

Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*

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Summary

1. In social mammals where group members cooperate to detect predators and raise young, members of small groups commonly show higher mortality or lower breeding success than members of large ones. It is generally assumed that this is because large group size allows individuals to detect or repel predators more effectively but other benefits of group size may also be involved, including reduced costs of raising young and more effective competition for resources with neighbouring groups.

2. To investigate the extent to which predation rate affects survival, we compared mortality rates in two populations of suricates (*Suricata suricatta*), one living in an area of high predator density (Kalahari Gemsbok Park) and one living in an area of relatively low predator density (neighbouring ranchland). Most aspects of feeding ecology and growth (including time spent feeding, daily weight gain, growth, adult body weight, breeding frequency and neonatal mortality) were similar in the two populations. In contrast, mortality of animals over 3 months old was 1.7 times higher in the Park than on ranchland.

3. Mortality of juveniles between emergence from the natal burrow and 6 months of age was higher in small groups than large ones in the Park but significantly lower in small groups than large ones on ranchland. Adult mortality declined in larger groups in both areas.

4. The tendency for survival to be low in small groups had far-reaching consequences for the risk of group extinction. During a year of low rainfall in the Park, all groups of less than nine animals became extinct and population density declined to around a third of its initial level. We argue that high group extinction rates are to be expected in species where survival declines in small groups and mortality rates are high.

Key-words: cooperative breeding, demography, mammals, mortality.

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Introduction

In social mammals where group members do not cooperate to rear offspring or to defend the group against predators, breeding success frequently declines with increasing group size while juvenile mortality increases (Clutton-Brock, Albon & Guinness 1982; van Schaik 1983). In contrast, where adults cooperate to rear young and detect predators, breeding success and survival commonly increase in large groups (Macdonald 1979; Moehlman 1979; Jennions &

Macdonald 1994). For example, in dwarf mongooses *Helogale parvula* Sundevall 1846, mortality of juveniles and adults is lower in large groups than in small ones (Rasa 1987a,b; Rasa 1989a,b; Rood 1990). Presumably, groups of cooperative breeders must sometimes grow to a size at which competition for resources reduces survival (Brown 1987) but few empirical studies of cooperative breeders have so far found evidence of this (Stacey & Koenig 1990).

The tendency for breeding success and survival to increase in large groups in cooperative breeders is commonly attributed to the effects of group size on predator detection and predation risk (Rasa 1987a; 1989b; Rood 1990). However, group size may have other beneficial consequences which could generate

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similar correlations. In particular, growing young may receive more food or better protection against infanticidal attacks by immigrants or neighbours, while the per capita workload of breeders and helpers is commonly reduced so that reductions in adult mortality might be expected (Brown 1987; Clutton-Brock *et al.* 1988; Packer *et al.* 1988). The ideal way to determine whether predation-related benefits are responsible for correlations between group size and survival would be to establish the presence of a relationship between group size and survival, and subsequently to eliminate predators, monitoring changes in the relationship between group size and survival. Though experiments of this magnitude are sometimes feasible (Krebs *et al.* 1995), more usually they are not. An alternative approach is to compare survival between prey populations living in sites where predators are abundant and sites where predators have been reduced or removed as a result of human interference and comparisons of this kind have proved useful in investigating the effects of predation on mortality in several mammals. For example, the density and breeding success of moose *Alces alces* L. varies inversely with the extent to which (human) hunting pressure reduces the density of their principal predators (Gasaway *et al.* 1992). Similarly, litters of cheetah, *Acinonyx jubatus* Schreber 1776 cubs in the Etosha National Park (where large carnivores are abundant) fall from an average of four cubs at birth to around two cubs by the end of the first year, while on neighbouring ranchland, litter sizes remain at four throughout the first year of life (McVitie 1979; Laurenson 1995).

In this paper, we compare mortality between two populations of the cooperative mongoose, *Suricata suricatta* Schreber 1776. One population, in the Kalahari Gemsbok Park, South Africa ('Park'), was subject to frequent predation while, in the other area ('Ranch'), which consisted of unimproved ranchland outside the Park, predator numbers had been reduced by human interference. Our analysis compares the relationship between mortality at different stages of the lifespan and group size in these two sites.

Methods

STUDY AREAS AND POPULATIONS

Reproduction and mortality periods were monitored in 17 groups of suricates living in the southern Kalahari between April 1993 and April 1996 (see Clutton-Brock *et al.* 1998). Ten groups, ranging in size from 5 to 14 adults occupied ranges along the (dry) bed of the Nossob river in the Kalahari Gemsbok National Park between Kwang Pan (25°17'S; 20°32'E) and Cheleka, 60 km to the south. A further seven groups, ranging in size from 3 to 10 adults, occupied ranges on fenced but uncultivated ranchland near Van Zyl's Rus (25°8'S; 20°49'E) along the (dry) bed of the

Kuruman river, 120 km to the south-east of Nossob. Both study areas consisted of similar habitat, which included stretches of dry river-bed and portions of vegetated dunes lying on either side, covered with a combination of annual and perennial grasses including *Eragrostis*, *Aristida*, *Stipagrostis* and *Schmidtia* species, interrupted by dispersed *Acacia* and *Boscia* trees (Doolan & Macdonald 1996a,b; Clutton-Brock *et al.* 1999). Groups varied in the timing and extent of habituation, so that not all forms of data could be collected for all groups and periods of data collection differed between groups. As a result, sample sizes varied between analyses.

