

# Delayed maturity, group fission and the limits of group size in female Cape ground squirrels (Sciuridae: *Xerus inauris*)

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## Abstract

Female Cape ground squirrels *Xerus inauris* live in matrilineal kin groups in which the number of reproductive positions is limited to three females. Field observations on a population in Namibia revealed that the mechanisms by which group size was limited were reproductive suppression and group fission. Sub-adult females attained sexual maturity at 8 months of age when only a single adult female was present in their social group, whereas sub-adult females in groups with more than one adult female matured at 12 months of age. Social groups with more than three breeding females subsequently split into smaller groups. Several hypotheses for limiting group size were considered. There was no evidence of higher ectoparasite loads on females in larger groups, nor was survival of adult females affected by group size. Although adult females have lower body masses and higher mortality during the winter when food is more scarce, feeding competition alone does not seem to limit group size. Groups that split continued to overlap in their feeding ranges and there was no seasonal difference in juvenile survival. However, juvenile survival was affected by group size. The greatest cost of being in a larger group was lower juvenile survival. Larger groups use larger feeding ranges, and because squirrels return to their sleeping burrow when threatened, not just to the nearest refuge, slower juveniles have greater exposure to predators. Thus, although competition for food resources may be important, predation seems to be a major constraint on female group size as well as the primary selective force leading to female group formation.

**Key words:** reproductive suppression, ground squirrels, group size, *Xerus inauris*

## INTRODUCTION

In many animals, group size is the result of a compromise between the benefits of co-operation and the costs of competition (Alexander, 1974; Hoogland, 1979; Armitage, 1986; Wrangham, Gittleman & Chapman, 1993; Rannala & Brown, 1994). In the social species of ground-dwelling sciurids, females live in cohesive, matrilineal social groups (Michener, 1983). The suggested benefits of such cohesive groups include enhanced thermoregulation, co-operative defence of resources, and predator avoidance (Hoogland, 1979, 1981a; Sherman, 1980; Armitage, 1988; Arnold, 1990a). In some species, however, reproductive success declines with increased group size (Hoogland, 1981b; Armitage, 1986), although the specific factors limiting reproductive success are unclear (Armitage, 1986). Armitage (1986) suggested that although resources are the ultimate constraint on group size, other more proximate factors determine reproductive strategies; such factors may include increased competition for resources, aggression,

and parasitism (Alexander, 1974). In addition, Armitage (1986, 1996) suggested that reproductive suppression could be a cost of grouping to some individuals. Such suppression, however, may be difficult to detect in hibernating species of ground squirrels that breed only once a year. The influence of older females on the age of maturity of younger females may be confounded by the effects of overwintering.

The Cape ground squirrel *Xerus inauris*, which lives in the arid regions of southern Africa, is active throughout the year (Herzig-Straschil, 1978; Waterman, 1996). Sociality in the Cape ground squirrel is characterized by female clusters of kin and associated non-kin bands of males. Male bands live independently of female groups, and males only interact with females during mating (Waterman, 1995). The major benefit of grouping for males is enhanced predator detection and deterrence through enhanced vigilance and mobbing (Waterman, 1997), and this is probably also a benefit for female groups. However, during an ongoing study of the social organization of this species, the number of reproductive positions within a female social group was rarely

observed to exceed three (Waterman, 1995), and social groups of greater than three breeding females did not persist, but broke up into two smaller groups that rarely interacted subsequently. It seemed apparent that even within these non-aggressive female groups there were costs to grouping and the potential for younger females to be prevented from breeding. As the Cape ground squirrel does not hibernate, it is a good species in which to address questions about delayed reproduction and the ecological constraints that may induce such suppression.

The objectives of the study were to: (1) identify the means by which female group size is limited; (2) investigate some potential costs of increased group size, such as increased parasite load, food competition, nest competition, and susceptibility to predation.

### BIOLOGY OF THE STUDY ANIMAL

Female Cape ground squirrels live in social groups of one to three adult females and usually two to three (but up to nine) sub-adults of either sex (Waterman, 1995). A social group was defined as a group of adult females and their sub-adult young living together in the same burrow system (after Herzig-Straschil, 1978). Social groups live in burrow clusters or aggregations of burrow openings clearly separated from adjacent clusters by areas without burrows that are larger than the cluster area (after Herzig-Straschil, 1978), usually a few hundred metres (Waterman, 1995). Each burrow cluster is inhabited by only a single female kin group (social group), and during any year, one to three burrow clusters were vacant (not occupied continuously by squirrels). Social groups are characterized by female philopatry and male-biased dispersal. Social group members share sleeping burrows and feeding ranges, and interactions within social groups are highly amicable. Before parturition, females isolate themselves from the social group by digging a nest burrow outside of the burrow cluster, and only return with their offspring after the emergence of the young. Once the weaned litters have joined the social group, interactions of mothers with their young are indistinguishable from the interactions of other members of the social group with the litter (Waterman, 1995). It was rare for more than one litter to be weaned at the same time due to the usual asynchrony of breeding within a group and high litter loss (Waterman, 1996).

