



# Mating tactics of male Cape ground squirrels, *Xerus inauris*: consequences of year-round breeding

JANE M. WATERMAN

Department of Ecology, Evolution and Behavior, University of Minnesota

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## ABSTRACT

The Cape ground squirrel is a highly social, tropical ground squirrel that does not hibernate, suggesting that female receptivity could be scattered throughout the year. Males in this species are very social, living in all-male bands. I studied the mating tactics of male Cape ground squirrels to examine the effects of year-round female receptivity and male grouping on these tactics and on the degree of intrasexual competition. Female breeding was highly irregular and unpredictable, and the average operational sex ratio during oestrus was 10:1 (males to females). However, the predicted high rates of aggression were not observed. Instead, competition among males was manifested by competitive searching, repeated copulations and disruptions of copulations. Dominant males had more copulations with more females, first access to females and were more likely to copulate below-ground where disruptions were unlikely to occur. I conclude that the mating patterns of males in this species are a product of the asynchrony of female oestrus, year-round breeding and the survival benefits of grouping.

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The distribution of females in space and time influences the mating strategies of males (Emlen & Oring 1977; Clutton-Brock 1989). The timing, or degree of synchrony, of sexual receptivity by females has a profound effect on the operational sex ratio (OSR), the 'ratio of fertilizable females to sexually active males at any given time' (Emlen & Oring 1977). As the degree of asynchrony of receptivity increases, the OSR should become more biased towards males (Emlen 1976), which should intensify male mating competition (Clutton-Brock & Parker 1992).

The spatial and temporal distribution of females has been suggested to have a large influence on the breeding systems of North American ground squirrels (Schwagmeyer 1990). Variation in the spatial distribution of female ground squirrels is reflected in the wide range of mating strategies displayed by male ground squirrels. Female social organization ranges from solitary and relatively asocial to highly clustered, colonial matrilineal groups (Michener 1983; Schwagmeyer 1990). Access to females and the relative reproductive success of males are determined through overt conflict, competitive mate searching and sperm competition (Schwagmeyer 1984; Schwagmeyer & Wootner 1985, 1986). In species where females are clustered in space, males appear to monopo-

lize females through overt conflict (Dobson 1984; Schwagmeyer 1990), which may occur through territoriality or dominance hierarchies. In species where females are scattered in space, males gain access to females by competitive searching, as it appears to be uneconomical for males to defend solitary females or those with highly asynchronous receptivity (Schwagmeyer 1990).

Studies examining the effects of the temporal distribution of females on male mating tactics (e.g. Davis & Murie 1985), however, have been limited by the relatively restricted breeding seasons of most North American ground squirrels, which are highly constrained by limitations imposed by winter. Females can mate only once a year, within a few weeks of emergence from hibernation, and thus are fairly synchronized by winter (Michener 1983; Dobson 1984). No study has examined the mating patterns of males in a species where receptivity extends over a long time span.

The Cape ground squirrel inhabits the desert areas of southern Africa. Although closer phylogenetically to African tree squirrels (Sciuridae: Black 1972), Cape ground squirrels are more similar ecologically to temperate ground squirrels (tribe Marmotini). Unlike most Marmotini, however, they do not hibernate and can breed throughout the year (Herzig-Straschil 1978; Waterman 1996). Sociality in the Cape ground squirrel is characterized by the presence of social female kin clusters and associated nonkin bands of males. The formation of

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

male bands results in a social organization unlike that described for other species of ground squirrel. The potential for breeding to be scattered over the entire year rather than restricted to a few weeks, and the occurrence of male groups in this species, suggest that male reproductive strategies may diverge from the patterns typical of North American ground squirrels.

The objectives of this study were to determine how male Cape ground squirrels obtain access to mates, and test the following predictions about the effect of scattered female receptivity on male mating patterns. (1) Because of a high OSR, males will be unable to monopolize females during oestrus. (2) Intense male competition will be exhibited by overt conflict. (3) Access to females will be determined by a stable dominance hierarchy instead of territoriality. (4) Males will interfere with the reproductive attempts of other males by copulating repeatedly with the female and disrupting copulating pairs.

## METHODS

### Biology of Cape Ground Squirrels

Cape ground squirrels live at fairly low densities compared with other species of ground squirrels (Waterman 1995). Adult sex ratios are 1:1 and individual females may breed at any time during the year and more than once in a year (Waterman 1995, 1996). Litter size is one to two and there is no male parental care. Litter loss is high in this species, with some 70% of all oestruses failing to produce successful litters. Females that do not give birth (either by failing to conceive or by miscarrying) have significantly shorter interoestrous intervals (76 days) than females that lose litters during lactation (90 days) and the interoestrous intervals of females whose litters successfully emerge are even longer (146 days; Waterman 1996). Females live in cohesive matrilineal kin clusters, usually composed of one to three adult females and up to nine subadults (Waterman 1995). Only one female group inhabits a burrow cluster (aggregation of burrow openings), and burrow clusters are usually separated by several hundred metres (Waterman 1995). Groups are characterized by female philopatry and male-biased dispersal. Female group members share sleeping burrows and feeding ranges, and interactions within social groups are nonaggressive.

