Foraging and feeding by bat-eared foxes *Otocyon megalotis* in the southwestern Kalahari

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Bat-eared foxes *Otocyon megalotis* feed in pairs or groups of three when utilizing clumped prey in patches, e.g. termites, and cover 0,87-1,28 km/h. When feeding on dispersed prey, e.g. insect larvae, they are widely spaced and cover 0,56-0,83 km/h. Food patches are never re-utilized on the same day. Patch size diameter varied from 6-30 m, and patches were 10 to >100 m apart, while from 1,17 min to 15 min were spent in patches. There were no significant correlations between patch size and distance moved to next patch, or time spent in a patch and distance moved to next patch, or time spent in a patch and patch size. Patches were seldom (1,6 %) returned to immediately. A male and a female had similar numbers of feeding bouts per sampling period during winter or summer, but when accompanied by cubs the male fed less frequently. The male had significantly longer feeding bouts than the female in winter, with the reverse applying in summer. Within-sex comparisons show that the number of feeding bouts of the male did not vary significantly between winter and summer. Conversely the female showed significant differences in the number but not the duration of feeding bouts in winter and summer. Optimal foraging in this species probably relates to prey profitability, i.e. highest ingestion rate.

Key words: foraging, feeding, bat-eared fox, *Otocyon megalotis*.

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Introduction

Bat-eared foxes *Otocyon megalotis* (Desmarest, 1822) are primarily insectivorous (e.g. Smithers 1971, 1983; Nel 1978; Lamprecht 1979) and in southern Africa forage diurnally during the colder winter months and at night during summer. This coincides with above-ground activity and thus availability of a major prey item, the harvester termite *Heotermes mossambicus*. Darkly-pigmented adults of this termite species are tolerant of ultraviolet radiation and can forage by day, although their above-ground activity is dependant on the prevailing temperature (Nel & Hewitt 1969). In summer, with soil surface temperatures up to 70 °C at midday in the study area they therefore forage at night. In winter, when temperatures can drop to -10 °C during the night, above-ground activity occurs from midday to late afternoon.

Bat-eared foxes preferentially forage in short grass or low shrub habitat (e.g. Smithers 1971; Nel 1978; Lamprecht 1979; Mackie & Nel 1989) but utilize tall or thick vegetation for cover. Prey is usually located by auditory means (Nel 1978; Malcolm 1986) and less frequently through smell or sight. When capturing prey the prominent ears are flipped back, which facilitates recognition and timing of feeding bouts.

The above characteristics of bat-eared foxes, and the presence in conservation areas of individuals or groups that allow very close (<30 m) approach by a vehicle permits at times sustained visual observation of a slow-moving forager that often feeds on a patchily distributed, time-depleted prey source such as harvester termites. This allows the accumulation of quantitative data on aspects of foraging, which can be related to some current

optimal foraging theories (for a review see Schoener 1987). This paper presents some preliminary data in this regard, which suggests that bat-eared foxes could well be suitable larger-than-normal experimental animals for testing submodels of optimal foraging theory.

Materials and methods

Focal animal (or group) sampling (Martin & Bateson 1986) was used, through 7x42 binoculars from a vehicle for varying periods during February 1976, July 1976, December 1976, January 1977, July 1978, April 1979 and July 1980, for a total of 220 h, or taking into account the number of foxes in the groups observed, >1 000 "fox-hours". Only groups easily habituated to the vehicle, and allowing close approach (<100 m) were followed; some groups tolerated the vehicle from less than 20 metres. Groups followed and observed foraged predominantly in a dry riverbed, adjacent flats, or dunes forming the riverbanks. Prey taken by foxes could sometimes be determined visually, e.g. active termites being licked up, or through subsequent digging for possible prey items in similar habitat, or else through later analysis of droppings passed by groups followed. Data on foraging were recorded on magnetic tape and later transcribed. Duration of feeding bouts was timed on electronic stop-watches. A "patch", i.e. an active termite colony fed upon was recognized as such if the giving up time was >1 minute. Feeding on termites for <1 min was regarded as sampling only. Size (diameter) of a patch fed in was estimated visually, extrapolating from the straightline distance nose-tailtip of a feeding fox being ca. 0.75 metres. Distances in metres between patches were estimated, or taken from the vehicle's odometer (to the nearest 100 m).

Study area

Bat-eared foxes were observed in and around the dry riverbed of the Nossob River in the vicinity of Nossob Camp (25° 25'S; 20° 36'E) in the Kalahari Gemsbok National Park, South Africa. Long-term (1966 - 1986) rainfall averages ca. 201 mm p.a. in the study area (National Parks Board 1990). Rainfall is in summer to early autumn (Nov-Apr) with more than 50 % falling between January and April. Two main habitats can be distinguished: the dry beds of the Auob and Nossob rivers, normally sparsely covered by grasses and/or ephemerals, with the adjacent flats covered with grasses (especially *Stipagrostis obtusa*) and shrubs (*Rhigozum trichotomum*); and the undulating duneveld which cover the major portion of the park,

as well as that of the contiguous Gemsbok National Park in Botswana. Detailed descriptions of the vegetation are provided by Leistner (1967) and Leistner & Werger (1973).

Results

Foraging groups

Foraging groups ($n=129$) comprised adults only ($n=69$), adults plus young ($n=50$), or subadult siblings ($n=10$). Groups consisting of two individuals had the highest incidence (43 %), followed (19 %) by groups of three (Nel, Mills & Van Aarde 1984). Single individuals were more common after family groups broke up in June-July; after the birth of cubs in October-December these singletons could have been lactating females foraging while the male guarded the cubs ($n=5$).

