

Why do male Cape ground squirrels live in groups?

JANE M. WATERMAN

Department of Ecology, Evolution and Behavior, University of Minnesota

(Received 29 January 1996; initial acceptance 22 March 1996;
final acceptance 2 July 1996; MS. number: A7509R)

Abstract. The Cape ground squirrel, *Xerus inauris*, is a social species of ground squirrel inhabiting the arid areas of southern Africa. The high degree of sociality in this species is due to the occurrence of all-male social groups. This study used scan and all-occurrence sampling to investigate male grouping in this species. Several hypotheses concerning the cause and function of all-male groups were addressed: aggregations around oestrous females, assessment of competitors, enhanced thermoregulation, reproductive alliances, satellite males, information exchange and enhanced predator avoidance. Males were able to detect the onset of oestrus in females. Although oestrus influenced male group size, males continued to group beyond the breeding period. These groups persisted throughout the year, regardless of ambient temperature. Older males were better at finding oestrous females than younger males, but younger males did not preferentially associate with older males to follow them to females. Results best support the hypothesis that males benefit from enhanced predator detection and deterrence. Aggregations of males roaming between groups of asynchronously breeding females may persist beyond the breeding period because the benefits to survival outweigh the relatively minor costs of reproductive competition.

© 1997 The Association for the Study of Animal Behaviour

Many hypotheses for the evolution of sociality in mammals are based on the premise that females form social groups (Wrangham 1986). All-male groups are uncommon among mammals, probably because male reproductive success is often determined by intra-sexual competition (Trivers 1972). In social mammals, males usually live with females in uni-male or multi-male groups, or they associate with females only during breeding (Rowell 1988; Clutton-Brock 1989). In some species, however, males form all-male groups living apart from females. Of the hypotheses that have been proposed to explain the evolution of grouping in mammals, seven may apply to the development of all-male groups (Table I).

Three of these hypotheses predict that adult male groups will occur only during specific time periods. The first hypothesis proposes that male grouping has no adaptive function but reflects the breeding system. Males gather near oestrous females, are highly agonistic to each other and do not maintain their aggregations beyond the

oestrous period (e.g. tree squirrels: *Sciurus aberti*, Farentinos 1972; *S. vulgaris*, Wauters et al. 1990; *S. carolinensis*, Koprowski 1991).

The second hypothesis suggests that males will congregate and interact outside the breeding period to assess their competitive abilities. Such a strategy might be important if access to females is determined by costly fighting during the breeding season, so that males may avoid potential injury during the mating season (Derocher & Stirling 1990).

Male groups may also form to gain energetic benefits through enhanced thermoregulation (Koprowski 1991). All-male sleeping groups occur during the winter in grey and fox squirrels, *S. carolinensis* and *S. niger*, respectively, and adult males rarely interact cohesively outside of the nesting area (Koprowski 1991). During warmer periods, when benefits of thermoregulation are absent, males sleep singly and interact agonistically (Koprowski 1991).

The four other hypotheses (reproductive alliances, satellites, information exchange and enhanced predator defence) generate no firm predictions about the timing of male groups. Male reproductive coalitions or alliances have been

Correspondence and present address: J. M. Waterman, Department of Biology, York University, North York, Ontario M3J 1P3, Canada (email: waterman@turing.sci.yorku.ca).

Table 1. The hypotheses addressing the function of grouping in males

Hypothesis	Predictions
1. Aggregations around oestrous females	Males only group when a female is receptive and in the vicinity of the female.
2. Assessing competitive abilities	Assumes that males can detect the onset of oestrus of the female. Males group outside breeding and interact in sparring competitions.
3. Enhanced thermoregulation	Assumes that fighting determines access to females. Males act cohesively only during cold times.
4. Reproductive alliances	Males cooperate to obtain resources or mates against other male groups.
5. Satellites	Dominant, territorial males tolerate subordinate males, especially if they share in territorial defence.
6. Information exchange	Males in larger groups find females better than males in smaller groups. Younger males preferentially associate with experienced males.
7. Enhanced predator defence	Assumes that older males are better at finding females. Groups have better overall vigilance than solitary individuals. Groups are able to mob dangerous predators.

described for lions, *Panthera leo* (Bygott et al. 1979; Packer et al. 1991); bottle-nosed dolphins, *Tursiops* spp. (Connor et al. 1992; Smolker et al. 1992), slender mongooses, *Galerella sanguinea* (Waser et al. 1994), chimpanzees, *Pan troglodytes* (Wrangham 1986), and other primates (Strier 1994). Males in such groups cooperate to obtain access to resources (usually females). Although interactions within male coalitions are usually amicable, coalitions aggressively compete with other coalitions (Packer & Pusey 1982; de Waal & Harcourt 1992).