The social system of Cape ground squirrels is unique among described species of ground squirrels because males live in all-male bands of up to 19 individuals that are essentially independent of females (Waterman 1995, 1997). Band home ranges encompass a number of female groups but are not defended against other male bands (Waterman 1995). When no female is in oestrus, males sleep in vacant burrow clusters away from female groups (Waterman 1995). Males form temporary sub-bands of four or five, whose size and composition change daily. It is in these sub-bands that the males forage, sleep and roam their home range (Waterman 1995, 1997). Outside breeding, interactions between males are rarely aggressive, and injury has never been observed. There is,

however, a linear dominance hierarchy in the band, which is correlated with age (Waterman 1995, 1997). This dominance hierarchy is formed and maintained by nonaggressive interactions (displacements), rather than fighting (Waterman 1995).

### Study Site and Trapping

The study area was a 3500-ha farm 185 km southeast of Windhoek, Namibia (23°25'S, 18°00'E). For details on the study site and the trapping, marking and observations of squirrels see Waterman (1995, 1996). Whenever a female was trapped, I recorded the degree of female vulval swelling (indicative of the onset of oestrus) to determine sexual receptivity. Adult and subadult males could be distinguished because subadult males were either non-scrotal or only partly scrotal, whereas adult males are scrotal year-round. 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.

### Observations and Analyses

I recorded behavioural observations of ground squirrels based on descriptions of Steiner (1970a, b) for *Spermophilus columbianus* and Ewer (1966) for *Xerus erythropus*. To determine time budgets, I recorded the activities of all squirrels every 5 min using scan sampling (Altmann 1974). To determine the dominance hierarchy in male groups, I used all-occurrence sampling to record the behaviours of 'approach' (one individual walking directly up to another, within 10 cm) and 'jumping back' by males engaged in a dyadic interaction (Waterman 1995). The most dominant male was assigned a rank of 1, and the ranks of subordinate individuals reflect the number of individuals dominating them (Lehner 1979). I calculated each individual's absolute rank (rank in the entire male group) and relative rank (rank relative to the other males attending an oestrous female). Dominance hierarchies in this species are highly linear and transitive (Waterman 1995, 1997). Behaviours used to calculate rates of aggressive behaviour were fighting, chasing and running at each other (see Waterman 1995 for descriptions of these behaviours). The only other interactive behaviour exhibited by males during oestrus was 'greeting' (mutual contact of the naso-oral areas).

Increased activity by males in the burrow cluster of a female coming into oestrus and interaction with that female a few days prior to oestrus (Waterman 1997) indicated that oestrus was imminent. Oestrus was considered to commence when a female first emerged in the morning and subsequently (usually within minutes) associated with a male. Oestrus was considered to be over when the female stopped copulating and one or more of the following criteria were met: (1) the female no longer submitted to males but fled or fought with any approaching male; (2) the oestrous female left the area completely or remained underground for 2–3 h; and (3) the attending males discontinued their search for the oestrous female and dispersed to feed.

I used focal-animal sampling of oestrous females to record the length of oestrus and the behaviour of all attending males towards the female. I calculated OSRs as the number of adult males present at a burrow cluster relative to the number of females in oestrus in that burrow cluster.

Copulations occurred both above and below ground. Observations of above-ground copulations indicated that a minimum of 25 s was necessary for ejaculation. An underground copulation was assumed to have occurred when an adult male followed a female closely and then both entered a burrow together, remaining underground for a minimum of 1 min. The pair often emerged at the same time, and either partner would often groom the genital area upon emergence. Two types of evidence lend support to the assumption that copulations took place below ground. First, females were usually aggressive towards males outside oestrus (Waterman 1995) and only once (in 1880 h of observation) was a nonoestrous female observed being followed into a burrow by an adult male. During oestrus, however, females were nonaggressive towards males and would often enter burrows with them (88 observations in 123 h of observation). Second, two females observed during oestrus, which had never been observed copulating above ground, entered burrows with males for only 1–2 min and later became pregnant. Although I am confident that a copulation did occur when a male and female went below ground for more than 1 min, I will use the term below-ground copulation to distinguish these interactions from above-ground copulations.