Squirrels move over relatively large home ranges, and during their daily feeding they often move quite far from their burrow cluster (Waterman, 1995). The feeding ranges of adjacent social groups overlap by an average of 26% (Waterman, 1995). Females from adjacent social groups sometimes fed together in the periphery of their feeding ranges, but interactions between neighbouring social groups were rare and females ignored each other 90% of the time when they were in close proximity (Waterman, 1995). Any interactions between females of adjacent social groups were

more likely to be aggressive than interactions within a group, but individuals did not co-operate in such aggression (Waterman, 1995).

### METHODS

The study was conducted on a 3500-ha farm, 185 km south-east of Windhoek, Namibia (23°25'S, 18°00'E). Temperatures in the area range from -5 to 42°C but are lowest during winter (June through August). This area has distinctly seasonal growing periods, with most of the annual rainfall occurring between November and April (Skarpe & Bergstrom, 1986; Thomas & Shaw, 1991). Rainfall that occurs outside of this time has little effect on the growth of annual grasses (Skarpe & Bergstrom, 1986) because colder temperatures and rainfall of < 10 mm do not stimulate plant growth (Leistner, 1967). For this study, the wet season was thus considered to include the 6-month period November to April and the dry season included the 6-month period May to October.

During the study, 123 adult females and sub-adults of either sex in 12 burrow clusters were trapped. 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 initially marked for identification using numbered metal tags in the ears (National Band & Tag Co., Monel No. 1). However, because the squirrels removed tags during allogrooming, small freeze-brands were used and found to be an effective permanent, well-visible means of identification (Rood & Nellis, 1980). Freeze-branding is regarded as painless as the tissue is numbed and nerves are believed to be inactivated for several weeks after freezing. Dye marks on the body (Lady Clairol Nice *n'*Easy and Nyanzol hair dye) were also used to aid identification at a distance. Individuals were weighed and examined for external parasites. Ectoparasites were counted on the dorsal region of the back and shoulders of individuals. Cape ground squirrels have short bristly thick hairs with no underfur (Skinner & Smithers, 1990), which allowed almost unobstructed vision of the dorsal region for ectoparasite counting. The sex, age, and reproductive condition of individuals were also recorded. After their initial capture, squirrels were captured periodically to renew dye marks when necessary, measure body masses and assess reproductive condition.

Adult females (reproductively mature individuals which had experienced at least 1 oestrus) could be distinguished from females that had not bred by examining the nipples, which swell during first gestation and remain permanently swollen (Waterman, 1995). The approximate ages of females were thus able to be determined on first arrival at the study site, even though precise ages for these females could not be determined. Females aged in this manner were not included in the analysis of age of maturity but were included in assessing the fission of social groups. To determine the

age at first maturity, only females of known age were analysed. These individuals were either trapped at first emergence at the natal burrow or the date of oestrus of their mother was known and thus date of emergence could be estimated. Their age of maturity was determined by observation of their first oestrus. Oestrus lasts about 3 h in this species (for details see Waterman, 1998), and the onset of the oestrus of a female Cape ground squirrel could be determined a few days before her actual oestrus by 2 criteria: (1) male behaviour towards females changed 3–4 days before oestrus (Waterman, 1997); (2) the female vulva swelled just before oestrus (indicative of the onset of oestrus), and this swelling was not only evident during trapping, but also, because of the short, sparse fur of this species, during observations. In addition, all the females included in this analysis did not have swollen nipples before the observed oestrus. Thus, it is unlikely that the first oestrus of any of these females was missed.

Detailed observations were made of squirrels at 8 burrow clusters from June 1989 to April 1990, June 1990 to February 1991, and July to December 1991, for a total of 2000 h. Each observation period is referred to by the year in which the observation began (e.g. the 1989 observation period includes June 1989 to April 1990). Observations focused on the times these squirrels interacted most, 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. All-occurrences sampling was used to record social interactions, and focal animal sampling to observe females during oestrus (Altmann, 1974). The agonistic behaviours used in the interaction analyses between female–female pairs (dyads) were chases, fights, running at another squirrel, and jumping back from another. These and other behavioural categories are described in detail elsewhere (Waterman, 1995). Interactions were calculated as the number of agonistic interactions per dyad per h.