Both study areas experienced a hot, wet summer (October–April) when most rain fell, followed by a cold, dry winter (May–September) (Mills 1990; Doolan & Macdonald 1996a,b). Much of the rain fell in a limited number of heavy storms, so that the timing of rainfall differed between study areas. Average annual rainfall calculated over 20 years was 240 mm in the Park and 217 mm for the Ranch. During the 5 years of the study, annual rainfall in the Park was 234 mm (1992/93), 375 mm (1993/94), 31 mm (1994/95), 262 mm (1995/96) and 276 mm (1996/97), while annual rainfall at the Ranch was 92 mm (1992/93), 301 mm (1993/94), 132 mm (1994/95), 187 mm (1995/96) and 326 mm (1996/97). Thus, there was little relationship between rainfall at the two sites in the same year. In particular 1994/95 was a year of unusually low rainfall in the Park ($\approx 10\%$ of the long-term average), while rainfall in this year at the Ranch was closer to the long-term average.

RECORDING METHODS

To provide a comparison of the relative numbers of medium sized carnivores and raptors in the two study areas, we recorded sightings of each species while driving 150 km through each study area between 6 am and 9 am in each month. In addition, we collected *ad lib* records of sightings of each species during 200 hours per month when we were walking with foraging suricate groups and standardized these to give the number of sightings per species per 100 h of observation. Data used for comparisons were summarized by month and covered the same period in the two study sites (August 1994–November 1995 for the road transects and January–December 1995 for the time-based data).

In both areas, suricate groups were located, counted and habituated to close observation by daily visits to the burrows. Approximately 75% of adults were caught and immobilized, while pups could be caught at the natal burrow once adults were habituated. All individuals could be recognized. Eight groups in the Park and six at the Ranch allowed observers to walk within a few metres of them while they foraged. In these groups, adults were trained to stand on an electronic platform balance by scattering crumbs of hard-

boiled egg in sand on a tray and could be weighed immediately after emergence from the sleeping burrow and last thing before entering the burrow in the evening.

Since most food items were caught after prolonged digging and the animals were extremely selective in their choice of feeding sites, it was not feasible to obtain direct measures of food availability at each site. However, as we could weigh animals at the start and end of each day (see above), we could compare daily weight gains between the two areas, providing an indication of variation in food availability. Measures of weight gain were supplemented by estimates of the proportion of daytime that the animals spent foraging, based on half-hourly scans of activity collected between 9 am and 5 pm and records of the number of food items caught per hour.

Around 80% of breeding attempts involved the dominant female in the group and 20% involved subordinate females, which usually bred synchronously with the dominant (Clutton-Brock *et al.* 1999). After birth, groups continued to use the natal burrow until the pups were 5–6 weeks old and were capable of travelling with the group. While they remained at the natal burrow, pups were guarded by a babysitter, which often remained at the burrow throughout the day and fed little (Clutton-Brock *et al.* 1998a). Subordinates of both sexes contributed to babysitting, while breeding females and dominant males rarely did so. After leaving the natal burrow, pups were fed by other group members until they were at least 3 months old. All group members participated in feeding pups, though dominant males fed them less than other individuals.

Litter size was counted at first emergence, around 21 days after birth (Clutton-Brock *et al.* 1999). Comparison of counts of foetuses based on ultrasonic imaging of pregnant females indicate that few pups are lost in the interval between birth and emergence, unless the entire litter dies (P. Brotherton, personal communication). Pups were weighed within a few days of emergence and were then weighed at least once a month after this. During the first 100 days of life, their growth rates were approximately linear and we used the (least squares) regression coefficient of weight on age (in days) to compare growth rates of pups born in different groups (see below). Animals reached adult weight (650 g) soon after 12 months, though less than 10% of females that survived to 2 years bred before they were 24 months old (Clutton-Brock *et al.*, unpublished). We classified animals as pups from 0 to 3 months, as juveniles from 3 to 12 months, and as adults at 12 months and over. In our analysis of the effects of group size on pup and juvenile survival, we used survival from emergence to 6 months because this covered the period when pups and juveniles depended on helpers. As in dwarf mongooses (Rasa 1987a; Rood 1989), groups contained one female and one male that were dominant to other group members of

the same sex. Dominant animals displaced other individuals when artificial food was provided, marked the substrate with their anal glands more frequently than other individuals and initiated a high frequency of digging attempts.

Groups were located and counted every 2 weeks. Animals rarely left their natal group before they were a year old and dispersing animals commonly left at the same time as several other individuals (Clutton-Brock *et al.* 1998b). Females were usually reluctant to leave their natal group and only did so when expelled by the dominant female (Clutton-Brock *et al.* 1998b). Males left of their own volition and typically began to forage separately from the group during the weeks before they dispersed. After leaving the group, they were usually seen at other burrows within the group's range before leaving the area. Animals were recorded as having died if we observed a predation event or saw their carcass or if they had not previously foraged away from the group or been attacked and disappeared suddenly on their own and were not seen again. They were recorded as having dispersed if they were no longer present in the group and had subsequently been seen on their own or with another group (Clutton-Brock *et al.* 1998b).