To test for the clustering of oestruses within social groups over time, I examined two 2-month periods because these intervals were just shorter than the 72-day interoestrous period of females that fail in pregnancy during or before gestation. A longer period could include a second oestrus for individuals that had already been included in the analysis. These periods also coincided with peak yearly breeding, at a time when adequate data would be available for testing (Waterman 1996; 15 July–15 September 1990 and 16 September–15 November 1990). The 1989 and 1991 field seasons were not included in this analysis because oestrous periods were not observed in enough social groups. I ranked oestruses by time of occurrence in each period, and compared the distribution of oestrous ranks among the different social groups using a Kruskal–Wallis test to determine whether oestruses were more clustered within social groups than among social groups.

I calculated the mating success of a male as the proportion of oestruses observed in which the male was successful in copulating with the female. I also determined a mating score for each male to include repeated copulations (multiple copulations by the same pair during the same oestrus) as well as the number of mates, by calculating the average number of copulations per oestrus. During copulations, I also recorded the identity of any male that caused disruptions (approaches or pouncing of males on or near a copulating pair such that the pair terminated the copulation abruptly).

Because the data were not normally distributed, I used nonparametric statistics (Conover 1980). A 0.05

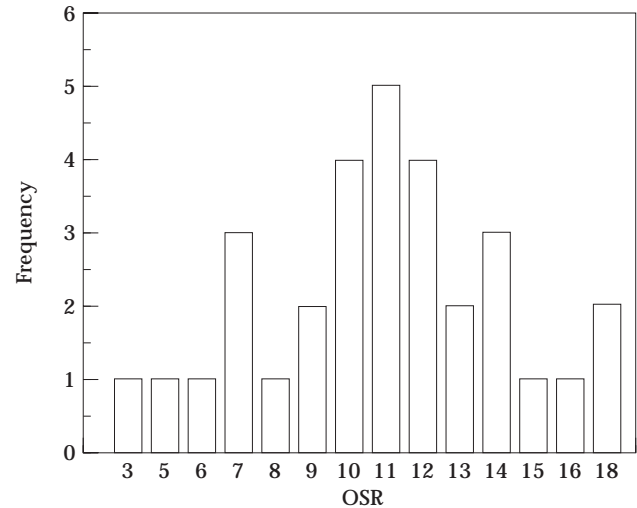


Figure 1. Frequency distribution of operational sex ratios of Cape ground squirrels for 31 oestruses (OSR was calculated as the number of adult males present at a burrow cluster relative to the number of females in oestrus in that burrow cluster).

probability of a type I error was considered significant. Results are expressed as mean  $\pm$  1 SE, unless otherwise stated.

## RESULTS

Thirty-one oestruses were observed in their entirety during the study. An additional 10 oestruses were observed at the beginning and end of the oestrus so that total duration could be measured, but only a portion of the interactions were observed during these oestruses. Oestrus began in the early morning and usually ended by noon, lasting  $3.1 \pm 0.3$  h ( $N=41$  oestruses where both the beginning and end of oestrus was observed). Only twice did more than one female in the study area come into oestrus on the same day (in each instance both females were in the same social group), suggesting oestrus overlap is rare. No greater clustering of receptivity occurred within social groups than between social groups (first period: Kruskal–Wallis test:  $K=5.71$ ,  $N=10$  oestruses in five female groups,  $P=0.22$ ; second period:  $K=0.86$ ,  $N=6$  oestruses in three groups,  $P=0.65$ ).

### Operational Sex Ratios and Male Mating

The night before a female came into oestrus, most males in the area entered the burrow cluster to sleep. On the morning of oestrus, males emerged up to half an hour earlier than the female social group and began to search the burrow cluster for the oestrous female. This continual searching lasted until the conclusion of oestrus.

The OSR during oestrus was  $10.9 \pm 0.6$  ( $N=31$  oestrous days where the entire oestrus was observed, Fig. 1). Copulations occurred both above and below ground (Table 1). Upon finding the oestrous female, males would either try to copulate immediately or follow and chase

