Afr. J. Ecol. 1999, Volume 37, pages 69–80

Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari

T. H. CLUTTON-BROCK[1], A. MACCOLL[1]*, P. CHADWICK[2], D. GAYNOR[2], R. KANSKY[2] and J. D. SKINNER[2]

[1]*Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K.;* [2]*Mammal Research Institute, University of Pretoria, 0002 Pretoria, Republic of South Africa*

Summary

In most respects, the demography of Kalahari suricates (*Suricata suricatta*) resembles that of other social mongooses. Average group size varies from four to nine, and groups typically include several mature females, of which one is responsible for the majority of breeding attempts. Breeding females show a postpartum oestrus; gestation is around 60 days; litter size is three to five pups at emergence and females rarely breed before the age of 24 months. In contrast, annual survival rates (0.20 for pups and 0.43 for animals over one year old) are lower than those recorded in other species. Breeding frequency is related to rainfall and breeding can cease altogether when rainfall is unusually low. In a year when this occurred, group size eroded rapidly and over 60% of groups became extinct. Total numbers were slow to recover during the following year because emigration by females was infrequent and new groups did not form in vacant ranges created by the extinction of groups. High rates of group extinction have been found in other cooperative breeders and may occur because breeding success and survival show inverse density dependence.

Key words: cooperative breeding, population dynamics, suricates

Résumé

Par bien des aspects, la démographie des suricates du Kalahari (*Suricata suricatta*) ressemble à celle des autres mangoustes sociales. La taille moyenne des groupes varie de quatre à neuf, et les groupes comprennent typiquement plusieurs femelles mâtures dont une est responsable de la majorité des tentatives de reproduction. Les femelles reproductrices présentent un oestrus de post-partum; la gestation dure environ 60 jours; la portée compte de trois á cinq jeunes á la naissance, et les femelles se reproduisent rarement avent l'âge de 24 mois. Par contre, les taux de survie annuels (0,20 pour les petits et 0,43 pour les animaux de plus d'un an) sont plus faibles que ceux des autres espèces. La fréquence des reproductions est liée aux chutes de pluie, et elles peuvent même s'arrêter quand les pluies sont extraordinairement rares. Une année où ceci est arrivé, la taille des groupes s'est réduite rapidement et plus de 60% des groupes ont disparu. Le nombre total a mis du temps à remonter l'année suivante

---

Correspondence: T. H. Clutton-Brock, e-mail: thcb@cam.ac.uk

* Present address: Institute of Terrestrial Ecology, Hill of Brathens, Glassel, Banchory, Kincardineshire A31 4BY, U.K.

parce que l'émigration des femelles était rare et que donc aucun nouveau groupe ne se formait dans les territoires laissés vacants par la disparition des groupes. On a trouvé de taux élevés de disparition des groupes chez d'autres reproducteurs communautaires; ils pourraient être dus au fait que le succès de la reproduction et la survie dépendent inversément de la densité.

Introduction

For the last 20 years, cooperative breeding in birds has been the focus of intensive research aimed at determining how individuals benefit by helping to rear the progeny of other animals (Brown, 1987; Stacey & Koenig, 1990; Emlen, 1991). In many (although not in all) communal breeding species, adult survival is relatively high and breeding habitat is saturated. Under these conditions, young animals that disperse have little chance of breeding successfully and may enhance both their survival and their chance of breeding by remaining in their natal group if this increases the chance that they will eventually breed in their natal territory (Brown, 1987; Emlen, 1991).

It is not yet clear whether high adult survival and saturated habitats are typical of all cooperative breeding mammals. Studies of the demography of cooperative or communal species are both less abundant and less advanced than in birds (Macdonald & Moehlman, 1982; Jennions & Macdonald, 1994) and few have yet measured the survival of adequate samples of individuals in natural populations (Sherman, Jarvis & Alexander, 1990).

The cooperative mongooses provide an unusual opportunity to investigate the demography of cooperative mammals as they are both relatively visible and have comparatively small ranges. The most detailed studies to date concern the dwarf mongooses, *Helogale parvula* Sudevoll 1846, where samples of groups have been monitored over extended periods at sites in Tanzania and Kenya (Rood, 1983; Rasa, 1986; Rood, 1990; Creel & Creel, 1991). Here, groups typically consist of five to ten animals, usually including a single breeding female (Creel & Waser, 1991). Most females do not breed before they are 2 years old and may produce four litters per year, averaging 2.4 pups at emergence (Creel & Waser, 1991). Emerging juveniles show relatively high survival rates (0.41 during the first year of life) for a carnivore of this size (354 g; see Gittleman 1986) and adults show even higher survival rates (0.68 per year; Waser *et al.*, 1995). Survival rates are also high in the larger banded mongoose, *Mungos mungo,* (1637 g) which lives in groups of up to 30 animals that include multiple breeding females (Rood, 1986): juveniles show survival rates of around 0.46 during their first year of life and annual survival rates for adults are around 0.63 (Waser *et al.*, 1995).