Similarly, the main benefit of male groups comprising a dominant male and one or more satellite males is also in the defence of resources (Wirtz 1981; Arcese et al. 1995). A satellite male is a subdominant, sexually mature male that exploits resources held by dominant (territorial) males (Wirtz 1981, 1982). Dominant males that allow subordinates to remain in their territory may have longer tenure than males without satellites (Wirtz 1982).

Zahavi's (1971) information centre hypothesis provides another reason for males to form groups, wherein grouping is a type of information exchange. Instead of acquiring information about the location of food resources, males, especially younger, less experienced individuals, might use other males to locate oestrous females.

Finally, males may benefit from grouping if the group has greater overall vigilance than a solitary individual, reducing predation risk. Such group

vigilance would also allow the individual to spend more time on more productive behaviours, such as feeding or resting (Bertram 1980).

The Cape ground squirrel, *Xerus inauris*, lives in the arid regions of southwestern Africa. Unlike any other species of ground squirrel documented, Cape ground squirrel males live independently of female groups in highly social all-male bands (Waterman 1995). The purpose of this study was to address how the predictions from the above hypotheses relate to the all-male groups that occur in the Cape ground squirrel.

METHODS

Study Site

The study area was a 14-ha site on a 3500-ha farm 185 km southeast of Windhoek, Namibia, in the Kalahari-bushveld region (23°25'S, 18°00'E). Ambient air temperatures (°C) were recorded using a maximum–minimum thermometer.

Biology of the Study Animal

Females live together in groups of one to three adult females and up to nine subadults, characterized by female philopatry and male-biased dispersal. In this study, I defined a burrow cluster as an aggregation of burrow openings separated from adjacent clusters by areas without burrows that

are larger than the cluster area (after Herzig-Straschil 1978). Burrow clusters are composed of a number of burrow systems, which are units of interconnecting burrows. Burrow systems are not connected to one another (Herzig-Straschil 1978). Only one female group inhabits a burrow cluster, and burrow clusters are usually separated by a few hundred metres ($\bar{X} \pm \text{SE} = 194.6 \pm 31.6$ m; Waterman 1995). Females can breed throughout the year, and breeding is highly asynchronous within and between female groups (Waterman 1996).

Male Cape ground squirrel bands can include up to 19 individuals. Temporary sub-bands of four to five males form but the individual composition and size changes daily (Waterman 1995). Sub-band membership rarely persists beyond 1 day, because of band males joining and leaving the sub-band, resulting in continuous fission and fusion of sub-bands (Waterman 1995). The male band shares a common home range that overlaps with those of a number of female groups (Waterman 1995). When no female is in oestrus, males sleep in vacant burrow clusters away from female groups (Waterman 1995). Interactions between the males in the band are amicable, but consist of a linear dominance hierarchy maintained by displacements (Waterman 1995).

Trapping and Observations

All individuals were live-trapped using Tomahawk ($15 \times 15 \times 50$ cm) and Havahart ($21 \times 21 \times 90$ cm) traps baited with peanut butter and oats. I marked individuals for identification using numbered metal tags (National Band and Tag Co., Monel No. 1) and dye marks on the body using hair dye (Lady Clairol Nice N'Easy and Nyanzol). Because tags were frequently removed, freeze branding was also used for permanent identification (Quick Freeze; Rood & Nellis 1980). Individuals were caught periodically to renew dye marks, obtain weight measures and assess reproductive condition. I also recorded male testes size and the degree of female vaginal swelling (indicative of the onset of oestrus) to determine reproductive condition. Adult and subadult males could be distinguished, because subadult males were either non-scrotal or only partly scrotal (adult males are scrotal year-round). By the second year of the study, male age could be further distinguished by fur condition. Males that

were older than 2 years had less fur on the face, and their body fur was sparser than that of younger males or females of any age.