**Table 1.** Data on mating parameters associated with mate order for male Cape ground squirrels

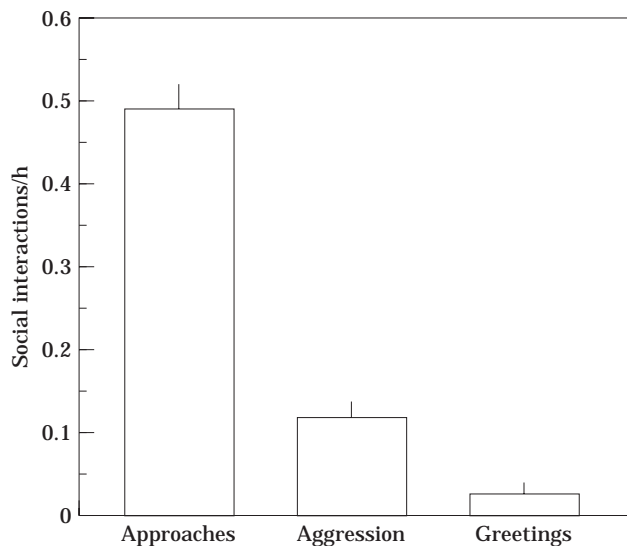
Mate order	Absolute rank	Relative rank	Weight (g)	Percentage			Duration (min)		Inter copulation interval (min)†	N‡
				Above	Below	Disrupted*	Above	Below		
1	2.8±0.5	2.3±0.4	638.8± 5.6	10.3	89.7	100.0	1.0±0.3	8.9±2.7	11.7±2.8	31
2	6.3±0.8	4.9±0.6	613.2± 9.8	28.1	71.9	56.0	2.6±0.8	4.0±0.8	19.8±5.5	31
3	6.2±0.8	6.2±0.8	610.9± 8.9	33.3	66.7	70.0	0.9±0.3	4.0±0.7	8.7±2.7	26
4	5.9±0.9	4.8±0.8	609.8±10.9	19.0	81.0	100.0	1.7±0.7	3.9±1.3	14.7±4.4	21
5	6.8±1.1	5.3±0.9	620.9± 8.2	35.3	64.7	67.0	5.4±3.9	4.6±2.5	18.6±6.4	15
6	7.9±1.0	6.1±0.6	629.3±15.1	35.7	64.3	80.0	2.5±1.0	4.2±1.9	4.9±3.0	12
7	5.4±1.2	4.0±0.9	619.3±16.5	22.2	77.8	75.0	4.8±2.0	4.7±1.0	8.1±2.8	12
8	5.4±1.0	4.1±0.6	632.4±17.0	12.5	87.5	0.0	1.1±0.9	4.4±1.4	13.0±7.2	8
Overall	—	—	601.5± 6.1§	25.0	75.0	72.0	2.4±0.4	5.4±0.6	12.0±1.3	33

\*Percentage of above-ground copulations that were disrupted.

†Delay until next copulation.

‡Number of oestruses.

§From Waterman (1996), adult male weight.



**Figure 2.** Rates of social interaction (i.e. per hour) between adult male Cape ground squirrels during female oestrus (averaged for 18 males) for approaches, aggression (chases, fights and running at each other) and greetings (see Methods).

her into a burrow. The OSR was unrelated to the number of mates accepted by the female (Spearman rank correlation:  $r_s=0.24$ ,  $N=31$  oestrous periods,  $P=0.20$ ).

### Male–Male Competition

During oestrus, males spent more time moving ( $22.6 \pm 1.7\%$ ,  $N=18$  males) and socializing ( $43.3 \pm 2.2\%$ ) than they did in other behaviours (feeding:  $16.2 \pm 2.0\%$ ; vigilance:  $12.5 \pm 1.1\%$ ; sitting:  $3.7 \pm 0.7\%$ ; and grooming:  $1.9 \pm 0.3\%$ ). Social interactions between males were dominated by approaches, and the occurrence of aggressive interactions (fights, chases and running at each other) were rare between males (Fig. 2). Fighting between males was also unlike that reported for other species of ground squirrel. Males first approached each other, side to side rather than head first, coming to within 10 cm.

They would then jump into the air almost simultaneously, arching backwards, heads held up and facing each other, legs splayed, bodies twisting and rarely touching. No wounding was ever observed in encounters between males. The OSR was unrelated to rates of male aggression ( $r_s = -0.21$ ,  $N=31$ ,  $P=0.27$ ).

### Dominance and Access to Females

Males copulated with  $0.20 \pm 0.03$  mates per oestrus,  $N=22$  males. The most dominant males had more mates than did subordinate males (median rank correlated with median number of mates per oestrus:  $r_s = -0.56$ ,  $N=22$ ,  $P=0.006$ ). The top-ranking males (ranks 1–10) mated with a median of three females during each study year (range 1–4,  $N=11$  males), significantly more than males of lower ranks, which mated with a median of one female (range 0–3,  $N=11$ ; Mann–Whitney  $U$  test:  $U=19.5$ ,  $N=22$ ,  $P=0.008$ ).

Access to females was strongly influenced by a male's position in the linear dominance hierarchy (absolute rank correlated with median mate order:  $r_s=0.95$ ,  $N=10$ ,  $P<0.0001$ ). The first male to copulate with the female was of higher rank than the male that followed (Mann–Whitney  $U$  test: absolute rank,  $U=201.5$ ,  $N=64$ ,  $P<0.0001$ ; relative rank,  $U=213$ ,  $N=64$ ,  $P=0.0001$ ; Table 1). There was, however, no difference between the absolute or relative ranks of second and third mates ( $U=380.0$ ,  $N=57$ ,  $P=0.72$  for absolute rank). Access to females was related to male weight for first versus third mates, but not between first versus second mates (Kruskal–Wallis test:  $K=6.5$ ,  $N=78$ ,  $P=0.039$ ; a posteriori multiple comparisons,  $P<0.05$  between the first versus third mates).