Locations of squirrels during observation and trapping 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. The sizes of feeding ranges for each study period were calculated from scan data by the minimum polygon method (Mohr, 1947) using RANGES IV (Kenward, 1990). Feeding ranges were estimated using all observation points as squirrels often fed in the peripheral areas of their ranges (Waterman, 1995). Adult females share a common group range and the movements of individuals within this common range overlap by almost 90% (Waterman, 1995). Thus social group range size was calculated as the median of the feeding range sizes of individual adult females in the social group. The range sizes of sub-adults were not included in this calculation, as range size changes during development (J. M. Waterman, pers. obs.). As the third year of the study concentrated only on morning and evening observa-

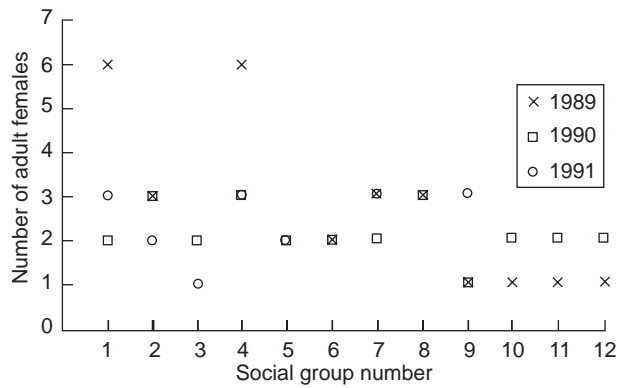
tions, with few all-day sessions, data for only the first 2 years of the study were used to calculate range sizes in 7 social groups. The eighth group was not included in the range analysis as it consisted of 2 immature females, who had split from their original social group in the second year. Overlap of the feeding range of an individual was calculated as the percentage of its feeding range that was shared with the feeding range of another individual within that group.

Maximum and minimum social group sizes were determined by the maximum or minimum number of adults and sub-adults (not juveniles) in a social group during the study period. As no difference was found in the results using either measure (there was little change in group size over a study period), the maximum number of individuals in a group was used to determine group size. Adult persistence on the study area was determined by calculating the fraction of adults in the area in 1 year that were still in the area in the next year. Juvenile persistence was determined by calculating the proportion of emerged juveniles that survived to 6 months. There are no sex differences in juvenile disappearance (Waterman, 1995). There was no evidence of female dispersal or recruitment (no female immigrant was ever observed), and females that disappeared were never observed again in the area, so they had probably died (Waterman, 1995). Likewise, sub-adult males do not disperse until 8 months of age, so the disappearance of a male <6 months of age most probably indicates death (Waterman, 1995). Squirrels >6 months of age that were not yet reproductive were considered sub-adults. Per capita reproductive success in groups was determined by dividing the number of juveniles that survived to 6 months of age by the number of breeding females in the group at first emergence of the juveniles from the natal burrow. Unless otherwise indicated, results are stated as mean  $\pm$  1 SE. Correlations determined by Spearman's rank correlation test are indicated by  $r_s$ .

## RESULTS

### How are groups limited in size?

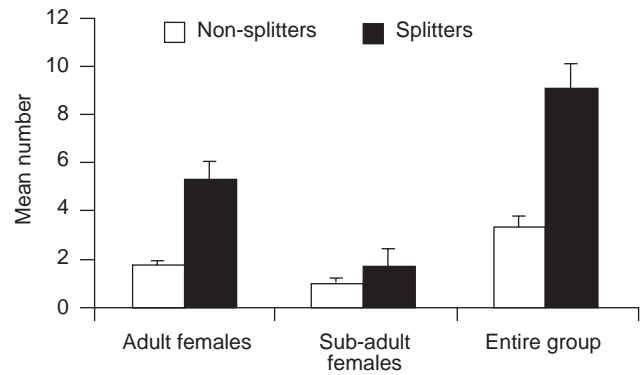
The number of adult females in a social group was usually three or less (1989:  $2.7 \pm 0.61$  females; 1990:  $2.2 \pm 0.16$ ; 1991:  $2.37 \pm 0.26$ ), however there were two occasions when the number of adult females in a social group was greater than three (Fig. 1). In both instances six females mated in a group, but fewer than three of the 12 females successfully gestated. Both groups subsequently divided into two distinct and independent groups, one in the first year of the study and the other in the second year. No data are available on how long these groups persisted before the split, but all groups persisted for the rest of the study. In one of these groups, three females left their social group, while in the second group two females left. Dates of maturity could be estimated in only the second of these groups, and of