In this paper, reproduction and survival is described in a third cooperative mongoose, the desert adapted suricate (*Suricata suricatta* Schreber 1776) in the Kalahari Gemsbok Park, Republic of South Africa. Like dwarf mongooses, suricates live in stable groups of 5–20 animals and breeding is commonly confined to a single female (Doolan & Macdonald, 1997). The animals show advanced cooperative behaviour: multiple females lactate in 40% of breeding attempts, all adult group members help to guard and feed the young and there is a coordinated system of vigilance with different individuals taking turns in going on guard (Doolan & Macdonald, 1996; Clutton-Brock *et al.*, 1998). These results extend those of a previous study in the same area which described reproduction and survival to 3 months in three groups (Doolan & Macdonald, 1997). Using the larger data set available to us, temporal changes in reproduction and population size were examined and the survival of adults as well as juveniles is described.

Methods

The study was based in the southern Kalahari at Nossob in the Kalahari Gemsbok National Park, Republic of South Africa (25°17′S, 20°32′E), and covered the period March 1994 to March 1996, although demographic data from April 1996–June 1997 are also included. Rainfall in this area averaged 217 mm/year between 1975 and 1995, falling mostly between December and March (Rooyen *et al.*, 1990). During the period of the study, rainfall was close to the average in 1992/3 (234 mm) and 1995/6 (247 mm), higher than average in 1993/4 (375 mm) but very low in 1994/5 (32 mm). The study area comprised the dry bed of the Nossob river, the terraces on either side and the dunes running down to the terraces. Vegetation consisted of tufted perennial grasses including *Eragrostis, Aristida, Stipagrostis* and *Schmidtia* spp. and low shrubs with widely spaced *Acacia erioloba* trees (see Leistner & Werger, 1973; Rooyen, Bredenkamp & Theron, 1991).

In an initial survey of the entire Park, all members of 33 groups were counted and sexed. The measure of group size excluded pups of less than 3 months but included all other animals. Adults could be sexed without difficulty with the use of a telescope when they were standing upright at the burrow entrance in the morning. Our survey showed that suricates were more numerous along the Nossob river between Kwang Pan and Cheleka than in other areas of the Park and the work was concentrated in this area. Initially, ten different groups used this stretch of the river bed (see Fig. 1a), seldom travelling more than 500 m into the dunes on either side. All members of these groups could be recognized by a combination of anatomical characteristics, natural markings and scars. During the course of the study (April 1993–96), seven of these groups became extinct and two new groups formed.

Groups were habituated to close observation and came to ignore observers within a few metres. Pregnancies could be identified by a visible extension of the abdomen during the last 6 weeks of gestation and birth dates could be identified by a sudden change in the female's shape. Pups were usually born at well established and frequently used burrow systems. For around the first 3 weeks after birth, the pups were left alone at the burrow during the day when the mother (and other group members) left to forage. During this time, a babysitter commonly remained to guard the burrow (Clutton-Brock *et al.*, 1998). When babysitters were habituated to the observer's presence it was possible to pick up and weigh pups using a spring balance. Adults were weighed after immobilization (using fluothane or ketamine), and in the later stages of the research, they were trained to stand on electronic balances.

Groups were checked every 2 to 4 weeks to monitor survival. Animals of less than 6 months and dominant females were not known to disperse (Clutton-Brock *et al.*, in press a). Dispersers typically foraged at a distance from their groups for several weeks before leaving and usually moved to neighbouring groups (Doolan & Macdonald, 1996). Where individuals disappeared without making temporary forays outside the group and were not sighted in surrounding groups or on their own, it was assumed that they had died.

As the population did not show a well-defined breeding season and groups were not known for exactly the same period, pups from different groups could not be

