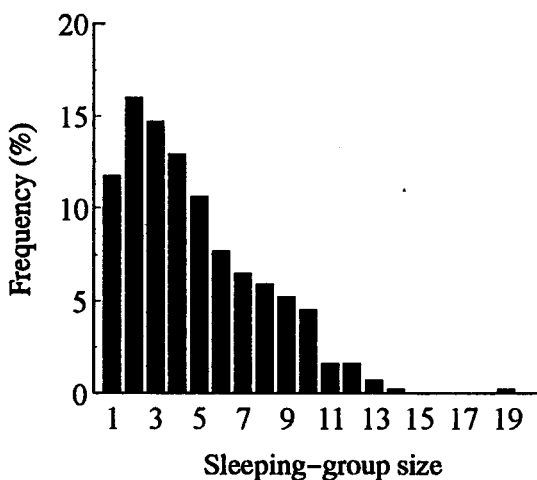


Fig. 6: Frequency distribution ($n = 443$) of male sleeping-group sizes for 1989-1991

young males would only join the male band during the oestrus of females, and spent the rest of their time with their natal social group.

Use of space: The entire male social group shared one home range, with no evidence of territoriality, as described by MURIE & HARRIS (1978; see below under Behaviour). Average range size of radio-collared individuals was 12.5 ± 2.5 ha ($n = 6$). The distance between male activity centres was 36.2 ± 3.3 m (distances between 10 males in 1990). Average shift in male activity centres between years was 39.8 ± 12.7 m ($n = 6$ for 1990–1991).

Behaviour: Although males spent most of their time feeding, they spent less time feeding and more time in sitting and locomotory behaviour than did females (Fig. 3). Males and females spent a similar amount of time in most social interactions (Mann-Whitney U, $p > 0.05$) except for approaches, allogrooming and greeting behaviour (males approached more than females, Mann-Whitney U = 26.5, $p < 0.0001$; females allogroomed and greeted more than males, Mann-Whitney U = 42, $p < 0.0001$ for the former and Mann-Whitney U = 87.5, $p < 0.002$ for the latter).

Males were within 10 m of another male in 78.1 % ($n = 14\ 057$) of observations. Of their time, 12 % was spent in social behaviour. Only a small percentage of the pairwise male interactions were agonistic (Table 3). No wounding between males was ever seen. The most common social behaviour (first-observed component of an interaction sequence) among males was the approach of one male to another (Table 3). Such an approach was defined as one individual walking directly up to another (within 10 cm). The response to such an approach (second-observed component of an interaction sequence) was usually that one of the individuals jumped back (Table 3).

Analysis of which individuals jumped back revealed consistent responses, indicative of a linear dominance hierarchy. Landau's index of linearity was greater than 0.9 in all 3 study years. This hierarchy did not appear to be strongly correlated with male weight or testis size (Spearman's rank correlation, $p > 0.05$ for all 3 yr). However, using fur condition and minimum known ages, comparison of rank between old and young males could be made for the second and third yr of the study. Older males were more dominant than younger males (median number of individuals dominated: 11.5 for older (2–18, $n = 24$), 6.0 for younger (0–10, $n = 12$), Mann-Whitney U, $U = 18.5$, $p < 0.0001$). Ranks changed from year to year, with individuals moving either up or down in the hierarchy (median change in the number dominated was 2 and 1.5 in 1989–1990 and 1990–1991, respectively). However, in 1989–1990, nine of 12 males moved down in the hierarchy with the arrival of two older males into the area because these new males moved into high positions in the hierarchy. In 1990–1991, 12 of 14 males moved up in the hierarchy after the disappearance of some of the higher-ranked males. Young males at the bottom of the hierarchy (who were usually either new recruits or non-dispersers) eventually did move up in the hierarchy.