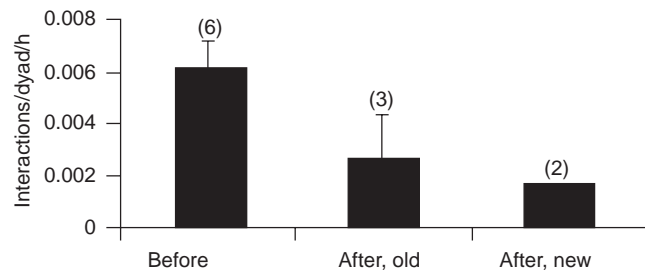
**Fig. 1.** The maximum number of adult female Cape ground squirrels *Xerus inauris* in 12 different social groups for the three study periods.

the three females that had a first oestrus (based on nipple swelling) 9 months before the split, the two that left were the youngest. Neither female successfully gestated while in their original social group but did so in the new group. A third young female remained in her natal group and bred when one of the three adult females disappeared at the time of the split. A third fission was also observed. The group of three females that split off in the first year of the study, subsequently split again in the second year. This group, with three adult females and four sub-adult females, divided with two immature females leaving. For all three fissions, the females that left moved into an adjacent empty burrow cluster and never returned to sleep with their old social group. However,  $63.5 \pm 9.3\%$  ( $n = 3$  separated groups) of their feeding range continued to overlap with their old social group. Where social groups split, two or three females formed the new social group. Groups that split had more adult and sub-adult females before separation and were larger overall (including adult females and sub-adults of both sexes) than groups that never split during the study (Fig. 2). In one group for which behavioural data were available both before and after the split (544.5 h of observation in 1989 before the split and 655.5 h in 1990 after the split), agonistic interactions within both the old group and the newly formed group were less frequent after the split than in the combined group before the split (Mann–Whitney  $U$ -test, one-tailed,  $U = 11.5$ ,  $P = 0.03$ ,  $n = 19$  dyads; Fig. 3).

The number of breeding females in a group influenced the age of maturity of young females. Six-month old females whose social groups contained two to three breeding females became reproductively mature (had their first oestrus) significantly later ( $12.0 \pm 0.32$  months,  $n = 5$ , range 11–13 months) than females of that age living in groups with only one breeding female ( $7.9 \pm 0.33$  months,  $n = 5$ , range 7–9 months; Mann–Whitney  $U$ -test,  $U = 0.00$ ,  $P = 0.008$ ). Between 6 months of age (1 month before the earliest observed oestrus) and the age of maturity, the number of adult females in the group often changed. By the time of first oestrus, all of these females resided in social groups containing



**Fig. 2.** Mean ( $\pm$  SE) number (adult females, sub-adult females and all individuals) in the social groups of Cape ground squirrels *Xerus inauris* for three groups that eventually underwent fission and seven groups that did not split.

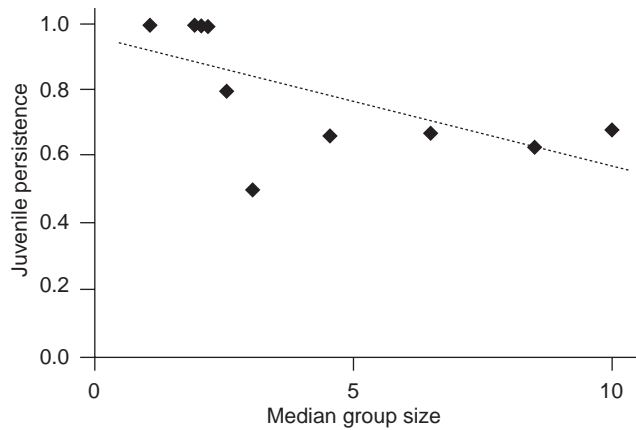


**Fig. 3.** Mean ( $\pm$  SE) rate of agonistic interactions/dyad per h within a group of six adult female Cape ground squirrels *Xerus inauris* (15 dyads) before the split and within the new (three dyads) and old groups (one dyad) after they split. Numbers in parentheses, number of females in the group (note: one adult female disappeared just before the split).

fewer than three adults. Thus, on the day of maturation, the age of females was unrelated to the number of adults in the group, as the age of first oestrus did not differ between females in groups with two breeding females and those with fewer than two ( $U = 7.0$ ,  $P = 0.35$ ,  $n = 10$  sub-adult females). Once females became reproductively mature they were no longer inhibited from future oestrus.

