Fluctuating group size in Bat-eared foxes (*Otocyon m. megalotis*) in the south-western Kalahari

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Introduction

Bat-eared foxes are small and primarily insectivorous carnivores (e.g. Nel, 1978; Lamprecht, 1979) and are considered to be more social than other fox-like canids (Kleiman, 1967; Kleiman & Eisenberg, 1972). Pair formation, as evidenced by pair bonding behaviour, takes place during June–July, and monogamy is probably the rule (Kleiman, 1977; pers. obs.). It is possible that monogamous pairs persist for several years. In the south-western Kalahari births occur from October to early December. Young first appear outside dens at an age of three weeks and are weaned at an age of roughly 10 weeks (Berry, 1978). Hereafter, family groups forage together for several months. Group size and the frequency distribution of group sizes are not fixed social parameters of the species and at any particular time will depend on litter size and mortality, population status, the "point" in the annual cycle, immigration and emigration, and seasonal changes in food availability.

The south-western Kalahari is an area of low rainfall. Precipitation, both spatially and temporally, is unpredictable and varies greatly from year to year (Table I). It is commonly known that primarily production is positively correlated with rainfall (Philipson, 1975), especially in arid areas (Seely, 1978; Rutherford, 1980), as is insect abundance (Seely & Louw, 1980).

Over the years it has become evident that both numbers and group sizes of Bat-eared foxes in the dry riverbeds of the Kalahari Gemsbok National Park varied, sometimes dramatically.

TABLE I

Total yearly rainfall (in mm) at Nossob Camp, Kalahari Gemsbok National Park, and mean group sizes in July. Sample sizes (no. of groups) given in parentheses

	1974	1975	1976	1977	1978	1979	1980
Total rainfall	532	239	602	263	107	224	151
Rainfall, July to June		224	638	268	139	140	194
$\bar{x}$ Group size (July)	—	3·5(2)	3·79(24)	3·3(9)	2·26(42)	2·0(7)	2·62(39)

The question arose as to what was responsible for these fluctuations. The present paper deals with the effects of changes in rainfall and therefore food availability.

Methods

Bat-eared foxes were counted and group sizes were noted from 1974 to 1980 during censuses and studies on their foraging behaviour in the Kalahari Gemsbok National Park. Counts were done from vehicles by day and night in the dry riverbed of the Nossob river, near Nossob Camp. Groups were only recognized as such if widely separated, when feeding aggregations broke up, or more usually from several counts of discrete groups over several days or nights in a given 21 km stretch of riverbed. Rainfall figures are from Nossob Camp.

Results

Between 1974 and 1980 mean group size throughout the year for 623 groups comprising 1694 individuals was 2·72 (range 1–10), while monthly mean group size varied between 2·26 and 4·19 (Table II). The frequency distribution of group sizes is given in Fig. 1, which shows that most groups (43·1%) comprised two individuals, far fewer (19%) of three individuals, with even fewer groups comprising one or four or more individuals. Frequency distribution of group sizes for the periods January to

TABLE II

Monthly mean group sizes (± 1 S.D.) of Bat-eared foxes in the south-western Kalahari; 1974–1980

	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
$\bar{x}$	3·19	4·19	3·07	2·50	2·55	2·88	2·76	2·35	2·88	2·28	2·95	2·26
S.D.	1·45	2·29	1·73	2·97	1·34	1·42	1·24	0·78	1·62	1·20	1·66	1·21
n	54	21	14	10	55	43	168	54	41	43	22	98

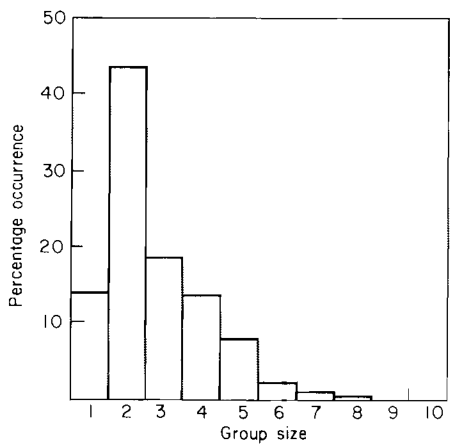

FIG. 1. Frequency distribution of group sizes in Bat-eared foxes in the south-western Kalahari.