Besides approaching, interactions between males are usually quite amicable (Table 3). Males spent about 4 % of their interactions allogrooming other males. Although, in years 2 and 3 the most dominant male allogroomed the most frequently, no relationship between rank and frequency of grooming or being

Table 3: Social interactions (mean %) between adult male Cape ground squirrels, averaged for 18 males, indicating the initial (first) behaviour in an interaction sequence and the response (second behaviour) in an interaction sequence

	Chase	Fight	Run at	Jump back	Approach	Greet	Allogroom	Play	No Reaction
Initial	1.5 ± 0.4	3.7 ± 0.8	3.7 ± 0.8	0.7 ± 0.3	80.3 ± 2.5	3.9 ± 1.5	6.8 ± 1.1	—	—
Response	0.4 ± 0.4	2.3 ± 0.7	—	68.8 ± 3.7	—	6.2 ± 0.8	0.8 ± 0.4	0.3 ± 0.2	18.0 ± 3.7

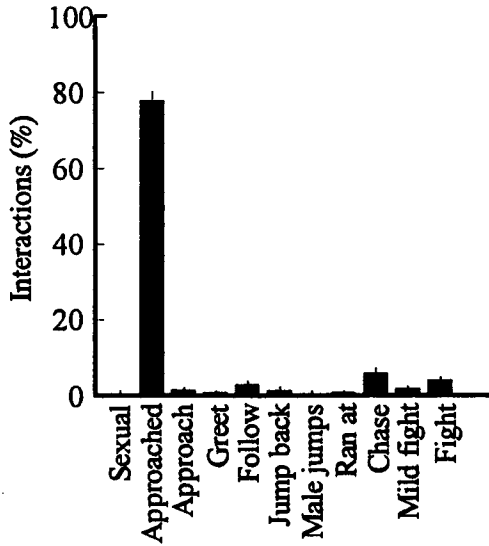


Fig. 7: Social interactions between female and male Cape ground squirrels (from the female perspective), excluding days of oestrus, averaged for 17 females

groomed existed (Spearman's rank correlation, $r_s = -0.2017$, $p > 0.05$, $n = 33$). Similarly allogrooming was not more frequent among adjacent-ranked males (Spearman's rank correlation, $r_s = -0.0753$, $p > 0.10$).

Male-female Interactions

Ranges: Males had much larger feeding ranges than females (ANOVA, $F = 54.4$, $df = 64$, $p < 0.0001$), resulting in male ranges overlapping with a number of female social groups (Fig. 2). Within this area, males travelled from one female social group to another. During the oestrus of a female, males sometimes slept in the females' burrow cluster, but they immersed into a different burrow system than the female social group.

Interactions: Most interactions between individuals of the opposite sex consisted of males approaching females (Fig. 7). Females usually responded to such approaches by jumping away ($64 \pm 5.1\%$, $n = 16$ females), running ($7.0 \pm 1.5\%$), fighting ($8.9 \pm 2.2\%$) or just ignoring the male ($9.6 \pm 1.9\%$).

Discussion

Many aspects of the social organization of the Cape ground squirrel are similar to North American species. Female Cape ground squirrels live in cohesive groups with little or no evidence of dominance hierarchies. Females within these social groups interact frequently and amicably, share sleeping burrows, and have

unrestricted use of space and burrows (with the exception of the natal burrow). Litter distinctions are not maintained following juvenile emergence from the natal burrow, and adults do not discriminate significantly between young from different litters. Sons disperse whereas daughters are recruited into the group, resulting in a matrilineal social structure. The aggregation of burrow clusters or female social groups in an area, separated from other aggregations of burrow clusters by a considerable distance, could be considered a dispersed colony. Certainly, the female social structure of the Cape ground squirrel is very similar to that of the black-tailed prairie dog and partially fits the description of the highest grade of sociality described by MICHENER (1983).

It is the social organization of males in the Cape ground squirrel that distinguish this species from other ground squirrels. In the black-tailed prairie dog, usually only a single male is associated with a female group (HOOGLAND 1981; HOOGLAND & FOLTZ 1982). This male is not dominant to the females and interacts amicably with the social group (MICHENER 1983), although he will act aggressively to unrelated males that come into his territory (HOOGLAND 1986). In Cape ground squirrels, however, males live independently of female social groups in highly structured all-male social bands. Male groups are maintained by the recruitment of young dispersed males. Within a band, males have a strictly linear dominance hierarchy, in which older males are more dominant over younger males. Although males maintain a common range throughout the year, all the males in the band do not group together all the time. Instead, males form temporary sub-bands, the size and composition of which changes daily. Within the band or between any of these sub-bands, there is no evidence of cooperative defence or territoriality, and new males are accepted into the band. Most interactions between males are amicable, including allogrooming, greeting, and sleeping together in the same burrow. Male bands have a home range that encompasses a number of female social groups, yet males do not live with these females.