STATISTICAL ANALYSIS

Non-parametric statistical tests were used to compare behavioural parameters: U denotes a Mann–Whitney U -test (Siegel 1956), T , a Wilcoxon Matched Pairs Signed Ranks Test and r_s , a Spearman Rank Order Correlation Coefficient (Siegel 1956) and t -tests (Snedecor & Cochran 1967) were used to compare body weights. Where we use parametric tests we quote means and standard errors, while for non-parametric tests we quote medians and ranges or interquartile ranges (IQR). Since neither population showed a well-defined breeding season (Clutton-Brock *et al.* 1999), we were unable to compare mortality between discrete cohorts. To compare mortality between years, we based our calculations on the mean number of animal-days per recorded death in each year. Annual mortality was calculated as total deaths

$$\text{Annual mortality} = 1 - [1 - (\text{Total deaths}/\text{Total days})]$$

In our analysis of the relationship between group size and mortality, group size was the average number of animals over 3 months in the group over the year. Group size was calculated by dividing the number of animal days by the number of days in the period during which the group was monitored.

Analysis of the effects of group size on survival involved the use of generalized linear modelling facilities in Genstat 5 Committee 1987 3.1 (Copyright 1992, Lawes Agricultural Trust; Payne 1993). We ran the model specifying binomial errors appropriate for percentage mortality (Crawley 1994) since we were principally interested in variation in the rate of mortality.

For mortality to 6 months, the dependent variable was number of deaths in a litter while the binomial denominator was the number of individuals in the litter at emergence. For mortality of adults, the dependent variable was the number of deaths while the number of animal days was the binomial denominator. Using binomial errors, Genstat carries out a weighted regression using the individual sample sizes (binomial denominators) as weights and the logit function to ensure linearity. We quote both the t -statistic which determines whether the slope of the model differs significantly from zero and the χ^2 statistic which shows whether the variable in question explains a significant amount of variation in the model. The 95% confidence limits for the fitted points of the models were calculated as outlined in Crawley (1994). Analysis of the effects of group size on growth was carried out using least squares linear regression since growth rates are continuous variables and the relationship between group size and growth rate showed no signs of non-linearity.

Results

PREDATORS

Both methods of estimating predator numbers showed that the density and diversity of potential predators was substantially higher in the Park than at the Ranch. Total predators seen per km: Ranch, $n = 14,14$, $t = 4.85$, $P < 0.001$; total predators seen per hour: $n = 14,14$ samples, $t = 4.19$, $P < 0.001$; (Table 1). Predators in the Park included lion *Panthera leo* L.1758, leopard *Panthera pardus* L.1758, cheetah *Acinonyx jubatus* Schreber 1776, caracal *Felis caracal* Schreber 1776, wild cat *Felis lybica* Foster 1780, black-backed jackal *Canis mesomelas* Schreber 1778, honey badger *Mellivora capensis* Schreber 1776 and Cape fox *Vulpes chama* A.Smith 1833 (Mills 1990). Of these, jackals were probably the most common predator of suricates. Raptors were abundant in the Park and included breeding populations of martial eagles *Polemaetus bellicosus* Daudin 1890, tawny eagles *Aquila rapax* Temminck 1823, bateleur eagles *Terathopius ecaudatus* Daudin 1800, brown snake eagles *Circaetus cinereus* Vieillot 1818, black-breasted snake eagles *Circaetus pectoralis* Smith 1829 and pale chanting goshawks *Melierax canorus* Thunberg 1799. Common migrants included steppe eagles *Aquila nipalensis* Hodgson 1833, booted eagles *Hieraetus pennantus* Gmelin 1788 and steppe buzzards *Buteo buteo* L.1758. Jackals, martial eagles and tawny eagles were the most dangerous predators: all three predators were seen to attempt to take suricates on one occasion during the course of the study and the suricates responded rapidly and strongly to all three. In addition, suricate carcasses were commonly found at the nests of martial eagles (J. Herholdt, unpublished data) and the animals were particularly alarmed by this species. Pale chant-

Table 1. Mean sightings of predators in the Park and at the Ranch (a) per 100 km of road census, (b) per 100 hours of group watches. Figures shown below each value are standard errors. Sightings per 100 km of road were calculated across 15 monthly drives along a fixed route; sightings per hour were calculated over 15 samples of 200 hours of observation for the same period (August 1994–November 1995)

Location	Black backed					Pale chanting					Total
	jackal	Honey badger	African wildcat	Martial eagle	Tawny eagle	Bateleur	Whalbergs eagle	Booted eagle	Gymnogene	goshawk	
(a) Park	23.46 ± 0.41	0.10 ± 0.36	0.29 ± 0.49	0.67 ± 0.88	2.21 ± 4.29	3.27 ± 4.78	0.00 ± 0.00	0.10 ± 0.36	0.10 ± 0.36	5.48 ± 2.24	35.68 ± 18.97
Ranch	0.03 ± 0.09	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.15	0.00 ± 0.00	0.02 ± 0.64	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.77 ± 1.26	1.94 ± 1.19
(b) Park	10.01 ± 9.75	1.11 ± 2.17	0.83 ± 1.51	2.22 ± 3.85	3.34 ± 4.98	1.11 ± 1.64	0.29 ± 0.96	0.00 ± 0.00	0.00 ± 0.00	1.39 ± 2.23	20.29 ± 11.24
Ranch	0.00 ± 0.00	0.00 ± 0.00	0.75 ± 2.59	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.74 ± 6.87	4.49 ± 6.38

ing goshawks were also a common predator of juveniles and were relatively common in both areas (Table 1).