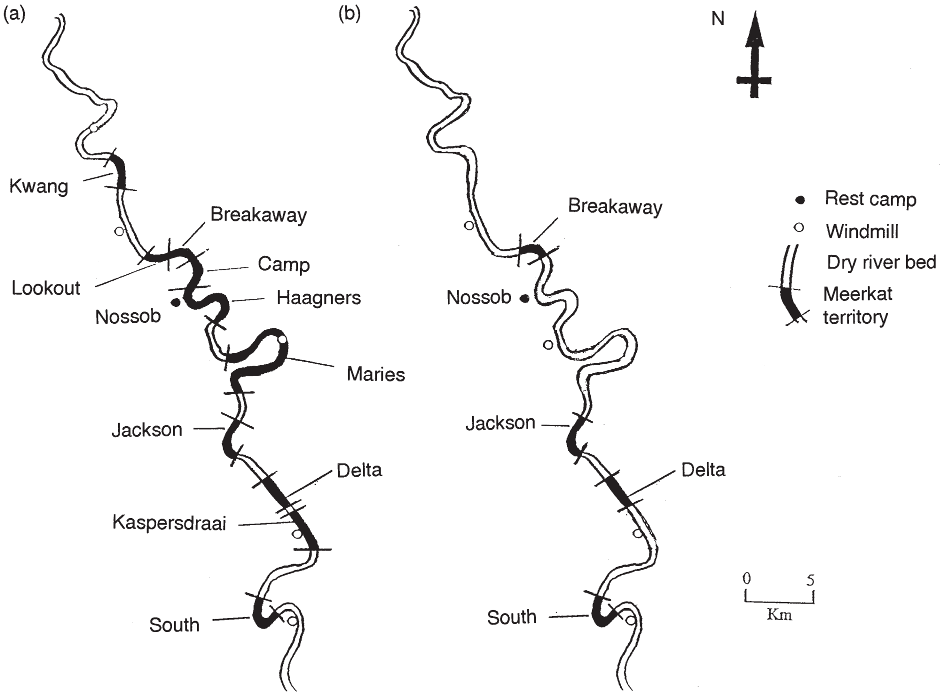

Fig. 1. Distribution of groups in April (a) 1994 and (b) 1995.

allocated to discrete cohorts. Consequently, the mean number of animal days per observed death was used to calculate annual survival and mortality. Annual survival (*S*) was calculated as:

$$S = 1 - (\text{deaths/days})^{365}$$

and annual mortality (see Fig. 5) was calculated as $1 - S$.

Results

Population density and group size

In an initial survey of suricate groups in the whole Park, 33 groups were counted, with a mean size (excluding juveniles < 2.5 months old) of 4.2 (Fig. 2). This was smaller than groups counted over the same area between 1976 and 1983 (mean size 8.5: J. Nel, unpublished), and between 1984 and 1988 (mean size 6.7: Doolan & Macdonald, 1997). The adult sex ratio was approximately equal: the average composition of 33 different groups whose members were counted in 1993 was 1.89 adult males, 1.90 females and 1.03 juveniles. The adult sex ratio did not differ between small and large groups (groups of ≤ 4: 33 males, 32 females; groups of ≥ 5: 16 males, 16 females). As numbers had apparently fallen since 1988 (see above), these ratios suggest that sex differences in survival are not pronounced.

In 1993, ten groups were resident in the 100-km^2 study area (Fig. 1a; Table 1). Groups holding ranges in the river bed rarely travelled more than 500 m into the dunes flanking the river and occupied ranges with an average size of 5 km^2. Ranges

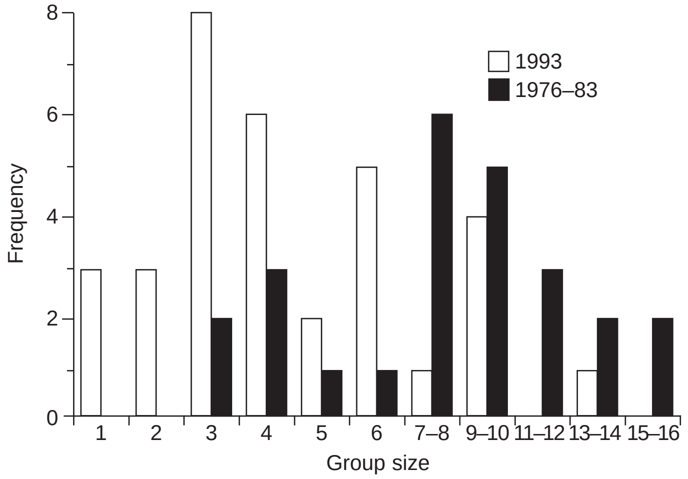

Fig. 2. Distribution of group sizes recorded during an initial survey of the Park in 1993 and previously recorded by Mills *et al.* (1984) and J. Nel (unpubl.) between 1976 and 1983.

Table 1. Group composition for the study area in April 1994

Group no.	Adult males	Juvenile males	Adult females	Juvenile females	Pups	Group size
1	1	6	1	4	0	12
2	7	0	3	0	4	14
3	2	2	3	0	0	7
4	1	0	4	3	0	8
5	3	3	1	5	0	12
6	1	5	0	3	0	9
7	3	1	2	4	3	13
8	1	0	2	0	0	3
9	1	0	1	3	0	5
10	3	5	4	2	0	14

were partly contiguous, although there were also substantial areas of vacant habitat.

Group membership was largely stable, although animals of both sexes commonly dispersed to join other groups (males only) or to found new groups (males and females) (Clutton-Brock *et al.*, in press a). During the course of this study, one new group (Sandile) was formed (by two males that emigrated from Jacksons and three females that emigrated from South).

Reproduction

Pregnancy could be identified during the last 3 months from the size and shape of the abdomen (Doolan & Macdonald, 1997). The minimum interval between births to the same female was 71 days, whereas interbirth intervals within the same season averaged 82±10.2 days ($n=22$).