I made behavioural observations (2000 hours) from June 1989 to April 1990, June 1990 to February 1991, and July 1991 to December 1991 using 10×50 binoculars and a $15\text{--}45 \times 60$ spotting scope. Observations were made from trees, windmills and a vehicle. Since these squirrels are most social in early morning and upon their return from feeding in late afternoon, observations concentrated on these times. Periodically, I also observed squirrels throughout the day. 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). I used focal animal sampling (Altmann 1974) on the day of oestrus to record the length of oestrus and the identity and behaviour of all attending males (Waterman 1995). Locations of squirrels were identified using a grid marked by coloured flags placed at 10-m intervals within burrow clusters and at 20-m intervals in adjacent areas.

Male sub-band size was determined by the number of males entering or leaving the sleeping burrow. I determined associations between individuals using a simple ratio index (Cairns & Schwager 1987; Ginsberg & Young 1992). This index is the least biased when the number of groups observed is both small and variable (Cairns & Schwager 1987). Associations in the Cape ground squirrel were determined by the frequency at which two males slept together in the same burrow system.

All-occurrence data on male–male interactions were used to determine the dominance hierarchy (Waterman 1995). I determined this hierarchy using the behaviour patterns of approach (one individual walking directly up to another, within 10 cm) and jumping back by males in a dyadic interaction (Waterman 1995). Dominance hierarchies are linear (Landau's index of linearity was greater than 0.9 in all years; mean number of interactions per dyad was 4.2 ± 0.2 ; interactions were seen for 67 of 79 dyads in 1989, 117 of 120 dyads in 1990 and 105 of 120 dyads in 1991; Waterman 1995). Older males (greater than 3 years of age) were significantly more dominant than younger males (between the ages of 8 months and 3 years; Waterman 1995). The most dominant male was assigned a rank of 1, and the ranks of

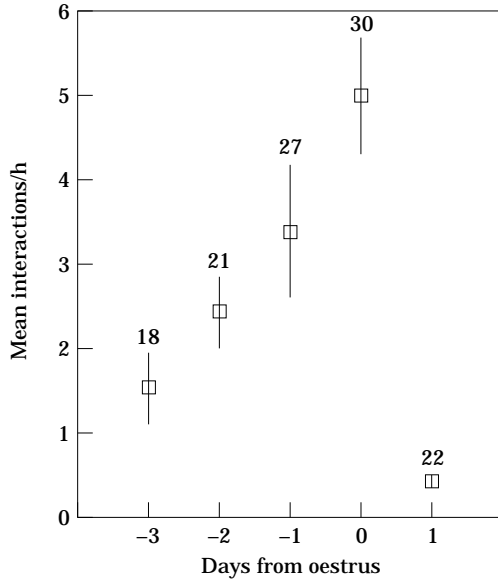


Figure 1. Mean number of interactions/hour between males and oestrous female Cape ground squirrels. Day of oestrus is 0. Numbers above error bars indicate number of females.

subordinate individuals reflect the number of individuals dominating them (Lehner 1979).

When data were found to be normal (Shapiro–Wilk test) and homoscedastic, I used parametric statistics (Sokal & Rohlf 1981; Snedecor & Cochran 1989); otherwise I used non-parametric statistics (Conover 1980). A 0.05 probability of a Type I error was considered significant. Results are expressed as mean \pm 1 SE unless otherwise stated.

RESULTS

Monthly median sub-band sizes varied from two to eight males, and males never consistently lived alone. Males rarely slept alone ($2.4 \pm 0.6\%$ of an average of 85.3 ± 13.2 sightings; $N=20$ males).