The permanent disappearance of adult females may influence the time of reproductive maturation of young females by opening up a reproductive position. Five of the 10 young females had lost an adult female from their social group in the previous 1.5–4 months ( $80.4 \pm 14.9$  days) before maturity (four of which then matured into groups of only two adult females). Of the other five young females, two were the pair that lived in a group of three adult females and subsequently split from their original group. There was no adult female disappearance before their split and thus no potential reproductive position. The last three young females were born into groups with a single adult female, had no adult female disappearances before maturity, and reached reproductive maturity before 9 months of age.

The temporary absence of adult females, which separate from their social group during parturition and



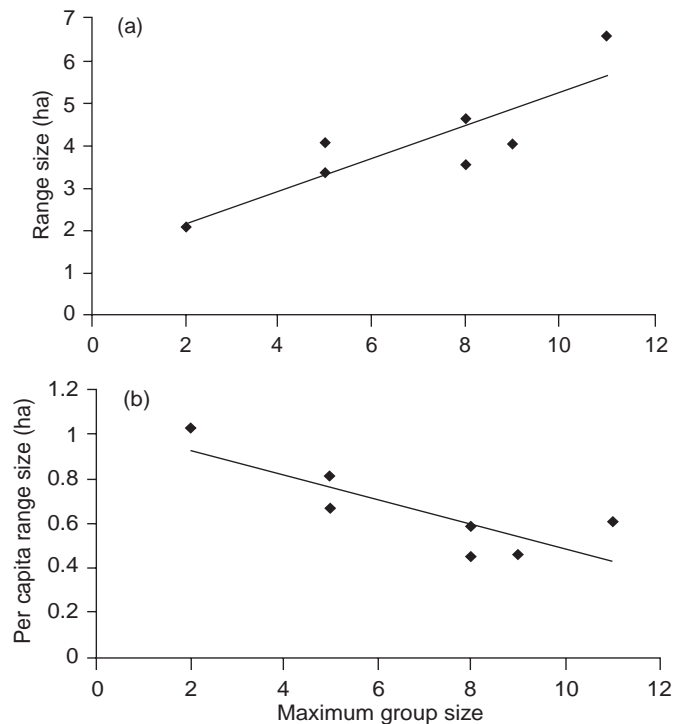
**Fig. 4.** Median juvenile persistence (survival) to 6 months of age of Cape ground squirrels *Xerus inauris* in 10 different social groups.

lactation, may also affect the age of maturity of young females. Eight of 10 females in whom the first oestrus was documented became reproductively mature within 1 month of a temporary absence of all adult females in their social group.

#### Why limit group size?

The only ectoparasites found on squirrels were ixodid ticks *Rhipicephalus theileri* (Walker, 1991). The incidence of these ticks was low (averaging  $0.21 \pm 0.04$  ticks per examination), and no ectoparasites were seen on females in 1991. The incidence of ectoparasites did not increase with maximum group size in either 1989 or 1990 (1989  $r_s = 0.35$ ,  $P = 0.26$ ,  $n = 12$  social groups; 1990  $r_s = 0.05$ ,  $P = 0.88$ ,  $n = 11$ ; social group size ranged from two to 11 individuals in both years). Annual persistence of adult females also was unrelated to group size (median group size *vs* median persistence,  $r_s = -0.36$ ,  $P = 0.15$ ,  $n = 10$  social groups that persisted at least two study periods), but there was a trend for lower per capita reproductive success in larger groups (median group size *vs* median per capita reproductive success,  $r_s = -0.53$ ,  $P = 0.06$ ,  $n = 10$ ). Juvenile persistence to 6 months of age decreased significantly with increasing group size (median group size *vs* median juvenile persistence,  $r_s = -0.77$ ,  $P = 0.004$ ,  $n = 10$ ; Fig. 4).