POPULATION DENSITY AND GROUP SIZE

There was no significant difference in group size between the study areas. In April 1994, the median size of 10 groups being monitored in the Park was 11, IQR 7.2–12.8 (excluding pups), while the median size of eight groups monitored at the Ranch was 7, IQR 6.25–9.25 ($U = 29$, $n = 10,8$, $P = 0.33$). Groups occupied partially overlapping ranges of 2–5 km² in both areas. On the Ranch, these were contiguous while, in the Park, there were unoccupied areas between group territories (Clutton-Brock *et al.* 1999). As a result, population density (calculated including unoccupied areas) was lower in the Park (approximately 0.95 animals km⁻²) than on the Ranch (1.69 animals km⁻²).

Group composition was similar in both areas. The 10 groups counted in the Park in April 1994 had an average sex ratio of 1.21 (males:females) among adults and of 0.92 among juveniles while the ratio of juveniles to adults was 1.10. Seven groups counted at the Ranch at the same time had a sex ratio of 1.09 among adults, 0.90 among juveniles and a juvenile/adult ratio of 0.82. The 10 groups in the Park contained 11 females that had given birth in the last year while the seven groups in the Ranch contained 9 females that had given birth in the past year.

GROUP MEMBERSHIP

Group membership was stable from day to day but both females and males left their natal groups from time to time. Subordinate adult females were commonly expelled from groups during the later stages of the dominant female's pregnancy (Clutton-Brock *et al.* 1998b). Males usually left groups of their own volition during their second or third year of life. Over the study period, eight adult males and 11 adult females left groups in the Park while 25 adult males and 19 adult females left groups at the Ranch. Relative rates of group leaving were calculated by dividing these totals by the number of animal-years for which individuals in each category were monitored. Rates of group leaving per animal year did not differ between the sexes (0.250 vs. 0.248, $\chi^2 = 0.008$, $P > 0.90$) nor between groups of fewer vs. more than six individuals (0.276 vs. 0.186, $\chi^2 = 0.187$, d.f. = 1, $P > 0.10$). When data for both sexes were combined, there was a tendency for leaving rates to be higher at the Ranch than the Park (0.284 vs. 0.194 per animal year, $\chi^2 = 2.71$, d.f. = 1, $P = 0.10$).

In both areas, around half of all emigrants returned to their natal group within three months of leaving it (Clutton-Brock *et al.* 1998b). Females that left their groups permanently either died or joined emigrant males and founded a new group, while males com-

monly immigrated into established groups as subordinates. Of 15 females that left their natal group and did not return to it, eight disappeared from our study population, seven became founder members of a new group and none joined groups with established breeding females. In contrast, of 33 males that left their natal group and did not return to it, 19 disappeared from the study area, six founded new groups and eight immigrated into established breeding groups.

While females were never seen to immigrate into established breeding groups, they commonly inherited the breeding position in their natal group. Of 12 dominant females whose origin was known, seven (58%) acquired the dominant role by remaining in their natal group and five did so by leaving and founding a new group. In contrast, of 19 dominant males whose origin was known, only two (11%) inherited the dominant position in their natal group, five were founding members of a new group and 12 (63%) had immigrated into the group as adults.

GROWTH AND WEIGHT GAIN

There was no evidence of any consistent difference in the percentage of daytime allocated to foraging or in daily weight gain between the two populations. The mean proportion of time spent foraging by members of nine different groups in each area did not differ significantly (Park: median = 44.3%, IQR 33.8–50.1; Ranch: median = 56.3, IQR 36.4–73.4) ($U = 28$, $n = 9,9$ groups, $P = 0.27$). Daily weight gain (measured as the difference between weight at emergence in the morning and weight at the end of the day) was also similar, averaging 25 ± 18.9 g day⁻¹ in the Park and 27.5 ± 14.1 g day⁻¹ on the Ranch for samples of nine and 13 subordinate adults, respectively ($t = 0.36$, $n = 9,13$ individuals, $P = 0.73$).

The growth and development of pups was similar in the two areas. The mean weights of recently emerged pups calculated across mean values for different litters did not differ significantly between them (Park: 106.7 g ± 25.8 , $n = 16$; Ranch: 122.8 ± 42.9 , $n = 6$) ($t = 1.09$, $n = 16,6$ litters, $P = 0.29$). Pups first emerged at around three weeks of age in both areas (Park: emergence date = 20.3 ± 3.9 days, range = 14–27; Ranch: emergence date = 18.0 ± 4.8 days, range = 9–28) ($U = 101.5$, $n = 11,26$ litters, $P = 0.16$) and left the burrow and began to move with the group around seven days afterwards (Park: median = 7 days, range = 2–14; Ranch: median = 7 days, range = 1–19; $U = 85$, $n = 14,14$ litters, $P = 0.87$). There was no significant difference in pup growth rates during the first 3 months of life: mean mass increase calculated across litters averaged 4.5 g day⁻¹ in the Park and 3.8 g day⁻¹ at the Ranch ($t = 1.49$, $n = 12,6$ litters, $P = 0.157$). Finally, the average weight of most categories of adults was similar in the two areas (Table

2). Dominant females averaged 721 ± 51 g in the Park compared to 720 ± 87 g at the Ranch ($t = 0.03$, $n = 6,10$ individuals, $P = 0.98$) while subordinate females averaged 640 ± 67 g in the Park compared to 632 ± 95 g at the Ranch ($t = 0.21$, $n = 9,9$ individuals, $P = 0.84$). Dominant males were heavier in the Park (808 ± 100 g) than on the Ranch (692 ± 88 g) ($t = 2.46$, $n = 8,8$ individuals, $P < 0.05$) though subordinate males in the Park ($= 680 \pm 100$ g) did not differ in weight from subordinates on the Ranch (663 ± 56 g) ($t = 0.55$, $n = 12,14$ individuals, $P = 0.59$).