Several authors have attempted to classify the social systems of the ground-dwelling squirrels into grades of sociality, from the asocial to the highly social. MICHENER (1983) classified sociality based on 'male territoriality extending beyond the breeding season, with territories encompassing the areas used by several females'. She described five grades of sociality: asocial, single-family female kin clusters, female kin clusters with male territoriality, polygynous harems with male dominance, and egalitarian polygynous harems. Cape ground squirrels cannot be described by any of these grades, because males are not territorial and male Cape ground squirrels do not live in the same burrow clusters as a female group, and breeding is not seasonal.

The definitions of sociality in ground squirrels have been based on the degree of association between adult males and females (MICHENER 1983; TRAVIS & SLOBODCHIKOFF 1993). ARMITAGE (1981) defined sociality as 'the state of group formation when members of differing sex and age structure share the same space'. Such sharing of space included overlapping home ranges, communication and cohesive social interactions (ARMITAGE 1981, 1987). Although Cape-ground-squirrel males and females do share the same space, such sharing is not continuous.

Based on the interactions of males and females, Cape ground squirrels would not be considered highly social. According to ARMITAGE's (1981) definition, Cape-ground-squirrel females would be highly social. If this definition was extended to the social groups that males form independently of females, they too would be considered highly social.

MICHENER's (1983) index of sociality makes the assumption that only a single male is associated with a group of females. Similarly, TRAVIS and SLOBODCHIKOFF's (1993) discussion on the influence of resources on sociality also defines the development of sociality as the association of a single male with two or more females. Yet, multi-male associations are not unknown in the North American ground-dwelling squirrels. Although a single male usually associates with a female coterie in the black-tailed prairie dog, some years up to 33 % of coterie may contain more than one male (HOOGLAND 1986). These males are usually related (HOOGLAND 1981, 1986; HOOGLAND & FOLTZ 1982). Black-tailed prairie-dog male relatives (father, son, brothers) sometimes disperse together into the same area (HOOGLAND 1986). While male relatives interact amicably outside of breeding in black-tailed prairie dogs, non-kin are not as amicable (HOOGLAND 1986).

The bands of male Cape ground squirrels are quite different from male groups in North American ground squirrels, because they are composed of unrelated individuals. Low litter sizes (average litter sizes range from 1.6 to 1.9; HERZIG-STRASCHIL 1978; WATERMAN 1996), and juvenile mortality make it unlikely that two male littermates will reach dispersal age. In addition, breeding occurs throughout the year, so females in the same social group are not likely to give birth synchronously. Thus, two subadults of dispersal age will rarely live in a social group simultaneously. The bands of males probably do not, therefore, contain close relatives, as new males usually arrive alone. However, regardless of being unrelated, interactions between male Cape ground squirrels are highly amicable.

A major hypothesis for the evolution of sociality in ground squirrels suggests a relationship between sociality and delayed dispersal (BARASH 1974; ARMITAGE 1981). Dispersal is assumed to be very costly. Animals living in severe environments require more time to gain body weight in order to successfully disperse and reproduce (BARASH 1974). ARMITAGE (1981) suggested that delayed dispersal is a form of direct parental investment, which has in turn led to the evolution of sociality and cohesive behaviour. Thus, in larger species of ground-dwelling squirrels, sociality will evolve if dispersal and reproductive maturity are delayed for 2 or more yr and if their active season is no longer than 6 mo (ARMITAGE 1981).