Female group size may be constrained by food resources. Overall, larger groups had larger feeding ranges than smaller groups, suggesting that they had to travel farther to feed (group size *vs* range size:  $y = 0.38x + 1.37$ ,  $r^2 = 0.72$ ,  $F_{(1,5)} = 12.98$ ,  $P = 0.01$ ; Fig. 5a). However, range sizes were not larger on a per capita basis, as larger groups had smaller per capita range sizes (Fig. 5b). Resources also varied throughout the year because of rainfall patterns. During the dry season when there was little standing grass, squirrels searched for seeds in the sand. Adult females weighed less during these dry months ( $540.5 \pm 22.0$  g in August) than during the summer months of rainfall ( $582.3 \pm$



**Fig. 5.** (a) Median feeding range of seven social groups of female Cape ground squirrels relative to maximum group size; (b) per capita feeding ranges of seven social groups relative to maximum group size.

16.0 g in January; paired *t*-test on 10 non-pregnant adult females,  $t = -2.77$ , d.f. = 9,  $P = 0.02$ ). Mortality of adult females may also be higher in the winter. Over the period of the study, 14 reproductively mature females disappeared, only two during the rainy season. However, juvenile disappearance did not differ between dry and wet months (24% ( $n = 29$ ) during the dry months July–September and 24% in the wet months December–February ( $n = 21$ )). Social group size also did not vary seasonally (two-way ANOVA, social group and month *vs* group size: June–December 1989,  $F_{(6,33)} = 1.64$ ,  $P = 0.18$ ; January–April and June–December 1990,  $F_{(10,54)} = 1.22$ ,  $P = 0.31$ ; January–February and July–December 1991,  $F_{(7,47)} = 0.84$ ,  $P = 0.56$ ).

#### DISCUSSION

The number of reproductive positions in social groups of Cape ground squirrels in my study area seems to be constrained to three females via two mechanisms. First, immature females may be reproductively suppressed through delayed maturity and this effect occurs when there is more than one adult female in a group. Reproductive suppression of sub-adults seems to be widespread in highly social ground-dwelling squirrels (Armitage, 1986, 1996; Barash, 1989) including alpine marmots (Arnold, 1990b), hoary marmots (Barash, 1989), yellow-bellied marmots (Armitage 1986; see

Armitage, 1996 for a discussion of suppression in other species of marmots) and black-tailed prairie dogs (Hoogland, 1995). Young females may be less likely to breed in the presence of their father, as in black-tailed prairie dogs (Hoogland, 1995) or social suppression by related adult females may occur, as in yellow-bellied marmots (Armitage, 1986, 1998). In Cape ground squirrels, adult males do not reside permanently with females, so presumably the timing of maturation in young females is influenced by the presence of adult females rather than males. Sub-adult females in a group with a single adult female could have more opportunity to sleep apart from the adult female than sub-adults in larger groups because adult females isolate themselves from their social group during parturition and lactation. For females in larger groups, the asynchrony of breeding and frequent failure in the reproduction of adult females (Waterman, 1996) could make it difficult for sub-adults to be separated from adults for any period of time.

One major cost to sub-adults that delay maturity is lost reproductive time. These sub-adults breed nearly one complete oestrous cycle later than females in groups with only a single adult female. The average inter-oestrous interval is 146 days for females that are successful in raising young (Waterman, 1996) whereas maturity for sub-adults in larger groups is delayed by 120 days.

Reproductive suppression is not only a mechanism for limiting breeding positions, but also a selective pressure that leads to fissioning. The fission of larger groups is a second mechanism by which the number of reproductive positions was maintained at a maximum of three and a means by which suppressed females can achieve reproductive status. In some other social mammals, when large social groups divide it is the least dominant animals that form new groups, such as in spotted hyenas (Holekamp *et al.*, 1993) and mountain baboons (Henzi, Lycett & Piper, 1997). However, there is no obvious dominance hierarchy in female social groups (Waterman, 1995). In other social mammals, such as yellow-bellied marmots (Armitage, 1984), kinship determines the composition of the new social groups when a large social group divides. In Cape ground squirrels, the younger females in the group split off together (where ages of the squirrels were known) and moved into adjacent, empty burrow clusters.

Thus, a female nearing reproductive age in a social group with three breeding females has two choices; either stay in the group and delay breeding while awaiting a reproductive position or separate from the group. Since annual mortality of adult females is nearly 30% (Waterman, 1996), a single sub-adult is fairly likely to have the opportunity to move into a breeding position. However, the delay could be substantial if more than one sub-adult is waiting for a breeding position. Females that attempt to breed in a natal group with more than three reproductively mature females risk the possible cost of increased aggression. Forming a new social group alone would also be risky if the main

benefit to sociality is enhanced predator avoidance (Waterman, 1997; Waterman & Fenton, 2000), and on all three occasions where social groups split, two or three females formed the new social group. Thus, the decision whether to stay and be suppressed or separate from the natal group probably depends not only on the number of breeding females, but also on the number of sub-adult females in the group.