### Repeated Copulations and Disruptions

The OSR was unrelated to the occurrence of repeated copulations (OSR correlated with median number of repeated copulations per oestrus:  $r_s=0.18$ ,  $N=31$ ,  $P=0.34$ ) and disruptions of copulations ( $r_s=0.09$ ,  $N=31$ ,  $P=0.63$ ). The number of males with which an oestrous female

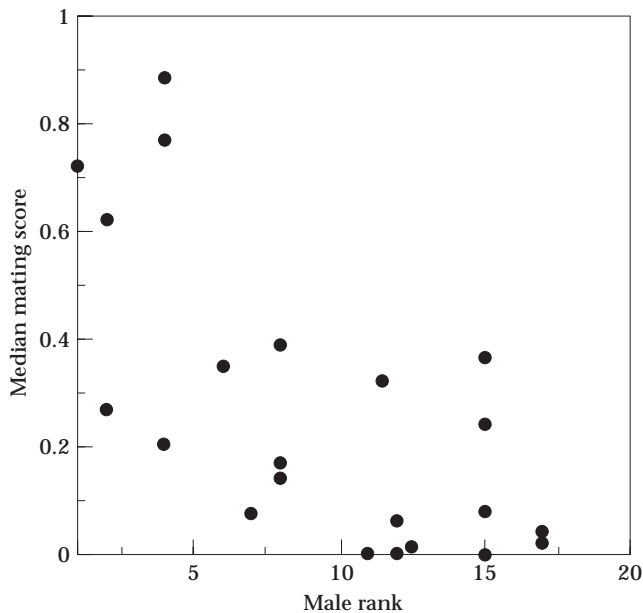


Figure 3. The median mate score for male Cape ground squirrels versus rank, calculated as the total number of copulations per female oestrus ( $N=22$  males).

copulated, however, was correlated with the median number of repeated copulations in that oestrus ( $r_s=0.54$ ,  $N=31$ ,  $P=0.0018$ ) and with the number of disruptions ( $r_s=0.78$ ,  $N=31$ ,  $P=0.0001$ ). Most males that were disrupted during their first copulation with a female later recopulated with the female (64% of 67 disruptions). The median number of repeated copulations was higher for males that were disrupted during an oestrus than males that were not disrupted (Wilcoxon signed-ranks test: one-tailed,  $T=25.5$ ,  $N=18$  oestruses in which copulations had been both disrupted (median=2, range 1–5) and undisrupted (median=1.5, range 1–4),  $P=0.047$ ).

The majority of males that disrupted copulations had not yet mated with the female (68.4%,  $N=57$  disruptions), and in 47.4% ( $N=57$ ) of disruptions, the disrupting male never gained access to the female during the oestrus. There was no relationship between a disrupting male's rank and his frequency of disruptions (weighted for number of oestruses attended; disturbances correlated with rank:  $r_s=-0.11$ ,  $N=22$  males,  $P=0.62$ ) nor between frequency of disrupting and number of mates per oestrus ( $r_s=-0.10$ ,  $N=22$ ,  $P=0.66$ ). However, mate score was significantly affected by rank ( $r_s=-0.50$ ,  $N=22$ ,  $P=0.016$ ; Fig. 3).

Although below-ground copulations were never seen to be disrupted by other males (no males were seen to enter a burrow successfully that a mating pair had entered), 72% of all above-ground copulations were disrupted (Table 1). Above-ground copulations of first mates were as likely to be disrupted as subsequent copulations (chi-square test:  $\chi^2_9=8.61$ ,  $P=0.47$ ), but first mates participated in below-ground copulations significantly more than second mates (Yates  $\chi^2_2=7.3$ ,  $P=0.026$ ; Table 1), and were thus less likely to be interrupted. The duration of above-ground copulation did not differ between first and second

mates (Mann-Whitney  $U$  test:  $U=27.0$ ,  $N=16$  above-ground copulations,  $P=0.44$ ; Table 1), nor did the duration of below-ground copulations ( $U=338.0$ ,  $N=56$  below-ground copulations,  $P=0.62$ ). The interval between the first and second mate was also not longer than the next interval ( $U=463.5$ ,  $N=63$ ,  $P=0.72$ ; Table 1).

Mate guarding, in which a male used aggressive behaviour to prevent other males from approaching the oestrous females, was rare, occurring only twice in 31 oestruses. In one case, a dominant male guarded a female that had not yet mated. He successfully sequestered her from other males and was the first male to copulate with her, but did not guard her after the copulation. In the second instance, another dominant male guarded a female with which he had not copulated, but which had already copulated with four other males. After guarding her for 2 min he left the area without copulating.