According to these predictions, the Cape ground squirrel should be asocial. Cape ground squirrels reach adult weight, reproductive maturity, and dispersal age at less than 1 yr, and are active throughout the entire year (WATERMAN 1996; this paper). However, despite these traits, this ground squirrel should be considered to be highly social. Sociality in this species may be a form of direct parental investment, as ARMITAGE (1988) suggests. However, the characteristics of the Cape ground squirrel are not consistent with the hypothesis that delayed

dispersal and delayed maturity lead to sociality. Most males reach maturity and disperse prior to 1 yr of age. Evidence supporting the assumption that dispersal is costly is scarce. Firstly, dispersing Columbian ground squirrels (*Spermophilus columbianus*) did not incur higher mortality than non-dispersers because of dispersal itself, but because they often settled in suboptimal habitat (HACKETT 1987). In non-territorial species, such as the Cape ground squirrel, males would not be excluded from the best habitats and therefore would not incur such costs. Secondly, the adult sex ratios of most ground squirrel species are biased toward females, which has been suggested as reflecting the cost of dispersal (SCHMUTZ et al. 1979; BOAG & MURIE 1981). Adult sex ratios in the Cape ground squirrel are not biased, suggesting that dispersal is not costly.

Many authors often discuss the social system of a species in terms of the mating system of the species (MICHENER 1983; TRAVIS & SLOBODCHIKOFF 1993). However, social systems are not necessarily equivalent to mating systems (ROWELL 1988). The breeding season in North American ground squirrels only lasts 1–3 wk (DOBSON 1984), after which males in many species often do not interact with females (MICHENER 1983). Classifying the entire social system of a species according to interactions that take place in such a short time period can be misleading. In the Cape ground squirrel, male groups are as social as female groups, and male and female groups live to a large extent independently. Thus, using only their mating system to describe their sociality would be both incomplete and inaccurate. Sociality in the Cape ground squirrel may be summarized as highly social female kin clusters and associated social non-kin bands of males.

In conclusion, the Cape ground squirrel has a highly unique social organization unlike that described for other species of ground squirrel. Females live in highly cohesive, matrilineal groups. Daughters are recruited into these groups whereas sons disperse. Males also live in amicable cohesive groups, independently of female social groups. Previous definitions and descriptions of sociality of North American ground squirrels are inadequate for describing the social system of the Cape ground squirrel as they are limited to single males and based on the interactions between males and females. The absence of extreme seasonality, which allows year-round activity and breeding in this species, has probably led to their unique social structure.

Acknowledgements

I would like to thank J. O. MURIE and J. D. ROTH for their advice and comments on earlier versions of this manuscript. E. C. BIRNEY, F. B. MARTIN, D. F. MCKINNEY, A. E. PUSEY, J. R. TESTER and two anonymous reviewers provided helpful suggestions for improving the manuscript. Mr and Mrs BARTSCH kindly allowed me access to their farm. I would especially like to thank J. D. ROTH for his friendship, support, and computer expertise. M. GRIFFIN of the Namibian Department of Conservation and Tourism provided much-appreciated logistic support. This research was supported by grants from the Dayton and Wilkie Funds of the Bell Museum of Natural History, Sigerfoos fellowships from the Zoology Program of the University of Minnesota, Sigma Xi, and the Graduate School of the University of Minnesota.

Literature Cited

ALTMANN, J. 1974: Observational study of behaviour: sampling methods. *Behaviour* 49, 227–267.