During their daily movements, males repeatedly approached adult females. The rate at which individual males approached females dramatically increased during the 3 days prior to oestrus and decreased rapidly the day after oestrus (Fig. 1). Male sub-band size tended to be larger on the day of oestrus, significantly so in 6 of the 10 days compared (Fig. 2). Male sub-band size outside of

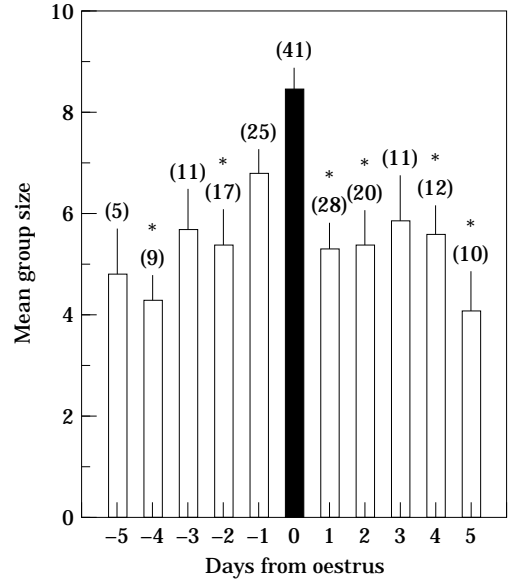


Figure 2. Mean number of male Cape ground squirrels in a sub-band. Day 0 is the day of oestrus. Numbers above bars refer to the number of sub-bands. Asterisks indicate which days differed from the mean sub-band size on the day of oestrus (Tukey pair-wise comparison, $P < 0.05$).

oestrus days remained at three to four individuals. Males continued to share sleeping burrows regardless of the oestrous state of females. When no females within their range were in oestrus, male sub-bands slept either in vacant burrow clusters (54%, $N=369$ nights) or in clusters that were occupied (46%).

Male sub-band size was not influenced by ambient minimum temperature ($Y=4.94 - 0.015X$, $F_{1,441}=0.40$, $P=0.53$, $R^2=0.001$). Furthermore, the frequency of individuals sleeping alone did not differ between the winter month of August and the summer month of December (August: $2.6 \pm 2.0\%$, December: $6.0 \pm 3.6\%$; Friedman's test: $\chi^2_r = -0.67$, $P=0.41$, $N=14$ males seen in both months).

During the night before a female's oestrus, the majority of males in attendance ($81.2 \pm 2.7\%$, $N=41$ oestrous periods) slept in the burrow cluster of the oestrous female. However, $16.3 \pm 2.2\%$ of males in attendance on any day of oestrus arrived alone, unaccompanied by other males. On average, the percentage of all oestruses that younger males attended after sleeping away from

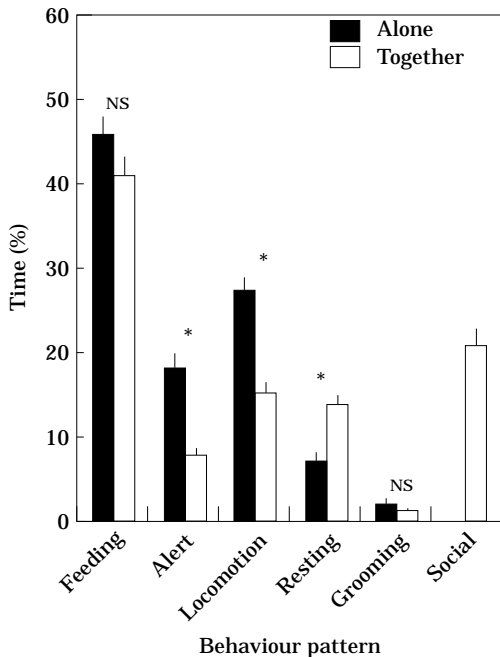


Figure 3. Comparison of male Cape ground squirrel behaviour when alone and when within 10 m of another male (asterisks indicate significant differences; Mann–Whitney U tests, $P < 0.01$ in all tests; $N = 18$ individuals).

other males was significantly greater than for older males ($53.4 \pm 11.0\%$, $N = 9$ young males; $10.6 \pm 1.9\%$, $N = 10$ older males; Mann–Whitney U -test: $U = 81.5$, $P = 0.0007$).

Frequency of attendance on a day of oestrus was independent of an individual's median sub-band size (Spearman's rank correlation, $r_s = 0.13$, $P > 0.05$, $N = 20$ males). There was also no relationship between an individual's rank and the median size of the sub-band it occupied ($r_s = 0.12$, $P > 0.05$, $N = 20$ males). Dominant males were more likely to attend oestrous females than were subordinates, however (average rank of a male versus

percentage of days in attendance, $r_s = -0.48$, $P < 0.025$, $N = 20$ males). Low-ranking males did not preferentially associate with high-ranking males, and there was no relationship between a male's rank and the rank of the other members in his sub-band ($r_s = -0.17$, $P > 0.05$, $N = 210$ dyads over 3 years, 20 males).