Litters were born in all months of the year except July, although more were born

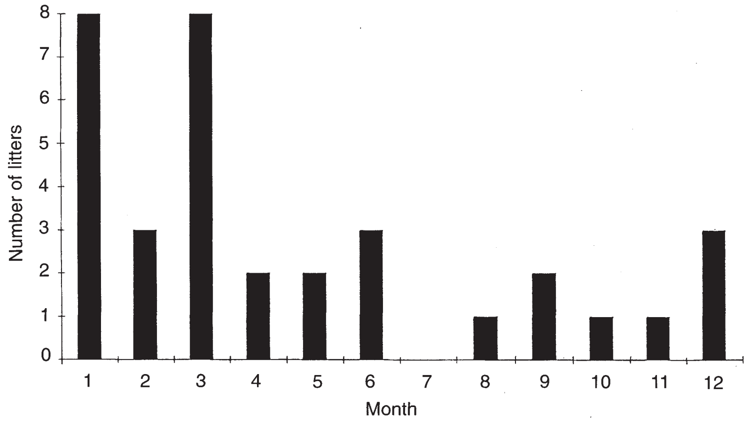

Fig. 3. Numbers of litters born in each month over the study period (1993–95): 1 = January, 12 = December.

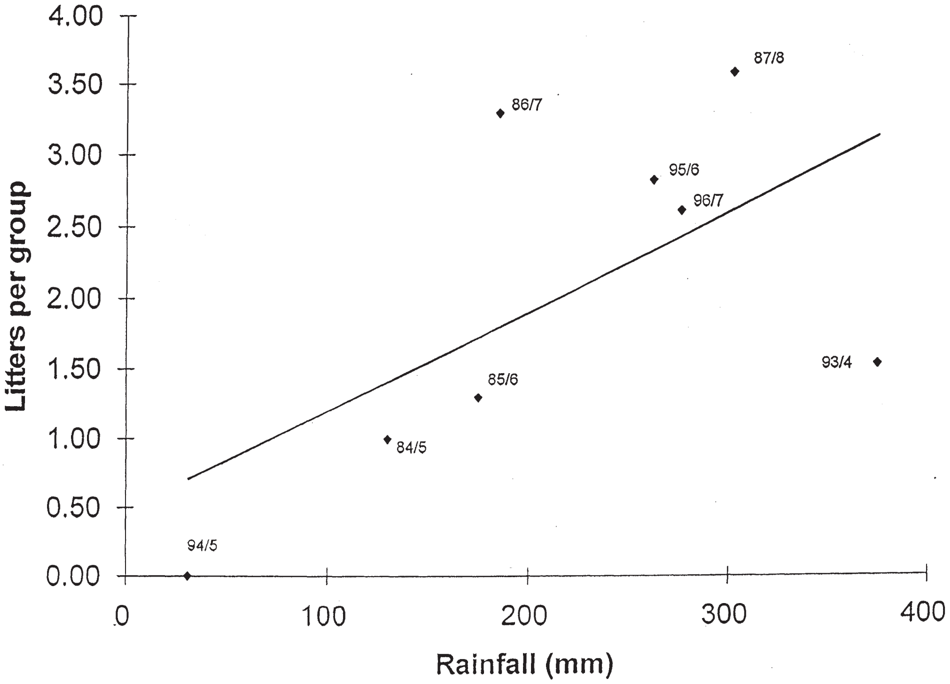

Fig. 4. Mean numbers of emerging litters per group plotted against rainfall for the years covered by this study and for the period between 1984 and 1988 covered by Doolan and Macdonald's previous study (1996).

between September and March than between April and August (Fig. 3). Over the entire period, the rate of (emerging) litter production for the eleven groups averaged 0.14 ± 0.1 litters per month or 1.8 litters per year. However, the frequency with which groups produced litters varied with rainfall (see Fig. 4, Spearman rank correlation: $r_s = 0.67$, $n = 8$, $P = 0.078$). In 1994/5, annual rainfall in the Park fell to around 10%

of the long-term average (31 mm) and there was a virtual cessation of breeding. When this year was excluded, estimates of the annual rate of litter production rose from 1.8 to 2.7 emerging litters per group per year.

Of 17 breeding attempts recorded in groups with more than one adult female, fourteen (82.3%) involved dominant females. Dominant (or only) females produced up to four litters per year but rarely did so if pups survived. Excluding data for 1994/5, the eleven dominant females monitored in the course of the study gave birth to 2.1 litters per year and reared 1.6 litters.

Where two females bred in a group, they usually (but not invariably) did so within a week of each other. Allosuckling occurred in around half of all breeding attempts in which more than one mature female was present in the group (8/17). All allosucklers were subordinate females and, in one case, three subordinate females suckled one litter.

Development and growth

After a female gave birth, the group typically continued to use the natal burrow for at least 3 weeks, leaving a babysitter at the burrow each day (Clutton-Brock *et al.*, 1998). Pups first emerged from the burrow around 3 weeks after birth. In 19 cases, the date of birth could be identified precisely and the number of days until the pups emerged recorded (mean = 18.9 ± 4.11). Litter size at emergence averaged 4.1 ± 1.5 pups, with a range of one to eight for a sample of 24 litters. Around 7 days after emergence (mean = 6.9, $n = 10$, range = 3–11), the pups left the natal burrow and began to travel with the group, foraging in different areas each day. Weaning was difficult to detect with certainty but appeared to occur by the time the young were around 2 months old.