- ARMITAGE, K. B. 1981: Sociality as a life-history tactic of ground squirrels. *Oecologia* 48, 36—49.
- — 1987: Social dynamics of mammals: reproductive success, kinship and individual fitness. *Trends Ecol. Evol.* 2, 279—284.
- — 1988: Resources and social organization of ground-dwelling squirrels. In: *The Ecology of Social Behavior* (SLOBODCHIKOFF, C. N., ed.). Acad. Press., San Diego. pp. 131—155.
- BARASH, D. P. 1974: The evolution of marmot societies: a general theory. *Science* 185, 415—420.
- BOAG, D. A. & MURIE, J. O. 1981: Population ecology of Columbian ground squirrels in southwestern Alberta, Canada. *Can. J. Zool.* 59, 2230—2240.
- CONOVER, W. J. 1980: *Practical Nonparametric Statistics*. Wiley & Sons Inc., New York.
- DOBSON, F. S. 1984: Environmental influences on sciurid mating systems. In: *The Biology of Ground-dwelling Squirrels* (MURIE, J. O. & MICHENER, G. R., eds). Univ. Nebraska Press, Lincoln. pp. 229—249.
- EMLEN, S. T. & ORING, L. W. 1977: Ecology, sexual selection and the evolution of mating systems. *Science* 197, 215—223.
- EWER, R. F. 1966: Juvenile behavior in the African ground squirrel, *Xerus erythropus* (E. Geoff.). *Z. Tierpsychol.* 23, 190—216.
- HACKETT, D. F. 1987: Dispersal of yearling Columbian ground squirrels. PhD diss., Univ. Alberta, Edmonton.
- HERZIG-STRASCHIL, B. 1978: On the biology of *Xerus inauris* (Zimmerman, 1780) (Rodentia, Sciuridae). *Z. Säugetierkde.* 43, 262—278.
- — 1979: *Xerus inauris* (Rodentia, Sciuridae) — an inhabitant of the arid regions of southern Africa. *Folia zool.* 28, 119—124.
- HOOGLAND, J. L. 1981: Nepotism and cooperative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). In: *Natural Selection and Social Behavior* (ALEXANDER, R. D. & TINKLE, D. W., eds). Chiron Press, New York. pp. 283—310.
- — 1986: Nepotism in prairie dogs (*Cynomys ludovicianus*) varies with competition but not with kinship. *Anim. Behav.* 34, 263—270.
- — & FOLTZ, D. W. 1982: Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). *Behav. Ecol. Sociobiol.* 11, 155—226.
- KENWARD, K. E. 1990: RANGES IV: Software for Analyzing Animal Location Data. Inst. of Terrestrial Ecol., Wareham.
- LEHNER, P. N. 1979: *Handbook of Ethological Methods*. Garland Press, New York.
- MICHENER, G. R. 1983: Kin identification, matriarchies and the evolution of sociality in ground-dwelling sciurids. In: *Recent Advances in the Study of Mammalian Behavior* (EISENBERG, J. F. & KLEIMAN D. G., eds). Spec. Publ., Am. Soc. Mammal. 7, pp. 528—572.
- MOHR, C. O. 1947: Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* 37, 223—249.
- MULLER, M. A. N. 1984: Grasses of Southwest Africa/Namibia. Directorate of Agriculture & Forestry, Windhoek.
- MURIE, J. O. & HARRIS, M. A. 1978: Territoriality and dominance in male Columbian ground squirrels (*Spermophilus columbianus*). *Can. J. Zool.* 56, 2402—2412.
- ROOD, J. P. & NELLIS, D. 1980: Freeze-marking mongooses. *J. Wildl. Manage.* 44, 500—502.
- ROWELL, T. E. 1988: Beyond the one-male group. *Behaviour* 104, 189—201.
- SCHMUTZ, S. M., BOAG, D. A. & SCHMUTZ, J. K. 1979: Causes of the unequal sex ratio in populations of Richardson's ground squirrels. *Can. J. Zool.* 57, 1849—1855.
- SNEDECOR, G. W. & COCHRAN, W. G. 1989: *Statistical Methods*, 8th Ed. Iowa State Univ. Press, Ames.
- SOKAL, R. R. & ROHLF, F. J. 1981: *Biometry*, 2nd. Ed. Freeman & Co., New York.
- STEINER, A. L. 1970a: Etude descriptive de quelques activités et comportements de base de *Spermophilus columbianus* (Ord.). Part I. *Rev. Comp. Anim.* 4, 3—21.
- — 1970b: Etude descriptive de quelques activités et comportements de base de *Spermophilus columbianus* (Ord.). Part II. *Rev. Comp. Anim.* 4, 23—42.
- TRAVIS, S. E. & SLOBODCHIKOFF, C. N. 1993: Effects of food resource distribution on the social system of Gunnison's prairie dog (*Cynomys gunnisoni*). *Can. J. Zool.* 71, 1186—1192.
- WATERMAN, J. M. 1994: The social organization of the Cape ground squirrel *Xerus inauris*. PhD diss., Univ. Minnesota, St. Paul.

- — 1996: Reproductive biology of a tropical, non-hibernating ground squirrel. *J. Mammal.*, in press.
- WRANGHAM, R. W. 1980: An ecological model of female-bonded primate groups. *Behaviour* 75, 262—300.

Received: July 18, 1994

Accepted: March 8, 1995 (J. Brockmann)