Males behaved differently when alone than when within 10 m of another male. Males that were solitary spent more time in alert postures and locomotion but less time resting (Fig. 3). Adult males also joined with females in mobbing potential predators, such as Cape cobras, *Naja nivea*, puff adders, *Bitis arietans*, and monitor lizards, *Varanus exanthematicus*. When Cape ground squirrels mob, they approach the predators and point their piloerected tails forward and parallel to their body. Squirrels jump forward in unison at the predator, and jump back when the predator strikes. During the predator's strike, the squirrel moves its tail in front of its body, positioning the tail between itself and the predator. Six instances of mobbing were recorded in this study, and adult males were involved in three cases (Table II). The squirrels mobbed only reptilian predators, and in all six cases drove the predator away from the burrow cluster.

DISCUSSION

Several results above are inconsistent with the predictions from hypotheses 1, 2 and 3 (Table I). There is also additional evidence for rejecting these hypotheses.

In tree squirrels, male groups are merely ephemeral by-products of the mating system. Males aggregate around the female a few days prior to oestrus and establish a dominance hierarchy by overt competition (Farentinos 1972; Thompson 1977; Wauters et al. 1990). Outside oestrus these males do not associate with squirrels of either sex.

Table II. Group composition of Cape ground squirrels during mobbing interactions

Mobbing group composition	Species mobbed
1 Adult female, 2 subadult males, 3 adult males	Cape cobra
5 Adult females, 3 subadult males	Puff adder
2 Adult females	Cape cobra
1 Adult female, 1 adult male	Cape cobra
1 Adult female, 1 subadult male	Cape cobra
2 Adult females, 2 subadult males	Monitor lizard

The hypothesis that grouping occurs as aggregations around females predicts that males detect the onset of oestrus in females and that groups form only around receptive females. Male Cape ground squirrels detect the onset of oestrus a few days in advance, and male sub-bands are larger on the day of oestrus. Sub-bands are maintained outside of the oestrous period, however, and often sleep in vacant burrow clusters away from the location of females. Furthermore, the male dominance hierarchy is maintained by non-aggressive interactions between band members outside oestrus, rather than by fights during oestrus (Waterman 1995). Male groups in Cape ground squirrels are not just aggregations around oestrous females.

Males in some species, such as polar bears, *Ursus maritimus*, appear to congregate outside of the breeding period to assess their competitive abilities (Latour 1981). A key assumption in this hypothesis is that fighting determines access to females (Latour 1981). No fighting or injuries associated with this type of assessment were ever seen in the Cape ground squirrel (Waterman 1995). Age, rather than size or fighting ability, is the most important factor determining dominance rank (Waterman 1995) and therefore access to females (Waterman 1994). Male Cape ground squirrels do not appear to form groups to assess their competitive abilities.

I found no support for the hypothesis that male Cape ground squirrels were grouping for enhanced thermoregulation. Temperatures in the burrows where Cape ground squirrels sleep fluctuate very little during the winter months, regardless of the ambient above ground temperature (Herzig-Straschil 1979). When ambient temperatures varied from 7.5 to 26°C, temperatures within burrows remained at 11.5–15°C, but these burrow temperatures could be even higher if more than one individual stayed together (Herzig-Straschil 1979). Unfortunately, there are no data for the summer months, when ambient temperatures can reach 40°C (Herzig-Straschil 1978; Waterman 1996). Thermoregulatory benefits of grouping do not explain why males continue to associate when above ground, however (Waterman 1995). Thus, although cool burrow temperatures could lead to huddling, temperature is unlikely to lead to male grouping above ground.

The final four hypotheses make no firm predictions about the timing of male groups. All-male

reproductive alliances could be a form of escalated mate competition (Waser et al. 1994). In many species with male coalitions, larger coalitions are usually (but not necessarily) composed of related individuals, presumably because the non-breeding individuals gain inclusive fitness benefits (Packer et al. 1991; Strier 1994).