## DISCUSSION

Three factors that can lead to a male-biased operational sex ratio are a relatively long mating season, relatively short and asynchronous receptive periods of oestrous females and an actual skew in the sex ratio of sexually active adults (Dobson 1984). Cape ground squirrels do not have a biased adult sex ratio, but they do have long mating seasons and short periods of receptivity.

In North American species, where any female emerging from hibernation will be receptive within the next few days, males have a predictable source of oestrous females during the 2–3 weeks that emergence occurs (Michener 1985; Boellstorff et al. 1994; Murie 1995; Lacey et al. 1997). Oestrus in Cape ground squirrels, however, is spread out over the entire year, and individual females have multiple oestruses in a year. Because interoestrous intervals depend on whether the female loses a litter, which depends on unpredictable climatic conditions or predation (Waterman 1996), the timing of oestrus is irregular and unpredictable to males. Thus, an oestrous female is an irregular and fleeting resource, which may occur at any time during the year. Overlap of receptivity, therefore, was rare in Cape ground squirrels, unlike most species in North America where a number of females may be receptive in a single day (Boellstorff et al. 1994; Murie 1995; Michener & McLean 1996; Lacey et al. 1997). The result is a high OSR whenever a female does come into oestrus, with no male able to monopolize the female (prediction 1).

The second prediction I tested is derived from Emlen & Oring (1977), who predicted that the high OSR caused by increased asynchrony of oestrus would result in more intense competition for mates. The OSRs for Cape ground squirrels were in the same range as that of California ground squirrels, *Spermophilus beecheyi* (range 2.86–20; Boellstorff et al. 1994), and Columbian ground squirrels, *S. columbianus* (range 2.3–26.0; Murie 1995), and much higher than that of Richardson's ground squirrels, *S. richardsonii* (range 1–3.3; Michener & McLean 1996), Belding's ground squirrels, *S. beldingi* (range 1.2–6; Sherman 1989) and Idaho ground squirrels, *S. brunneus* (range 2–4; Sherman 1989). Male Cape ground squirrels,

however, appeared to be less aggressive than these North American species, which are often found with severe wounds during the breeding season (*S. columbianus*, Steiner 1970b; *S. richardsonii*, Michener 1983; *S. beldingi*, Sherman & Morton 1984; *S. beecheyi*, Boellstorff et al. 1994). The intense combat observed in these species was never seen in Cape ground squirrels, nor was there any evidence of wounding.

The value of the OSR as a predictor of the intensity of male competition in ground squirrels, however, has been questioned (Schwagmeyer & Wootner 1985; Michener & McLean 1996). Michener & McLean (1996) found that the OSR was not a good predictor of the intensity of competition, as more overt conflict was found during low OSR in Richardson's ground squirrels. Similarly, Schwagmeyer & Wootner (1985) determined that the density of female thirteen-lined ground squirrels, *S. tridecemlineatus*, was more closely related to male-male competition than was the OSR. Often, however, the OSR is determined by the average number of receptive mates over a breeding season, which may be an inappropriate measure (see Michener & McLean 1996 for a discussion). Alternatively, the OSR has often been calculated as the number of receptive males and females in the entire study area, even though these individuals would be unlikely to have access to all potential mates in the study area. I calculated the OSR as the actual number of receptive males present at the same burrow cluster as the oestrous female on the day of oestrus. Thus, only males that actually had access to the female during oestrus were included. Even with this more accurate estimate, the OSR was not related to the number of mates that a female accepted, rates of aggression, or repeated matings.

Competitive searching is a less aggressive form of competition exhibited by Cape ground squirrels (Waterman 1997). If females are widely dispersed, differential ability to locate mates may be more important to a male's reproductive success than overt conflict (Schwagmeyer & Wootner 1986). For example, female thirteen-lined ground squirrels are scattered and difficult to find, and males rarely fight over a female but instead compete indirectly through competitive searching (Schwagmeyer & Parker 1987). Female Cape ground squirrels are clustered in matrilineal kin groups and are not scattered, yet competitive searching appears to influence male copulatory success (Waterman 1997). Female social groups are dispersed throughout the home range of the male band, and the asynchrony of oestrus results in receptive females being scattered in time and space (both within and between social groups). Male Cape ground squirrels must continually travel from one female group to another and monitor the reproductive state of females, and some males are better than others at finding oestrous females (see below; Waterman 1995, 1997). Thus, competition between males was apparent through competitive searching, even though rates of aggression were low.