The mean weight of 70 pups weighed within 5 days of emergence was 100.7 ± 24.4 g. Pups grew rapidly during their first month, averaging 179 ± 35.1 g at 6 weeks, and showed a daily growth rate of around 4.5 g/day over the first 3 months of life. Pups averaged 394.8 ± 50.25 g at 3 months ($n = 40$), 529.3 ± 64.2 g at 6 months ($n = 28$) and 636.2 ± 57.4 g at 12 months ($n = 9$), ≈90% of adult body weight.

Dominant animals were older and heavier than other group members. Six dominant females over one year old averaged 721 ± 51 g, whereas nine subordinate adult females averaged 640 ± 66.8 g (Mann–Whitney *U*-test: U = 6, $n = 6,9$, $P < 0.01$). Nine dominant males averaged 808 ± 86.1 g, whereas twelve adult, subordinate males averaged 659 ± 69.5 g (U = 11.0, $n = 9,12$, $P < 0.001$). Females usually begin to breed between 24 and 36 months of age. Only one of 16 female juveniles that lived to 2 years became pregnant and gave birth before the age of 24 months, whereas 83.3% of twelve living to 3 years became pregnant before the age of 36 months and all animals reaching 4 years had bred at least once.

Survival

Seven out of 34 (20.6%) litters died before emergence. In most cases, the likely cause of litter failure could not be determined. However, in two cases, litters were killed when a neighbouring group visited the natal burrow. In one of these cases, no babysitter was left at the burrow whereas, in the other, the babysitter was displaced by the invading group.

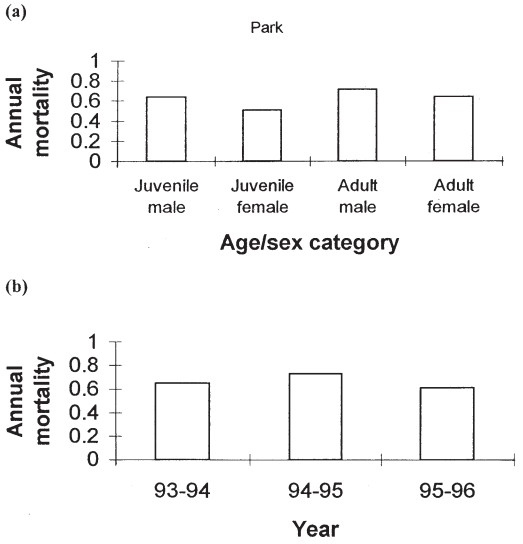

Fig. 5. Annual mortality for: (a) adults (> 12 months) during the 3 years of the study, (b) adults and juveniles of each sex between April 1993 and April 1996.

A total of 137 young emerged from 39 litters during the 3 years of this study and the survival of 119 young from 17 litters could be monitored. Of these pups, 89% survived to 2 weeks, 69% to 8 weeks, 43% to 6 months and 20% to 1 year.

Over the 3 years of this study, annual mortality of adults was 0.68. There was no significant difference in mortality between the sexes ($\chi^2 = 1.587$, $P = 0.208$) or between juveniles and adults ($\chi^2 = 0.245$, $P = 0.65$: see Fig. 5a) and annual mortality did not vary significantly between years (Fig. 5b).

Changes in population size

Although mortality was not significantly higher when annual rainfall was unusually low in 1994/5 than in other years (see Fig. 5a), the cessation of breeding combined with high overall mortality led to a rapid decline in average group size and population density. Between March 1994 and May 1995, the number of suricates in the study area fell from 100 to 35; six of the ten original groups (Kwang, Lookout, Camp, Haagners, Maries and Kaspersdraai) became extinct; the mean size of surviving groups (see Fig. 1b) fell from ten to four animals; and population density within the ranges of the remaining groups fell from 0.95–0.32 animals/km^2 (see Fig. 6). The extinction of over half of the original groups left large areas of vacant habitat between the remaining four groups (see Fig. 1b). In 1995, one further group (Delta) moved to a new range outside the study area and one new group formed betwen Kaspersdraai and Cheleka, consisting of emigrants from Jacksons and South. Following the return of normal rainfall in 1995/6 (181 mm), group size and population size began to recover (see Fig. 6). However, emigration was rare and the number of groups remained low. Because reproduction is dominated by a single female, both the number of breeding females and the total number of litters produced per year also remained relatively low until the end of 1997.