Two features of male bands of Cape ground squirrel do not support the predictions of the coalitions hypothesis. First, the large male groups are maintained by the recruitment of young males that have dispersed into the area and are unlikely to contain closely related individuals (Waterman 1995). Second, there is no evidence of territoriality or cooperative defence by male bands against other bands (Waterman 1995). New males in the area are accepted into the band without conflict (Waterman 1995). This lack of territoriality by Cape ground squirrel males also does not support hypothesis 5, in that these groups are not composed of a dominant male and satellite males defending a common territory.

Males could be grouping to exchange information. The prediction that males in larger sub-bands were more successful in finding oestrous females than were males in smaller sub-bands was not supported. Alternatively, young males could use older males as a source of information. This hypothesis assumes that older males are better at finding females than are younger males. In Cape ground squirrels, older males were more likely to attend oestrous females than were younger males. Younger males located oestrous females independently of other males, however, and did not preferentially associate with older males. There is no evidence that benefits from information exchange would be a major selective force on grouping in this species.

Predator detection and deterrence is another benefit of grouping (Pusey & Packer 1986; Rodman 1988; Rowell 1988). Struhsaker (1969) suggested that open habitats are more suitable to grouping as an anti-predator strategy, and he found that all-male groups were more common in terrestrial than arboreal primates. In open areas, where hiding is difficult, early detection would be the best way of avoiding predators (Jarman 1974; van Schaik & van Hooft 1983). Male Cape ground squirrels are more vigilant when alone than when in groups. Zumpt (1970) suggested that aerial predators are a major predator of Cape ground squirrels, so improved vigilance could be an

important benefit of grouping. Groups can also deter some terrestrial predators, and both male and female Cape ground squirrels mob potential reptilian predators. Similar harassment of predators has been documented in the banded mongoose, *Mungos mungo* (Rood 1975), and Rood (1983) suggested that predation is the most important selective factor leading to sociality in the small, diurnal social mongooses.

Although the hypotheses of enhanced thermoregulation and enhanced predator avoidance are functional explanations of grouping, neither addressed why males would group exclusively with other males. Males could just join female social groups. In situations where males are excluded from female groups (i.e. bachelor herds) either by the females themselves or by resident males, selective pressures could lead to grouping by single males (Sinclair 1977; Arcese et al. 1995). These males group either outside of the breeding season (e.g. mountain sheep, Geist 1971; red deer, Clutton-Brock et al. 1979), while they wait to obtain a reproductive position in a group (e.g. patas monkeys, *Erythrocebus patas*; Gartlan 1975; guenons, *Cercopithecus* spp.; Rowell 1988) or while they wait to gain a territory (e.g. white rhinoceros, *Ceratotherium simum*; Owen-Smith 1975). Interactions between bachelor males are usually amicable, but become agonistic in the presence of oestrous females.

The term 'bachelor herd' is not an appropriate description of the all-male groups in Cape ground squirrels, because these males are not merely awaiting reproductive positions in a female group or to gain a territory. Males form bands that exist independently of female groups, and the individuals within these bands interact amicably regardless of female oestrous condition (Waterman 1995, this paper).

Individual Cape ground squirrel males could join female groups instead of remaining in bands or living solitarily, which would produce a social system nearly identical to that of the black-tailed prairie dog, *Cynomys ludovicianus*. Unlike Cape ground squirrels, however, black-tailed prairie dogs breed fairly synchronously (Hoogland 1995). Asynchrony of female reproduction may make roaming between female groups more reproductively successful for male Cape ground squirrels than joining a female group, even though such roaming could increase the risk of predation. Since males can detect the onset of oestrus, most

of these roaming males would aggregate around the female. Because oestrus is asynchronous and year-round, males would end up associating regularly. The benefits of enhanced predator avoidance may have led to these groups persisting beyond the oestrous period.

The all-male bands of the Cape ground squirrel are unusual male associations. Groups of adult male Cape ground squirrel do not cooperatively defend any resource or territory, nor do they dissolve during or after breeding. The groups are highly cohesive, amicable and persist throughout the year. They also cannot be characterized as bachelor herds. The results provide some support that grouping is a response to the risk of predation. Further manipulative experiments (e.g. alarm calling using playback experiments and snake mobbing trials) are required to determine the effects of predation on group size and male behaviour.