This interplay between spatial distribution and temporal receptivity of females caused the highly male-biased OSR and made defence of space uneconomical (prediction 3; Emlen & Oring 1977). There is no evidence of

territoriality in this species, or any site-dependent dominance (Waterman 1995). Instead of defending territories, males establish stable dominance relationships (male dominance polygyny). The highly linear dominance hierarchy, established between males through displacements independent of mating, influenced the mating success of males in a number of ways. The most dominant males had more copulations with more mates than subordinates, and participated in more below-ground copulations where disruptions were not likely to occur. Dominance was not correlated with body weight, as might be expected if dominance were determined by combat (Schwagmeyer 1990). Rank, however, is strongly correlated with age, with older males being more dominant (Waterman 1995). Even competitive searching in Cape ground squirrels is influenced by dominance, as dominant (older) males are more successful in locating oestrous females than subordinate males (Waterman 1997). This higher proficiency could be due to greater experience. Schwagmeyer & Brown (1983) found a similar pattern in thirteen-lined ground squirrels, in that older males were more likely than younger males to be found with oestrous females, and they attributed this tendency to either female preference or the older males' greater skill in locating females.

Male dominance also affected access to a female, which may be an important determinant of male reproductive success (Michener & McLean 1996). In thirteen-lined ground squirrels, the first male to mate sires most of the offspring, and although females may mate with more than two males, only the first two sire offspring (Foltz & Schwagmeyer 1989). A first-male advantage has also been documented for Belding's ground squirrels (Sherman 1989), and Arctic ground squirrels, *S. parryii* (Lacey et al. 1997) and males do not guard females in either species. In contrast, male Idaho ground squirrels that copulate longest or last with the female sire the most offspring and mate guarding does occur in this species (Sherman 1989).

Three lines of evidence suggest that a first-male advantage could exist in the Cape ground squirrel. First, the most dominant male usually had first access to the female, suggesting that this mating is most critical. Second, females only reject copulation attempts by males in the early stages of oestrus, when the reproductive cost to mating with an inferior male may be higher (Waterman 1994). Third, mate guarding was rare. Dominant males with this first-male advantage, therefore, suffer reduced competition with other band members, minimizing their reproductive cost of remaining in these groups.

The unaggressive means by which dominance is determined in Cape ground squirrels is likely to be due to the persistence of male associations. Overt conflict would be very costly in this species because males would be constantly suffering injuries, since mating can occur throughout the year. Therefore, less aggressive (and less costly) methods of establishing and maintaining dominance have developed.

Reproductive interference is another mating tactic that male Cape ground squirrels appear to employ (prediction 4). The potential for sperm competition is very high in

this species because females mate with several males during oestrus. Cape ground squirrels have large testes (4.8 cm or 19.8% of the head and body length, Waterman 1994), a trait that often occurs in species where sperm competition is important (Harcourt et al. 1981; Kenagy & Trombulak 1986). In addition, repeated copulations by males increased as females mated with more males. These repeated copulations may be a way to deposit as much sperm as possible and to displace rival sperm (Parker 1984). Although not conclusive, this evidence certainly suggests that sperm competition has possibly been a significant evolutionary influence.

Disrupting copulations is a more direct form of reproductive interference, and during oestrus, males continually interrupted each other's copulation attempts. These disruptions might be the stimulus for repeated copulations, as males attempted to complete copulations that were interrupted, and the frequency of repeated matings increased with the number of disruptions. Males that were not disrupted, however, subsequently copulated with females, so disruptions could not be the sole stimulus for such repeated copulations. Thus, males appear to attempt to maximize their own sperm input, while minimizing the sperm input of competitors, through interference.

In Cape ground squirrels, male bands roam their home range, continually checking on the status of the female groups their range encompasses. Dominance relationships among males influences their ability to find females, their access to oestrous females, and the likelihood of disruption. Dominant males, therefore, enjoy a reproductive advantage without the cost of defending females or territories and with the benefits of enhanced predator avoidance that come with grouping (Waterman 1997). Subordinate males enjoy the same benefits of grouping, and as they would probably be unable to defend against dominant males, at least have potential access to females by roaming in these amicable male bands. Thus, the predictable location of females in space, the irregularity and unpredictability of their oestrus, and the ability to breed throughout the year have led to a unique male social organization in this species.