REPRODUCTION AND MORTALITY

Breeding frequency was similar in the two study areas throughout most of the period. In the Park, groups produced a median of 0.11 litters per group per month over the whole study period (IQR calculated across groups = 0.09–0.13), while at the Ranch they produced a median of 0.11 litters per group per month (IQR = 0.01–0.24) ($U = 79$, $n = 11,16$ groups, $P = 0.66$). Median litter size at emergence was 4 with an IQR of 1–5 in both areas ($U = 336.5$, $n = 24,19$ litters, $P = 0.84$).

Mortality between birth and emergence was also similar in the two areas. In the Park, 20.6% (7 of 34) litters failed and all neonates died before emergence while 22.5% (9 of 40) litters failed at the Ranch (Fisher's Exact Test: $P = 0.89$). Of 119 pups from 27 litters whose survival we were able to monitor in the Park, 89% survived to 2 weeks and 70% to 8 weeks, while of 123 pups from 40 litters monitored at the Ranch, 89% survived to 2 weeks and 69% to 8 weeks.

In contrast, mortality of animals over 3 months was 1.7 times higher in the Park (0.62) than at the Ranch

(0.38) (Fig. 1a). In the Park, adults (> 1 years) showed a mean mortality rate of 0.68 calculated across three years while, at the Ranch, the mean mortality rate of adults calculated over the same period was 0.32 (G -test with Yates' correction: $\chi^2 = 93.3$, $P < 0.001$). In neither area was there a significant difference in mortality between the sexes (Park: $\chi^2 = 1.587$, $P = 0.208$; Ranch: $\chi^2 = 0.37$, $P = 0.54$; see Fig. 1b). In the Park,

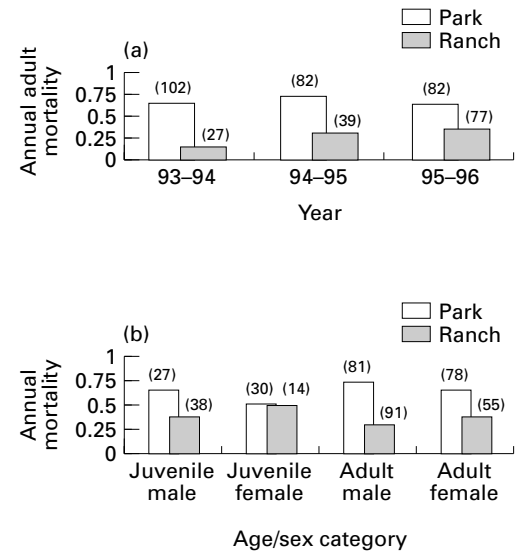


Fig. 1. (a) Mean annual mortality for adults during 3 years in the park and at the Ranch. Figures above each histogram show the number of animals monitored. No measures of variance are shown since all animals in the study population were included and the figure shows actual rates rather than estimates. (b) Mean annual mortality for male and female juveniles (3–12 months) and adults (> 12 months) in the Park and at the Ranch calculated across years (April 1993 and April 1996). Figures above each histogram show the number of individuals monitored.

Table 2. Mean body mass of suricates of different ages, sexes and dominance categories. Dominant and subordinate categories only include adults (individuals over a year old)

	All			Males			Females		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Park									
Dominants	771	87.0	14	808	86.0	8	721	51.0	6
Subordinates	651	72.0	21	659	70.0	12	640	67.0	9
6 Months	515	69.1	19	533	68.7	14	465	44.2	5
3 Months	372	62.1	28	386	65.1	20	338	38.8	8
Ranch									
Dominants	704	90.0	18	692	88.0	8	720	87.0	10
Subordinates	659	92.0	17	679	70.0	8	632	95.0	9
6 Months	438	68.3	21	464	57.8	10	415	71.2	11
3 Months	325	31.7	11	330	23.9	8	310	50.8	3

there was no difference in mortality between adults and juveniles (Park: $\chi^2 = 0.245$, $P = 0.65$) but, at the Ranch, juveniles showed significantly higher mortality than adults ($\chi^2 = 4.02$, $P = 0.045$; see Fig. 1b).

GROUP SIZE, REPRODUCTION AND MORTALITY

There was no significant difference in breeding frequency between small and large groups in either area. In the Park, small groups (≤ 6 individuals excluding pups, $n = 15$) produced 0.17 ± 0.13 litters per month while large groups (> 6 individuals, $n = 6$) produced 0.11 ± 0.08 ($t = -0.913$, $P = 0.396$). On the Ranch, small groups ($n = 7$) produced 0.21 litters per month while large groups ($n = 4$) produced 0.19 litters per month ($t = -0.238$, $P = 0.827$). Mortality between birth and emergence did not vary with group size in either area. In the Park, 25% of litters produced by small groups failed to emerge while 15.4% of litters produced by large ones failed ($\chi^2 = 0.012$, $P = 0.91$). On the Ranch, 25% of litters produced by small groups failed to emerge while 22.2% of litters produced by large groups failed ($\chi^2 = 0$, $P = 1$).