July, and August to December, differed significantly ($\chi^2=19{\cdot}37$; d.f. $=7$; $P<0{\cdot}05$). Nearly twice as many groups of single individuals were counted during the second half of the year, about equal numbers of groups of two and three throughout the year, but twice as many groups of four, five and six during the first half of the year. This agrees with other observational data that the young stay with the parents till June–July, when nuclear family groups split up. There is some evidence (unpubl. data) to suggest that the adult pair re-affirms their pair bond at this time by, especially, urine-marking and allogrooming, while the young remain together as a sibling group.

The sex and age composition of groups could often not be determined. Although sexes squat differently when urinating, this was not always observable at long distances. Cubs grow rapidly and at an age of three to four months are about fully grown (Berry, 1978) and nearly indistinguishable from adults.

Inadequate sampling did not permit a year-to-year analysis of the frequency distribution of group sizes for each month. A contingency table analysis for July of each year did, however, indicate that frequency distribution of group size for this month changed significantly from year to year ($\chi^2=20{\cdot}58$; d.f. $=8$; $P<0{\cdot}01$). This is probably related to rainfall the previous 12 months; less rainfall equated with smaller group sizes, and vice versa (Table I).

Frequency distribution of group sizes also appears to differ from area to area. A comparison of the Kalahari population with Serengeti population (Lamprecht, 1979) revealed a statistically significant dependence of group size frequency distribution on study site ($\chi^2=25{\cdot}55$, d.f. $=7$; $P<0{\cdot}01$), although in both areas groups of two were most common. In the Kalahari, however, groups comprising more than two individuals were more numerous than in the Serengeti.

The influence of rainfall ($\simeq$food supply) on group size frequency distribution was investigated through regression analysis. Monthly percentage occurrence of groups of one, two or more than two individuals (dependent variables) based on the three point moving average and mean monthly rainfall figures (independent variables) were calculated as the mean for the years 1974–80. From this analysis the following was revealed (Fig. 2):

A linear increase in the frequency of occurrence of groups larger than two with an increase in rainfall, where 81% of the changes in frequency of occurrence can be ascribed to changes in rainfall;

A linear decrease in the frequency of occurrence of pairs of foxes with a decrease in mean monthly rainfall where 77% of the changes in the above can be ascribed to changes in rainfall;

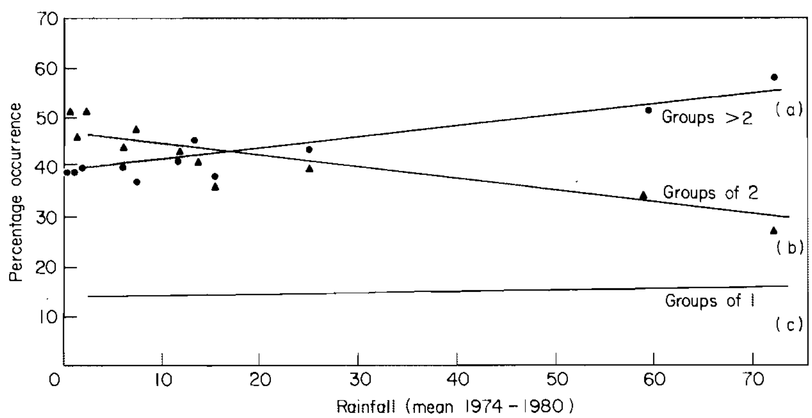

FIG. 2. The relationship between the percentage occurrence of groups of Bat-eared foxes and mean rainfall. (a) Groups >2; (b) groups of 2; (c) groups of 1. For (a) $y=39{\cdot}72+0{\cdot}21x$ ($r^2=0{\cdot}81$; $P<0{\cdot}01$; d.f. $=10$). For (b) $y=46{\cdot}59-0{\cdot}24x$ ($r^2=0{\cdot}77$; $P<0{\cdot}01$; d.f. $=10$). For (c) $y=13{\cdot}42+0{\cdot}04x$ ($r^2=0{\cdot}06$; $P=$ not significant; d.f. $=10$).