ACKNOWLEDGMENTS

E. C. Birney, M. B. Fenton, D. F. McKinney, A. E. Pusey, J. D. Roth and three anonymous referees provided many suggestions for improving the manuscript. Mr and Mrs Bartsch kindly allowed me access to their farm. In addition, the scientists of Windhoek were especially supportive, including B. Curtis, C. Roberts, R. Swart and J. Mendelssohn. M. Griffin of the Namibian Department of Conservation and Tourism provided much appreciated logistic support. I especially thank J. Roth for his friendship and 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.

REFERENCES

- Altman, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–267.
- Arcese, P., Jongejan, G. & Sinclair, A. R. E. 1995. Behavioural flexibility in a small African antelope: group size and composition in the Oribi (*Ourebia ourebi*, Bovidae). *Ethology*, **99**, 1–23.
- Bertram, B. C. R. 1980. Vigilance and group size in ostriches. *Anim. Behav.*, **28**, 278–286.

- Bygott, J. D., Bertram, B. C. & Hanby, J. P. 1979. Male lions in large coalitions gain reproductive advantages. *Nature, Lond.*, **282**, 839–841.
- Cairns, S. J. & Schwager, S. J. 1987. A comparison of association indices. *Anim. Behav.*, **35**, 1454–1469.
- Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proc. R. Soc. Lond. Ser. B.*, **236**, 339–372.
- Clutton-Brock, T. H., Albon, S. D., Gibson, R. M. & Guinness, F. E. 1979. The logical stag: adaptive aspects of fighting behaviour in red deer. *Anim. Behav.*, **27**, 211–225.
- Connor, R. C., Smolker, R. & Richards, A. F. 1992. Dolphin alliances and coalitions. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 415–442. New York: Oxford University Press.
- Conover, W. J. 1980. *Practical Nonparametric Statistics*. New York: John Wiley.
- Derocher, A. E. & Stirling, I. 1990. Observations on aggregating behaviour in adult male polar bears (*Ursus maritimus*). *Can. J. Zool.*, **68**, 1390–1394.
- Farentinos, R. C. 1972. Social dominance and mating activity in the tassel-eared squirrel, *Sciurus aberti ferreus*. *Anim. Behav.*, **20**, 316–326.
- Garlan, J. S. 1975. Adaptive aspects of social structure in *Erythrocebus patas*. In: *Proceedings from the Symp. 5th Congr. Int. Primatol. Soc.* (Ed. by S. Kondo, M. Kawai, A. Ehara & S. Kawamura), pp. 161–171. Tokyo: Japan Science Press.
- Geist, V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. Chicago: The University of Chicago Press.
- Ginsberg, J. R. & Young, T. P. 1992. Measuring association between individuals or groups in behavioural studies. *Anim. Behav.*, **44**, 377–379.
- Herzig-Straschil, B. 1978. On the biology of *Xerus inauris* (Zimmerman, 1780) (Rodentia, Sciuridae). *Z. Säugetierk.*, **43**, 262–278.
- Herzig-Straschil, B. 1979. *Xerus inauris* (Rodentia, Sciuridae): an inhabitant of the arid regions of southern Africa. *Folia Zool.*, **28**, 119–124.
- Hoogland, J. L. 1995. *The Black-tailed Prairie Dog: Social Life of a Burrowing Mammal*. Chicago: The University of Chicago Press.
- Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour*, **48**, 215–267.
- Koprowski, J. L. 1991. The evolution of sociality in tree squirrels: the comparative behavioral ecology of fox squirrels and eastern gray squirrels. Ph.D. dissertation, University of Kansas, Lawrence.
- Latour, P. B. 1981. Interactions between free-ranging, adult male polar bears (*Ursus maritimus* Phipps): a case of adult social play. *Can. J. Zool.*, **59**, 1775–1783.
- Lehner, P. N. 1979. *Handbook of Ethological Methods*. New York: Garland Press.
- Owen-Smith, N. 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell 1817). *Z. Tierpsychol.*, **38**, 337–384.
- Packer, C. & Pusey, A. E. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? *Nature, Lond.*, **296**, 740–742.