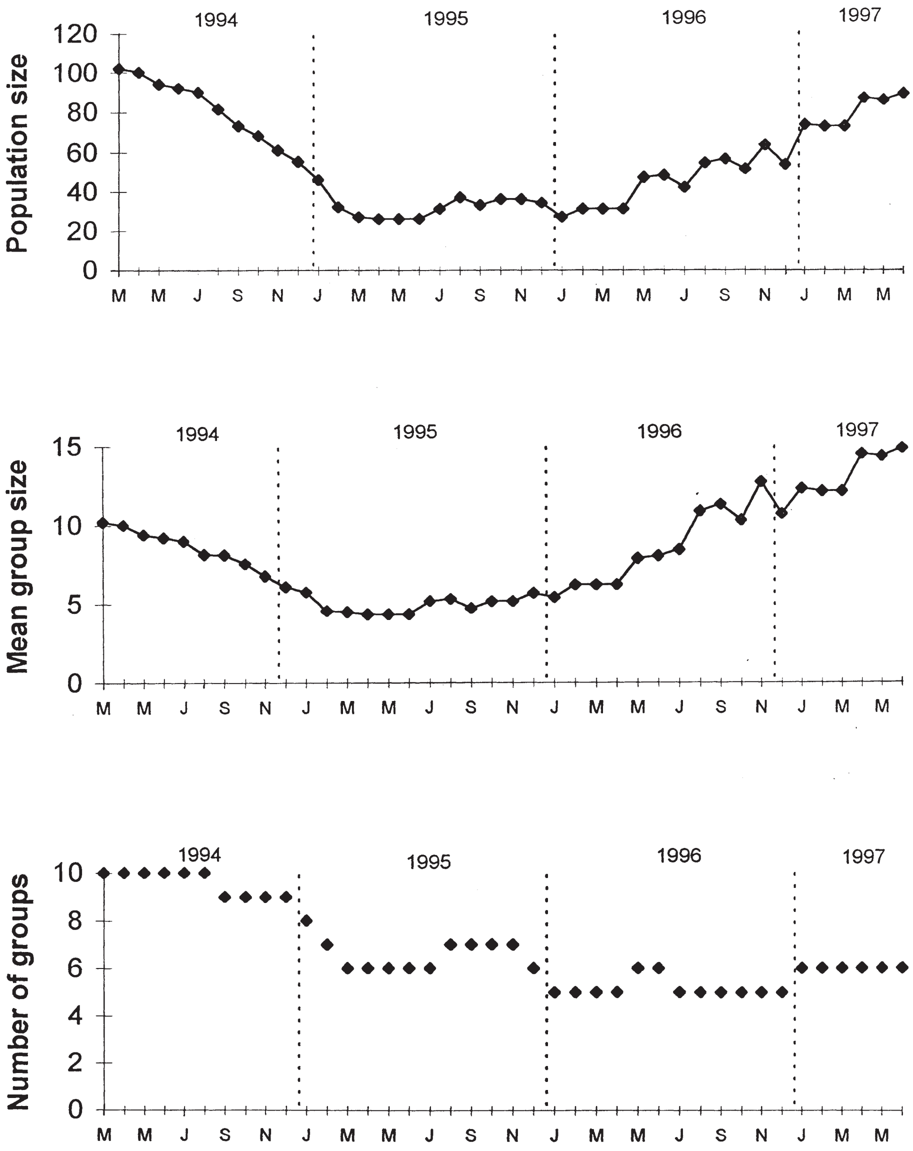

Fig. 6. Demographic changes between July 1993 and June 1997: (a) population size, (b) mean group size, and (c) number of groups in study area.

Discussion

In most respects, reproduction in suricates resembles that of dwarf mongooses (Rasa, 1986; Rood, 1990; Creel & Creel, 1991): gestation is around 60 days, litter size usually lies between three and five pups at emergence, young leave the natal burrow and begin to travel with the group at around 5 weeks of age and are weaned at around 2 months, females rarely breed before they are 2 years old, and non-breeding females commonly lactate (Lynch, 1980; Creel *et al.*, 1991). In contrast to dwarf and banded mongooses and suricates, the solitary-feeding mongooses (including slender, *Herpestes sanguineus* Rüppell 1836, and yellow *Cynictis penicillata* G. Cuvier 1829 mongooses) have small litters of one or two pups which remain at the natal burrow for around 10 weeks before they begin to forage independently (Rasa *et al*., 1992). It seems likely that the reduced time spent at the burrow by the offspring of group-living species reflects the protection that they are able to provide for young compared to solitary-feeding species. The alternative explanation that delayed development of the young occurs in solitary species because they cannot cover the energetic costs of rapid development in their young, is less likely as, in yellow mongooses (which live in groups of two to twelve), all group members cooperate to feed pups at the natal burrow (Rasa *et al*., 1992). However, the high costs of feeding young at the natal burrow for the first 10 weeks of life may constrain litter size, as yellow mongooses typically produce small litters despite the evolution of cooperative feeding.