There may be costs to sociality for all or some members of a Cape ground squirrel group, especially when groups become large. Larger groups tend to have lower per capita reproductive success, as in black-tailed prairie dogs and yellow-bellied marmots (Hoogland, 1981*b*; Armitage, 1986). Both of these species live in habitats where space and, potentially, food are limited, whereas the population of Cape ground squirrels in this study does not seem to be living in a saturated habitat. Larger groups did have larger feeding ranges (but smaller per capita feeding ranges) and in winter, when food may be more limited, females had lighter weights and potentially higher mortality, suggesting competition for food. In addition, home ranges increased in size during a drought subsequent to this study (Waterman & Fenton, 2000). However, two reasons suggest that food shortage is not the only factor limiting group size. First, even in the face of extreme food shortage during the drought, group sizes did not decrease (Waterman & Fenton, 2000). Second, social groups that split continued to share much of their feeding ranges, suggesting that the social group did not split only to alleviate food competition. Thus, some other selective advantage must maintain these groups.

Competition for nesting burrows may be a consequence of larger groups, as Hoogland (1995) suggested for black-tailed prairie dogs. This hypothesis is unlikely for Cape ground squirrels for three reasons. First, as suggested above, their habitat is not saturated, and there are empty burrow clusters available in the veldt at any time. Second, females isolate themselves during lactation outside the burrow cluster area, within the larger feeding range, in newly dug nest burrows, suggesting that they would not compete over old nest burrows. Third, because of high litter loss and year-round breeding (Waterman, 1996), females in the same burrow cluster are unlikely to be lactating at the same time and thus unlikely to compete for nesting space.

Parasite load increases in larger colonies of black-tailed prairie dogs, which could increase disease transmission (Hoogland, 1979). However, no such relationship was apparent in Cape ground squirrels. External ectoparasites were not numerous and in 1991 were not even seen on females. As allogrooming accounts for over 40% of adult female social interactions (Waterman, 1995), the lack of relationship between group size and external parasite load was not surprising.

Cape ground squirrels most probably group to improve predator detection (Waterman, 1997; Waterman & Fenton, 2000). However, when threatened with a potential predator, Cape ground squirrels tend to

run not merely to the closest refuge but all the way to their own burrow cluster, where they meet up with the other members of their social group (Smithers, 1971; Herzig-Straschil, 1978). Thus individuals in larger groups, with larger ranges, have farther to travel to safety and could be more susceptible to predation, especially the slower, more vulnerable juveniles. The lower survivorship of juveniles in larger groups supports this hypothesis. As juveniles disappeared in summer and winter at the same rate, it is unlikely that food stress caused that survival difference. Thus predation seems to be the major constraint on female group size as well as the major selective force leading to female group formation in the first place. Male bands, which do not have the constraints of slower juveniles, can be nearly twice as large as female groups (Waterman, 1995).

In conclusion, the number of breeding positions in Cape ground squirrel groups in my study area seems to be limited to a maximum of three through the reproductive suppression of sub-adult females. If the number of potentially adult females in a group rises above this limit, the group divides. Although some competition for food resources is apparent, increased vulnerability of juveniles to predation when in larger groups seems to be an important factor limiting the size of these groups. The mechanism behind reproductive suppression in this species is unknown, and studies into hormonal and pheromonal influences on sub-adult maturation are warranted.