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#### References

- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–267.
- Black, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). In: *Evolutionary Biology* (Ed. by T. Dobzhansky, M. K. Hecht & W. C. Steere), pp. 305–322. New York: Appleton-Century-Crofts.
- Boellstorff, D. E., Owings, D. H., Penedo, M. C. T. & Hersek, M. J. 1994. Reproductive behaviour and multiple paternity of California ground squirrels. *Animal Behaviour*, **47**, 1057–1064.
- Clutton-Brock, T. H. 1989. Mammalian mating systems. *Proceedings of the Royal Society of London, Series B*, **236**, 339–372.
- Clutton-Brock, T. H. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.
- Conover, W. J. 1980. *Practical Nonparametric Statistics*. New York: J. Wiley.
- Davis, L. S. & Murie, J. O. 1985. Male territoriality and the mating system of Richardson's ground squirrels. *Journal of Mammalogy*, **66**, 268–279.
- Dobson, F. S. 1984. Environmental influences of sciurid mating systems. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 229–249. Lincoln, Nebraska: University of Nebraska Press.
- Emlen, S. T. 1976. Lek organization and mating strategies in the bullfrog. *Behavioral Ecology and Sociobiology*, **1**, 283–313.
- 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 behaviour in the African ground squirrel, *Xerus erythropus* (E. Geoff.). *Zeitschrift für Tierpsychologie*, **23**, 190–216.
- Foltz, D. W. & Schwagmeyer, P. L. 1989. Sperm competition in the thirteen-lined ground squirrel: differential fertilization success under field conditions. *American Naturalist*, **133**, 257–265.
- Harcourt, A. H., Harvey, P. H., Larson, S. G. & Short, R. V. 1981. Testis weight, body weight and breeding system in primates. *Nature*, **293**, 55–57.
- Herzig-Straschil, B. 1978. On the biology of *Xerus inauris* (Zimmerman, 1780) (Rodentia, Sciuridae). *Zeitschrift für Säugetierkunde*, **43**, 262–278.
- Kenagy, G. J. & Trombulak, S. C. 1986. Size and function of mammalian testes in relation to body size. *Journal of Mammalogy*, **67**, 1–22.
- Lacey, E. A., Wieczorek, J. R. & Tucker, P. K. 1997. Male mating behaviour and patterns of sperm precedence in Arctic ground squirrels. *Animal Behaviour*, **53**, 767–779.
- Lehner, P. 1979. *Handbook of Ethological Methods*. New York: Garland Press.
- Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground dwelling sciurids. In: *Advances in the Study of Mammalian Behaviour* (Ed. by J. Eisenberg & D. G. Kleiman), pp. 528–572. Shippensburg, Pennsylvania: American Society of Mammalogists.
- Michener, G. R. 1985. Chronology of reproductive events for female Richardson's ground squirrels. *Journal of Mammalogy*, **66**, 280–288.
- Michener, G. R. & McLean, I. G. 1996. Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. *Animal Behaviour*, **52**, 743–758.
- Murie, J. O. 1995. Mating behavior of Columbian ground squirrels. I. Multiple mating by females and multiple paternity. *Canadian Journal of Zoology*, **73**, 1819–1826.
- Parker, G. A. 1984. Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 1–60. Orlando, Florida: Academic Press.

- Schwagmeyer, P. L. 1984. Multiple mating and intersexual selection in thirteen-lined ground squirrels. In: *The Biology of Ground-dwelling Squirrels* (Ed. by J. O. Murie & G. R. Michener), pp. 275–294. Lincoln, Nebraska: University of Nebraska Press.
- Schwagmeyer, P. L. 1990. Ground squirrel reproductive behaviour and mating competition: a comparative perspective. In: *Contemporary Issues in Comparative Psychology* (Ed. by D. Dewsbury), pp. 175–196. Sunderland, Massachusetts: Sinauer.
- Schwagmeyer, P. L. & Brown, C. H. 1983. Factors affecting male-male competition in thirteen-lined ground squirrels. *Behavioral Ecology and Sociobiology*, **13**, 1–6.
- Schwagmeyer, P. L. & Parker, G. A. 1987. Queuing for mates in thirteen-lined ground squirrels. *Animal Behaviour*, **35**, 1015–1025.
- Schwagmeyer, P. L. & Wootner, S. J. 1985. Mating competition in an asocial ground squirrel, *Spermophilus tridecemlineatus*. *Behavioral Ecology and Sociobiology*, **17**, 291–296.
- Schwagmeyer, P. L. & Wootner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Animal Behaviour*, **31**, 359–364.
- Sherman, P. W. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. *Nature*, **338**, 418–420.
- Sherman, P. W. & Morton, M. L. 1984. Demography of Belding's ground squirrels. *Ecology*, **65**, 1617–1628.
- Steiner, A. L. 1970a. Etude descriptive de quelques activites et comportements de base de *Spermophilus columbianus columbianus* (Ord.). Part I. *Revue Comparative de l'Animal*, **4**, 3–21.
- Steiner, A. L. 1970b. Etude descriptive de quelques activites et comportements de base de *Spermophilus columbianus columbianus* (Ord.). Part II. *Revue Comparative de l'Animal*, **4**, 23–42.
- Waterman, J. M. 1994. The social organization of the Cape ground squirrel *Xerus inauris*. Ph.D. thesis, University of Minnesota.
- Waterman, J. M. 1995. The social organization of the Cape ground squirrel. *Ethology*, **101**, 130–147.
- Waterman, J. M. 1996. Reproductive biology of a tropical, non-hibernating ground squirrel. *Journal of Mammalogy*, **77**, 134–146.
- Waterman, J. M. 1997. Why do male Cape ground squirrels live in groups? *Animal Behaviour*, **53**, 809–817.