Survival was lower in the study population than in most other mongoose populations that have been studied. Around 0.20 of emerging pups survived to 1 year compared to 0.41 and 0.46 in dwarf and banded mongooses in the Serengeti, respectively (Waser *et al*., 1995). Similarly, in this study, estimates of survival for animals over 1 year old (0.32 with no difference between the sexes) were substantially lower than estimates of adult survival in dwarf (males: 0.68, females: 0.74), banded (males: 0.65, females: 0.69) or slender (males: 0.82, females: 0.79) mongooses in the Serengeti (Waser *et al*., 1995). However, it is clear that survival rates vary widely between populations and may be higher in more heavily vegetated habitat: compared to Serengeti populations, dwarf mongooses in the arid Taru desert of Kenya show lower survival rates (Rasa, 1986), whereas banded mongooses living in thickets in the Mweya peninsula in Uganda show higher survival rates (0.89) than in the Serengeti (Rood, 1975, 1986; Waser *et al*., 1995). The study site at Nossob in the Kalahari Gemsbok Park lies towards the edge of the species range in the Kalahari, and suricate populations occupying more heavily vegetated areas of southern Africa probably show higher survival.

Most aspects of demography measured in this study were similar to Doolan and Macdonald's (1997) estimates based on a smaller number of suricate groups between 1984 and 1988, despite the fact that group size and population density were more than 50% greater during the earlier period (see Fig. 1). Average litter sizes in the two studies were 4.1 ± 1.5 and 4.4 ± 0.6 pups at emergence, respectively. Estimates of breeding rate (1.8 and 1.9 emerging litters per group per year) and interbirth interval (82 ± 10.2 and 90 ± 18 days between births to the same female) were also similar. The survival of litters between birth and emergence (20.6%) was slightly lower in this study than Doolan and Macdonald's (24.1%), as were estimates of the subsequent survival of pups.

The longer data set available in this study allowed exploration of the causes and consequences of changes in breeding rate. Over the 8 years for which data were available, annual rainfall varied from 31 mm in 1994/5 to over 350 mm in 1993/4. These changes were associated with variation in the numbers of emerging litters produced by groups, which ranged from zero to 3.5 per year (see Fig. 4). The cessation of breeding in 1994/5 led to a rapid erosion of group size, although mortality was not significantly higher in 1994/5 than in other years (Fig. 5): six of the ten groups using the study area became extinct and numbers fell by over 70%. These changes were paralleled by declines in the numbers of other small carnivores:

over the same period, the density of bat-eared foxes fell by 85% and the density of silver-backed jackals fell by 60% (Clutton-Brock, unpublished data). Relatively high rates of group extinction have been reported by studies of several other cooperative mammals, including African wild dogs (Burrows, 1995) and Damaraland mole-rats (Jarvis, unpublished).

Group size began to recover in the study population following the return of normal rainfall (187 mm) in 1995/6, but few animals emigrated and the number of groups did not increase during the next 2 years. Because, in most groups, a single breeding female was responsible for all successful breeding attempts, the increase in group size has little effect on the total number of emerging litters, which was determined principally by the number of groups in the study area. As a result, the rate of population recovery was slow. The failure of non-breeding females to emigrate and colonize the substantial areas of vacant habitat that were available (see Fig. 1b) during 1996 and 1997 suggests that habitat saturation is not necessary for dispersal to be delayed. Both survival and breeding success increase with group size in this population (Clutton-Brock *et al.*, in press b) and females maximize their fitness by remaining in their natal group until they have an opportunity to breed there (Clutton-Brock *et al.*, in press a).

Both high rates of group extinction and slow rates of population recovery following periods of decline may be a common feature of cooperative breeders. In social but non-cooperative species, small group size is typically associated with reduced competition for resources and improved breeding success and survival (Clutton-Brock, Albon & Guiness, 1982; Van Schaik, 1983), with the result that groups whose size has been reduced recover quickly. In cooperative breeders, by contrast, the low survival and breeding success typical of small groups will increase the risk that they will continue to decline, raising the probability of group extinction. Where few females emigrate and the rate at which new groups are established is low, populations of cooperative breeders often may be slow to recover from periods of population decline induced by food shortage or disease. As a result, they may spend more time below ecological carrying capacity than populations of other social species, where small groups recover more quickly and successful emigration is more frequent.

Acknowledgements

We are most grateful to the National Parks Board of the Republic of South Africa for permission to work in the Park and for their hospitality at Nossob. In particular, we are grateful to Dr Antony Hall-Martin and Dr Peter Novellie, to Mr Elias Le Riche and Mr Dries Engelbrecht, Wardens of the Kalahari Gemsbok National Park, and to the National Parks staff based at Nossob, including Rangers J. Herrholdt, S. De Waal and G. de Kock. We are also grateful for the support of members of the Department of Zoology and the Mammal Research Institute, University of Pretoria, including Dr Phillip Richardson, Dr Andrew MacKenzie, Martin Haupt, Tim Jackson and Gus van Dyk. Seven volunteer assistants made important contributions to data collection: Laurence Postgate, Henry Nicholls, Kerry McKay, Paul Dixon, Catriona McLeod, Alex Toole and Catriona MacCallum. For comments on the manuscript, we are grateful to Professor A. E. Rasa and Dr D. W. Macdonald.

References

Brown, J.L. (1987) *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton.

BURROWS, R. (1995) Demographic changes and social consequences in wild dogs, 1964–92. In: *Serengeti II. Dynamics, Management and Conservation of an Ecosystem* (Eds A.R.E. Sinclair and P. Arcese). Chicago University Press.