In contrast, mortality of pups and juveniles between emergence and 6 months varied with group size in both study areas. In the Park, juvenile mortality declined in larger groups (logistic regression: $\chi^2 = 6.7$, d.f. = 1, $P < 0.05$, t ratio = -2.29 , d.f. = 8, $P < 0.05$) (see Fig. 2a). In contrast, juvenile mortality on the Ranch increased with group size (Fig. 2b; logistic regression: $\chi^2 = 13.55$, d.f. = 1, $P < 0.01$, t ratio = 3.01 , d.f. = 7, $P < 0.01$).

Adult mortality declined with increasing group size in both areas. In the Park, there was a non-significant tendency for adult mortality to decline with group size in the sample overall (logistic regression: $\chi^2 = 2.07$, d.f. = 1, $P > 0.05$, t ratio = -1.37 , d.f. = 10, $P < 0.1$; Fig. 2c), but during the period between June 1994 and June 1995 when the population size declined rapidly (see below), there was a significant decline in adult mortality in larger groups (Fig. 2d; logistic regression: $\chi^2 = 10.313$, d.f. = 1, $P < 0.005$, t ratio = 3.25 , d.f. = 8, $P < 0.01$). On the Ranch, adult mortality declined with increasing group size over the whole period (logistic regression: $\chi^2 = 43.05$, d.f. = 1, $P < 0.001$, t ratio = 6.28 , d.f. = 11, $P < 0.001$; Fig. 2e). These associations were not caused by changes in group size and survival between years, for there was no significant difference in survival between years in either site (see Fig. 1a).

GROUP EXTINCTION

The tendency for animals living in small groups to show high mortality had far reaching effects on the dynamics of groups. In 1994/5, annual rainfall in the

Park fell to around 10% of the long-term average (31 mm) while rainfall at the Ranch remained close to average levels. Low rainfall in the Park was not associated with any significant increase in overall annual mortality, which was not significantly higher in 1994/95 than in the other 2 years combined ($\chi^2 = 0.73$, $P = 0.39$; see Fig. 1a). However, during 1994/45, there was a virtual cessation of breeding in the Park: the rate of litter production fell from 0.28 ± 0.190 litters per group per month in 1993/94, to 0.03 ± 0.05 litters per group per month in 1994/95, and was significantly lower than at the Ranch, where groups averaged 0.16 ± 0.03 litters per group per month over the same period ($U = 7$, $n = 11,8$ groups, $P < 0.01$). When data from the 5 years covered by this study in the Park were combined with similar data collected in the same area between 1984 and 1988 by Doolan and Macdonald, breeding frequency declined with rainfall ($r_s = 0.62$, $n = 9$, $P = 0.008$; Fig. 3). Mortality of litters before emergence was also high in the Park during 1994/95: of the three litters born in the Park during this period, one failed before emergence, a total of three pups emerged from the other two litters and all three died before 6 months. As a result of these changes, the ratio of juveniles:adults in the Park fell from 0.43 in 1993/94 to 0.19 by April 1995.

Combined with the high levels of mortality, the cessation of breeding in the Park led to a rapid decline in population size from 0.95 animals km^{-2} in April 1994 to 0.32 km^{-2} by May 1995. Six of the 10 groups using the study area in April 1994 became extinct in the course of the year and the median size of the remaining groups fell from 9.5 adults in April 1994 to 3.2 in May 1995 (Clutton-Brock *et al.* 1999). No similar changes occurred at the Ranch: group size remained approximately constant (April 1994: median = 11.0, $n = 10$; May 1995: median = 10, $n = 10$) and none of the 10 study groups became extinct.

The tendency for members of small groups to show high levels of mortality had an important influence on the frequency of group extinction. As might be expected, the size at which groups entered the period of drought in 1994 was related to their probability of survival: all of the five groups that entered 1994/95 at sizes of 9 animals or below became extinct during the year while only one of the five groups of 10 or more animals did so (Binomial test, $P < 0.05$). To examine the effects of the relationship between group size and mortality on the probability of group extinction, we used the observed distribution of mortality in groups of different sizes in 1994/95 (Fig. 4a) to calculate the probability of an individual dying at each group size during the year (Fig. 4b) and used this to calculate the probability that the groups of different sizes would become extinct during the year in the absence of recruitment. Figure 4c compares the probability of group extinction for groups of different size estimated in this way with the probability based on calculations