A non-significant relationship between the occurrence of solitary individuals and mean monthly rainfall ($r^2 = 0{\cdot}06$).

A multiple linear regression analysis, furthermore, indicated that 83 and 81% of the variability in frequency of occurrence of groups of two or more than two individuals, respectively, can be ascribed to changes in rainfall and season (month of the year), the rest of the variation being ascribed to unknown factors.

A decline in rainfall did not only affect the mean group size, with fewer large groups occurring as rainfall decreased, but also the number of groups and thus total number of Bat-eared foxes in the riverbed habitat. For example, in a 21 km stretch regularly censused 17 groups totalling 38 foxes were counted in July 1978, while only six groups totalling 22 foxes were present during July 1980.

Discussion

Group size in Bat-eared foxes does not seem to be dependent on enhanced or lowered ability to procure food. They call each other to rich food patches (Nel & Bester, In press) so that a particular group size does not seem to increase foraging efficiency. They do not defend prey caught, so this factor would have no influence on group size, as is postulated to be the case in certain other carnivores (Lamprecht, 1981).

The hypothesis that rainfall, and, as a result, amount of food available influences group size distribution and numbers of Bat-eared foxes in a particular habitat, however, seems justified from the results obtained. The reasons for this could be that rainfall influences food availability and, therefore, either litter size, pup survival, or both. This equates with group size (up to July at least) and of course with eventual total numbers. A correlation between group size and food availability has been found in other carnivores (Macdonald, 1980; Kruuk & Parish, 1982; Mills, 1982). The duration of group cohesion in Bat-eared foxes may also be affected by food availability, with low availability forcing earlier breakup. Our data are, however, insufficient to substantiate this. The occurrence of family groups during the first half of the year, and break up during July-August, is shown by the significant difference in group size frequency distribution before and after this period. What happens to the sibling groups is uncertain. Probably from these groups new breeding pairs are formed during the following June-July, as these foxes only breed at an age of 18 months (Smithers, 1971). Disintegration of these sibling groups could also account for the greater number of solitary individuals seen during the second half of the year.

Rainfall, therefore, acts as the proximate agent affecting group size in Bat-eared foxes in the south-western Kalahari. Apart though from mean group size fluctuating in synchrony with a change in amount of rainfall, numbers of groups and thus total numbers also change. Similar fluctuations in population size of Bat-eared foxes have been reported in Kenya (Leakey, 1969), where disease has been suggested as precipitating the decline, and in Serengeti (Lamprecht, 1979), where movements between habitats probably accounted for the disappearance of foxes from a particular area. Here there were also monthly changes in mean group size, but on the whole, larger group sizes tended to occur late in the year or during the first months of the year (Lamprecht, 1979; fig. 9) as in the Kalahari. It seems possible that in the Kalahari local movements also occurred. As food supplies in the riverbed dwindle, more groups may utilize the adjoining dune veld. However, as we have no comparable figures for fox numbers in the dunes over the years, this explanation must remain tentative. Other studies, on rodents and insectivores in the south-western Kalahari, do suggest that survival in the dunes is much higher in times of food shortage than in the riverbed (unpubl. data). In the case of the Bat-eared foxes the dunes could conceivably also act as the ultimate "survival" habitat.

All this points to the Bat-eared fox being an opportunistic *r*-strategist, with group sizes tracking, and depending on, food availability and ultimately rainfall. This may well apply to other insectivorous carnivores in similarly unpredictable environments as well.

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