CLUTTON-BROCK, T.H., ALBON, S.D. & GUINNESS, F.E. (1982) Competition between female relatives in the matrilocal mammal. *Nature* **300,** 178–180.

CLUTTON-BROCK, T.H., BROTHERTON, P.N.M., SMITH, R., MCILRATH, G.M., KANSKY, R., GAYNOR, D., O'RIAIN, J. & SKINNER, J.D. (in press a) Infanticide and the expulsion of females in a cooperative mammal. *Proc. Roy. Soc. Lond. B.*

CLUTTON-BROCK, T.H., GAYNOR, D., KANSKY, R., MACCOLL, A.D.C., MCILRATH, G., CHADWICK, P. (1998) Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. Lond. B.* **265,** 185–190.

CREEL, S.R. & CREEL, N.M. (1991a) Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behav. Ecol. Sociobiol.* **28,** 263–270.

CREEL, S.R. & WASER, P.M. (1991) Failures of reproductive suppression in dwarf mongooses: accident or adaptation? *Behav. Ecol.* **2,** 7–15.

CREEL, S.R., MONFORT, S.L., WILDT, D.E. & WASER, P.M. (1991) Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature* **351,** 660–662.

DOOLAN, S.P. & MACDONALD, D.W. (1996) Dispersal and extra-territorial prospecting by slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari. *J. Zool.* **240,** 59–73.

DOOLAN, S.P. & MACDONALD, D.W. (1997) Breeding and juvenile survival among slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari: ecological and social influences. *J. Zool.* **242,** 309–327.

EMLEN, S.T. (1991) Evolution of cooperative breeding in birds and mammals. In: *Behavioural Ecology: an Evolutionary Approach* (Eds J.R. Krebs and N.B. Davies). Blackwell Scientific Publications, Oxford.

GITTLEMAN, J.L. (1986) Carnivore life history patterns: allometric, phylogenetic, and ecological associations. *Am. Nat.* **127,** 744–771.

JENNIONS, M.D. & MACDONALD, D.W. (1994) Cooperative breeding in mammals. *Trends Ecol. Evol.* **9,** 89–93.

LEISTNER, O.A. & WERGER, M.J.A. (1973) Southern Kalahari phytosociology. *Vegetation* **28,** 353–399.

LYNCH, C.D. (1980) Ecology of the suricate, *Suricata suricatta*, and the yellow mongoose, *Cynictis penilcillata*, with special reference to their reproduction. *Mém. Nas. Mus. Bloemfontein* **14,** 1–145.

MACDONALD, D.W. & MOEHLMAN, P.D. (1982) Cooperation, altruism and restraint in the reproduction of carnivores. *Perspective Ecol.* **5,** 433–467.

MILLS, M.G.L., NEL, J.A. & BOTHMA, J.d.P. (1984) Notes on some smaller carnivores from the Kalahari Gemsbok National Park. *Koedoe* **7,** 221–227.

RASA, O.A.E. (1986) Ecological factors and their relationship to group size, mortality and behaviour in the dwarf mongoose, *Helogale undulata. Cimbebasia* **8,** 15–21.

RASA, O.A.E., WENHOLD, B.A., HOWARD, P.A., MARAIS, A. & PALLETT, J. (1992) Reproduction in the yellow mongoose revisited. *S. Afr. J. Zool.* **27,** 192–195.

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* (Eds J.F. Eisenberg and D.G. Kleiman). American Society of Mammalogists, Washington.

ROOD, J.P. (1986) Ecology and social evolution in the mongooses. In: *Ecological Aspects of Social Evolution* (Eds D. Rubenstein and R.W. Wrangham). Princeton University Press, Princeton.

ROOD, J.P. (1990) Group size, survival, reproduction and routes to breeding in dwarf mongooses. *Anim. Behav.* **39,** 566–572.

ROOYEN, N.V., BEZUIDENHOUT, D., THEROOU, G.K. & BOTHMA, J.d.P. (1990) Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe* **33,** 63–68.

ROOYEN, N. VAN., BREDENKAMP, G.J. & THERON, G.K. (1991) Kalahari vegetation: veld condition trends and ecological status of species. *Koedoe* **34,** 61–72.

SHERMAN, P.W., JARVIS, J.U.M. & ALEXANDER, R.D. (1990) *The Biology of the Naked Mole-Rat*. Princeton University Press, Princeton.

STACEY, P.B. & KOENIG, W.D. eds (1990) *Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.

VAN SCHAIK, C.P. (1983) Why are diurnal primates in groups? *Behaviour.* **87,** 120–144.

WASER, P.M., ELLIOTT, L.F., CREEL, N.M. & CREEL, S.R. (1995) Habitat variation and mongoose demography. In: *Serengeti II. Dynamics, Management and Conservation of an Ecosystem* (Eds A.R.E. Sinclair and P. Arcese). Chicago University Press, Chicago.

(Manuscript accepted 25 February 1998)