- Packer, C., Gilbert, D. A., Pusey, A. E. & O'Brien, S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature, Lond.*, **351**, 562–565.
- Pusey, A. E. & Packer, C. 1986. Dispersal and philopatry. In: *Primate Societies* (Ed. by B. B. Smuts, D. C. Cheney, R. M. Seyfarth, R. W. Wrangham & T. H. Struhsaker), pp. 250–266. Chicago: The University of Chicago Press.
- Rodman, P. S. 1988. Resources and group sizes of primates. In: *The Ecology of Social Behavior* (Ed. by C. N. Slobodkinoff), pp. 83–108. San Diego: Academic Press.
- Rood, J. P. 1975. Population dynamics and food habits of the banded mongoose. *E. Afr. Wildl. J.*, **13**, 89–111.
- Rood, J. P. 1983. The social system of the dwarf mongoose. In: *Advances in the Study of Mammalian Behavior* (Ed. by J. F. Eisenberg & D. G. Kleiman), pp. 454–488. Lawrence, Kansas: Allen Press.
- Rood, J. P. & Nellis, D. 1980. Freeze-marking mongooses. *J. Wildl. Mgmt.*, **44**, 500–502.
- Rowell, T. E. 1988. Beyond the one-male group. *Behaviour*, **104**, 189–201.
- van Schaik, C. P. & van Hooff, J. A. R. A. M. 1983. On the ultimate causes of primate social systems. *Behaviour*, **85**, 91–117.
- Sinclair, A. R. E. 1977. *The African Buffalo*. Chicago: The University of Chicago Press.
- Smolker, R. A., Richards, A. F., Connor, R. C. & Pepper, J. W. 1992. Sex differences in patterns of association among Indian ocean bottlenose dolphins. *Behaviour*, **123**, 38–69.
- Snedecor, G. W. & Cochran, W. G. 1989. *Statistical Methods*. 8th edn. Ames, Iowa: Iowa State University Press.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. New York: W. H. Freeman.
- Strier, K. 1994. Brotherhoods among atelins: kinship, affiliation, and competition. *Behaviour*, **130**, 151–167.
- Struhsaker, T. T. 1969. Correlates of ecology and social organization among African cercopithecines. *Folia Primatol.*, **11**, 80–118.
- Thompson, D. C. 1977. Reproductive behavior of the grey squirrel. *Can. J. Zool.*, **55**, 1176–1184.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 139–179. Chicago: Aldine Press.
- de Waal, F. B. M. & Harcourt, A. H. 1992. Coalitions and alliances: a history of ethological research. In: *Coalitions and Alliances in Humans and Other Animals* (Ed. by A. H. Harcourt & F. B. M. de Waal), pp. 1–22. Oxford: Oxford Scientific Press.
- Waser, P. M., Keane, B., Creel, S. R., Elliot, L. F. & Minchella, D. J. 1994. Possible male coalitions in a solitary mongoose. *Anim. Behav.*, **47**, 289–294.
- Waterman, J. M. 1994. The social organization of the Cape ground squirrel. Ph.D. dissertation, University of Minnesota, St Paul, Minnesota.
- Waterman, J. M. 1995. The social organization of the Cape ground squirrel (*Xerus inauris*, Rodentia: Sciuridae). *Ethology*, **101**, 130–147.

- Waterman, J. M. 1996. The reproductive biology of a tropical, non-hibernating ground squirrel. *J. Mammal*, **77**, 134–146.
- Wauters, L., Dhondt, A. A. & De Vos, R. 1990. Factors affecting male mating success in red squirrels (*Sciurus vulgaris*). *Ethol. Ecol. Evol.*, **2**, 195–205.
- Wirtz, P. 1981. Territorial defence and territory takeover by satellite males in the waterbuck *Kobus ellipsiprymnus* (Bovidae). *Behav. Ecol. Sociobiol.*, **8**, 161–162.
- Wirtz, P. 1982. Territory holders, satellite males and bachelor males in a high density population of waterbuck (*Kobus ellipsiprymnus*) and their associations with conspecifics. *Z. Tierpsychol.*, **58**, 277–300.
- Wrangham, R. W. 1986. Ecology and social relationships in two species of chimpanzee. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 352–378. Princeton, New Jersey: Princeton University Press.
- Zahavi, A. 1971. The function of pre-roost gatherings and communal roosts. *Ibis*, **113**, 106–109.
- Zumt, I. 1970. The ground squirrel. *Afr. Wildl.*, **24**, 115–121.