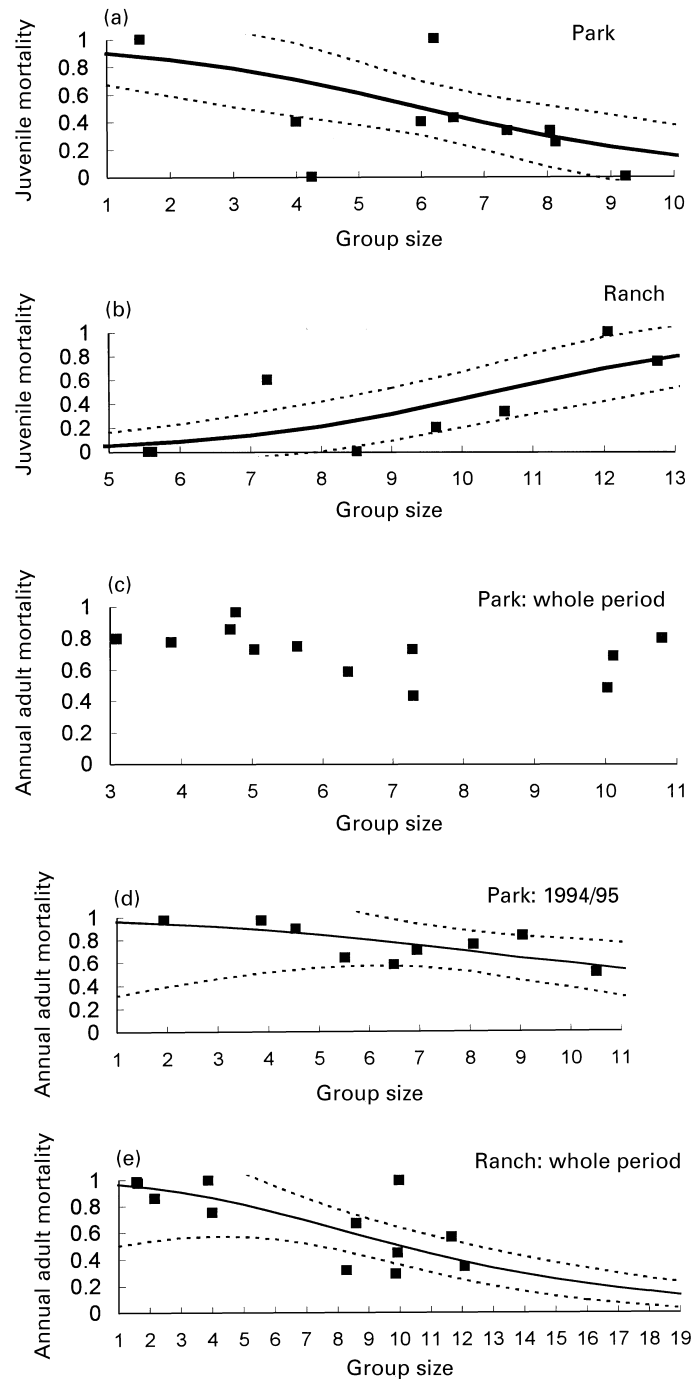


Fig. 2. Annual rates of mortality for: (a) juveniles between emergence and 6 months in the Park, April 1993 – April 1996; (b) juveniles between emergence and 6 months, April 1993 – April 1996 on the Ranch; (c) adults (> 12-month-old), April 1993–April 1996 in the Park; (d) adults, April 1994–April 1995 in the Park; (e) adults, April 1993–April 1996 on the Ranch. Solid lines show predicted relationship from the logistic regression analysis, dashed lines show 95% confidence limits.

assuming stochastic variation in mortality across all group sizes. This emphasizes the extent to which the relationship between group size and mortality contributes to the risk of group extinction. Had reproduction persisted, the effects of group size on adult

survival might have had a lesser influence on group extinction rates, though the negative effects of small group size on juvenile survival would have contributed to the increased risk of extinction in small groups.

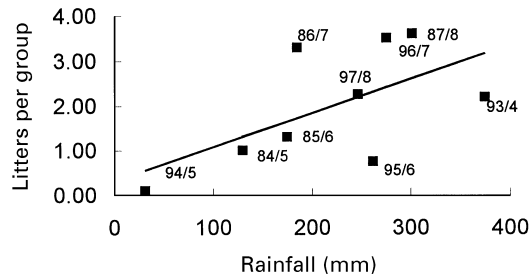


Fig. 3. Mean numbers of emerging litters per group plotted against rainfall for the years covered by this study and for the period between 1984 and 1988 when Doolan and Macdonald were working at the same site.

Discussion

Compared to other social mongooses, suricates in the Park showed high annual mortality. Our estimates of mortality in the Park (0.62 for juveniles and adults combined) are similar to Doolan and Macdonald's estimates for the same population between 1984 and 1988 (Doolan & Macdonald 1997a,b). Both estimates are higher than similar measures for two other social mongooses in the Serengeti National Park, Tanzania where dwarf mongooses (*Helogale parvula*) show annual mortality rates of 0.59 to 1 year and of 0.29 among adults and banded mongooses (*Mungos mungo* Gmelin 1788) show mortality rates of around 0.54 during their first 2 years of life and mortality rates of around 0.33 among adults (Waser *et al.* 1995). In contrast, mortality on the Ranch was similar or lower than levels observed in other mongooses in the Serengeti.

Our results confirm previous studies showing that predation rates on diurnal mongooses are high (Rasa 1987a; 1989b; Waser *et al.* 1995) and that, as in many other small mammals, predation exerts an important influence on population dynamics (Krebs *et al.* 1995; Stenseth, Bjornstad & Falck 1996). The contrast in overall mortality rates between the Park and the Ranch can presumably be attributed to predation, for there was no evidence that food availability was higher at the Ranch: neither daily weight gain, pup growth nor female body weight differed between the two areas, while males were heavier and pups tended to grow faster in the Park than at the Ranch. Nor does it seem likely that the difference in survival was a consequence of any misclassification of emigration as mortality, for rates of confirmed emigration tended to be higher at the Ranch than in the Park.