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### REFERENCES

- Alexander, R. D. (1974). The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**: 324–383.
- Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **49**: 227–267.
- Armitage, K. B. (1984). Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. In *The biology of ground-dwelling squirrels*: 377–403. Murie, J. O. & Michener, G. R. (Eds). Lincoln: University of Nebraska Press.
- Armitage, K. B. (1986). Marmot polygyny revisited: determinants of male and female reproductive strategies. In *Ecological aspects of social evolution*: 303–331. Rubenstein, D. I. & Wrangham, R. W. (Eds). Princeton: Princeton University Press.
- Armitage, K. B. (1988). Resources and social organization of ground-dwelling squirrels. In *The ecology of social behavior*: 131–155. Slobodchikoff, C. N. (Ed.). San Diego: Academic Press.
- Armitage, K. B. (1996). Social dynamics, kinship, and population dynamics of marmots. In *Biodiversity in marmots*: 113–128. Le Berre, M., Ramousse, R. & Le Guelte, L. (Eds). Moscow-Lyon: International Marmot Network.
- Armitage, K. B. (1998). Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. *J. Mammal.* **79**: 385–393.
- Arnold, W. (1990a). The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behav. Ecol. Sociobiol.* **27**: 239–246.
- Arnold, W. (1990b). The evolution of marmot sociality: I. Why disperse late? *Behav. Ecol. Sociobiol.* **27**: 229–237.
- Barash, D. P. (1989). *Marmots: social behavior and ecology*. Stanford: Stanford University Press.
- Henzi, S. P., Lycett, J. E. & Piper, S. E. (1997). Fission and troop size in a mountain baboon population. *Anim. Behav.* **53**: 525–535.
- Herzig-Straschil, B. (1978). On the biology of *Xerus inauris* (Zimmerman, 1780)(Rodentia, Sciuridae). *Z. Säugetierkd.* **43**: 262–278.
- Holekamp, K. E., Ogutu, J. O., Dublin, H. T., Frank, L. G. & Smale, L. (1993). Fission of a spotted hyena clan: consequences of prolonged female absenteeism and causes of female emigration. *Ethology* **93**: 285–299.
- Hoogland, J. L. (1979). Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae: *Cynomys* spp.) coloniality. *Behaviour* **69**: 1–35.
- Hoogland, J. L. (1981a). The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* **62**: 252–272.
- Hoogland, J. L. (1981b). Nepotism and co-operative breeding in the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). In *Natural selection and social behavior*: 283–310. Alexander, R. D. & Tinkle, D. W. (Eds). New York: Chiron Press.
- Hoogland, J. L. (1995). The black-tailed prairie dog: social life of a burrowing mammal. Chicago: University of Chicago Press.
- Kenward, K. E. (1990). *RANGES IV: software for analysing animal location data*. Wareham: Institute of Terrestrial Ecology.
- Leistner, O. A. (1967). The plant ecology of the southern Kalahari. *Mem. Bot. Surv. S. Afr.* **38**: 1–172.
- Michener, G. R. (1983). Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In *Advances in the study of mammalian behavior*: 528–572. *American Society of Mammalogists Special Publication* No. 7. Eisenberg, J. F. & Kleiman, D. G. (Eds). Shippenberg, PA: American Society of Mammalogists.
- Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**: 223–249.
- Rannala, B. H. & Brown, C. R. (1994). Relatedness and conflict over optimal group size. *Trends Ecol. Evol.* **9**: 117–119.
- Rood, J. P. & Nellis, D. (1980). Freeze-marking mongooses. *J. Wildl. Manage.* **44**: 500–502.
- Sherman, P. W. (1980). The limits of ground squirrel nepotism. In *Sociobiology: beyond nature/nurture?*: 505–544. Barlow, G. W. & Silverberg, J. (Eds). Boulder, CO: Westview Press.
- Skarpe, C. & Bergstrom, R. (1986). Nutrient content and digestibility of forage plants in relation to plant phenology and rainfall in the Kalahari, Botswana. *J. Arid Environ.* **11**: 147–64.
- Skinner, J. D. & Smithers, R. H. N. (1990). *The mammals of the southern African subregion*. 2nd edn. Pretoria: University of Pretoria Press.

- Smithers, R. H. N. (1971). The mammals of Botswana. *Mem. Natl Mus. Rhodesia* **4**: 1–340.
- Thomas, D. S. G. & Shaw, P. A. (1991). *The Kalahari environment*. Cambridge: Cambridge University Press.
- Walker, J. B. (1991). A review of the ixodid ticks (Acari, Ixodidae) occurring in southern Africa. *Onderstepoort J. Vet. Res.* **58**: 81–105.
- Waterman, J. M. (1995). The social organization of the Cape ground squirrel (*Xerus inauris*; Rodentia: Sciuridae). *Ethology* **101**: 130–147.
- Waterman, J. M. (1996). Reproductive biology of a tropical, non-hibernating ground squirrel. *J. Mammal.* **77**: 134–146.
- Waterman, J. M. (1997). Why do male Cape ground squirrels live in groups? *Anim. Behav.* **53**: 809–817.
- Waterman, J. M. (1998). Mating tactics of male Cape ground squirrels, *Xerus inauris*: consequences of year-round breeding. *Anim. Behav.* **56**: 459–466.
- Waterman, J. M. & Fenton, M. B. (2000). The effect of drought on the social structure and use of space in Cape ground squirrels, *Xerus inauris*. *EcoScience* **7**: 131–136.
- Wrangham, R. W., Gittleman, J. L. & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav. Ecol. Sociobiol.* **32**: 199–209.