Mortality of pups between birth and emergence was not related to group size in either study area. This was probably because helpers in smaller groups compensated for reductions in their number by increasing the amount of time they spent guarding the burrow and the pups, so that there was no reduction in the proportion of time that a babysitter was present

(Clutton-Brock *et al.* 1998). In contrast, the mortality of pups between emergence and 6 months was significantly related to group size in both areas, though in opposite directions: juvenile mortality declined in larger groups in the Park but increased in larger groups on the Ranch. The most likely explanation of the negative relationship between group size and mortality in the Park is that helpers provided less effective defence of juveniles when the ratio of helpers to juveniles was low. The tendency for juvenile mortality to increase in large groups on the Ranch may suggest that the benefits of increased helper number may be offset by increased competition between juveniles and helpers for resources where population density is relatively high and predation rates are relatively low. Helpers commonly carried pups in their mouth when they fell behind the group and defended them against predators by standing over them. Where helper numbers were low, there were often not enough individuals to carry or protect all pups which may have led to higher pup mortality.

The tendency for adult mortality rates to show similar relationships with group size in the two areas was surprising. There are at least three possible explanations that we cannot currently distinguish between: (i) that stochastic variation in mortality is too large and sample size too small to reveal differences in the relationship between group size and predation rate; (ii) that increased group size has additional benefits on the Ranch, possibly associated with the higher density of groups (see below); and (iii) that changes in predation rate are not responsible for the relationship between group size and survival in both areas. Group size has multiple benefits in social mammals (Wrangham 1980; van Schaik 1983). In cooperative societies, increases in the number of helpers generally dilute individual work loads, reducing the per capita costs of caring to helpers and breeders (see Clutton-Brock *et al.* 1998). In addition, larger suricate groups usually displaced smaller ones, sometimes pursuing them until they left their usual home range. Interactions between groups were commonly associated with changes in territory boundaries and, on several occasions, small groups moved to other territories after repeated interactions with larger groups.

Whatever its causes, the tendency for mortality to increase in small groups had important consequences for the stability of groups in suricates and other cooperative breeders. In social mammals where breeding success and survival decline in large groups (e.g. Clutton-Brock *et al.* 1982; van Schaik 1983), reductions in group size lead to improvements in the rate of recruitment, allowing groups whose size has been reduced to regain their original size rapidly. In contrast, where reproductive success or survival fall in small groups (as in suricates and several other cooperative breeders), density-independent factors affecting group size may reduce recruitment rates in smaller groups, delaying the rate at which they can regain

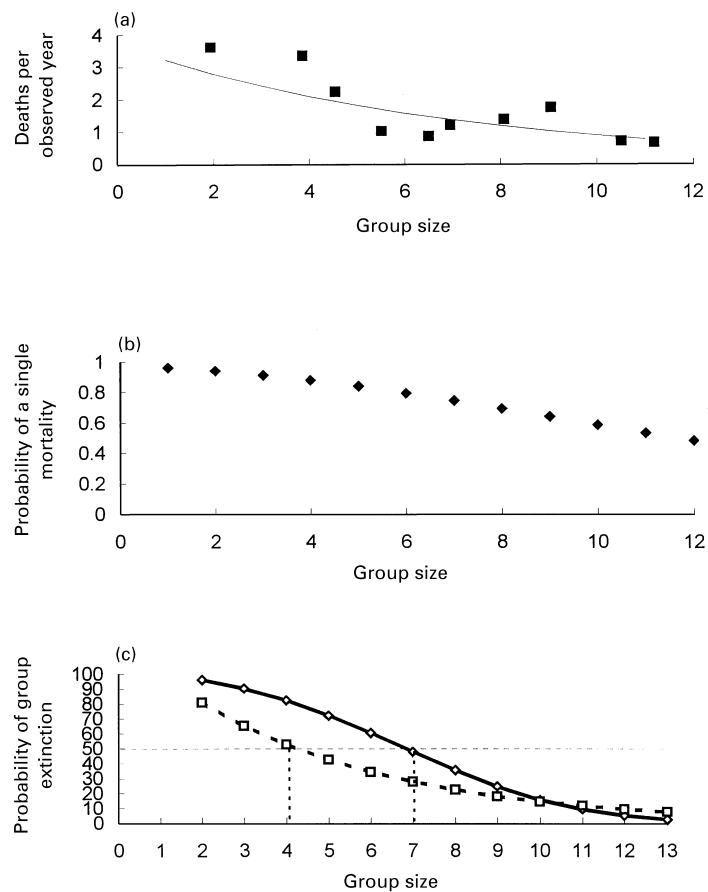


Fig. 4. Survival and group size for 1994/95. (a) Numbers of deaths per head in groups of different sizes (filled squares). Curve fitted using values predicted from the logistic regression model. (b) Probability per head of dying during the year. (c) Probability of all animals but one within the group dying during the year, the solid line shows the probability calculated using a stochastic model assuming that mortality is random across group sizes.

their original size. Over half of the groups in our study population became extinct during the course of a single dry year and research on two other cooperative mammals has recently shown that rates of group extinction are relatively high (R. Burrows 1995; J. Jarvis, personal communication). Our model of the relationship between group size and survival emphasizes the substantial impact that inverse density dependence may have on the probability of group extinction. For example, once group size has fallen to six members, the inverse relationship between group size and mortality nearly doubles the risk of group extinction (see Fig. 4c). Other features of cooperative breeders that may add to the risk of group extinction include low rates of immigration by females and the tendency for females to cease breeding rather than to mate with a close relative. In conjunction with effects on survival, these may reduce the chance that small groups will recover. As a result, groups of cooperative breeders may be substantially more likely to suffer extinction than groups of other social

species where survival and breeding success increase as group size declines.

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Dedication

This paper is dedicated to the memory of Ben Themen, who died in a road accident in the course of the work at Van Zyl's Rus.

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