Time of foraging

In midsummer (Dec-Jan) foraging commenced around sunset or earlier on overcast or rainy days. It continued throughout the night to peter out during early morning, or later if overcast or rainy. This regime gradually shifted to a nearly exclusive diurnal pattern during winter; in June-July foraging usually commenced between 11:00 to 12:00 and continued till after dark (Fig. 1). Although not specifically monitored, fox foraging periods seemed to coincide with those of harvester termites *H. mossambicus* during winter, when termite activity was very noticeable and audible (see also Malcolm 1986).

Foraging and feeding patterns

When resting, before or during foraging, group members huddled together, lay or sat <5 m apart ($n=44$). Spacing of group members when foraging depended on the prey type utilized at the particular time. When feeding on (and presumably foraging for) predominantly termites, linear movements by single foxes, pairs or groups of three, were interspersed with feeding bouts in patches. Feed-

Fig. 1. Percentage of *Otocyon megalotis* encountered in the Kalahari Gemsbok National Park foraging at different times during summer or winter. Time is abbreviated as follows: 1 = 01:00, 12 = 12:00 etc. "Day" is from sunrise

ing in patches ($n=60$) commenced at or near the centre of a patch, with foxes milling around while licking up and ingesting termites, and gradually shifting to the periphery. On five occasions, when one of a pair or group located a patch, the other(s) were "called" with a low whistling sound. Otherwise they reacted to the feeding behaviour of the locator, and ran to join it. These linear movements between patches averaged 68 m (± 112 m), although 61 out of the 64 movements were 100 m or less.

By contrast, when feeding predominantly on beetles, beetle and other larvae usually dug up

at the base of shrubs, or grasshoppers, group members commonly ($n=47$) foraged as a loose assemblage, sometimes one behind the other or in line abreast, spaced apart according to the location of shrubs harbouring prey. In this case foxes fed singly on presumably dispersed prey.

When specifically monitored most foraging occurred on the plains or riverbanks (Table 1).

Foraging rate

The prey type (termites or larvae, grasshoppers, etc.) influenced the straight line distance

Table 1
Percentage time spent foraging and feeding in different habitats in the
southwestern Kalahari by *Otocyon megalotis*

Period	Sampling period (duration)	Habitat		
		Riverbed (short grass)	Riverbank/plains (short grass, <i>Rhigo- zum</i> shrubs)	Dunes (tall grass)
Feb. '79 (summer)	6h 14 min	0	92,5	7,5
April '79 (autumn)	4h 40 min	10,5	89,25	0
July '78 (winter)	10 h 03 min	32,2	67,8	0
July '80 (winter)	7 h 54 min	3,4	96,6	0

covered per unit time by foraging groups. During summer (Dec-Jan), feeding primarily on termites in patches, foxes covered a mean of 1,28 km per hour ($SD = 0,42$, $n=5$); in winter this rate dropped to $\bar{x} = 0,87$ km/h ($\pm 0,24$, $n=4$). When feeding primarily on larvae or grasshoppers (i.e. non-patch feeding) the foraging rate was lower. In summer groups moved at a mean rate of $0,83 (\pm 0,25)$ km/h ($n=4$), and in winter at $0,56 (\pm 0,08)$ km/h ($n=6$).

Foraging rates when feeding on termites during winter or summer did not differ significantly ($t=1,565$, $P > 0,05$), or when feeding on larvae and grasshoppers ($t=2,211$, $P > 0,05$). The foraging rates when feeding on termites or on larvae in summer also did not differ significantly ($t=1,735$, $P > 0,05$), but differed significantly in winter ($t=2,43$, $P < 0,05$).

Feeding patch use (Table 2)

If a food patch (i.e. a termite colony) was encountered it was never ignored. Patches were never re-utilized on the same day, but on consecutive or 2-3 day intervals.

No significant correlation between the size of a patch and the distance moved to the next patch emerged (Spearman's rank correlation $0,3991$, $P > 0,05$), where the size of feeding patches varied between 6 m - 30 m in diameter ($\bar{x}=24,2 \pm 9,84$ m, $n=14$) and the distance moved to the following patch varied from 10-100 m ($\bar{x}=46,1 \pm 32,08$ m, $n=14$).

Similarly, there was no significant correlation between time spent feeding in a patch and distance moved to the next patch (Spearman's rank correlation $0,0755$, $P > 0,05$). In this case time in patches varied from 1,17 to 15 min ($\bar{x}=7,95$ min $\pm 3,4$ min, $n=18$). Also, no significant correlation was found between time spent feeding in a patch and patch size (diameter) both in winter (Spearman's rank correlation $0,0376$, $P > 0,05$, $n=16$) or autumn ($0,4008$, $P > 0,05$, $n=17$).

Return to a patch immediately after it was abandoned occurred in 1,6 % of cases ($n=39$) and then for a brief period (< 2 min) only.

Similarly, pairs or threesomes normally abandoned a patch simultaneously; again only in 1,6 % cases did one leave before the other. In this case the singleton or pair never remained for > 1 min before also leaving.

Table 2
Patch feeding on *Hodotermes mossambicus* by *Otocyon megalotis*
in the southwestern Kalahari

Season	Habitat	Time in patches	Patch diameter(m)	Distance to next patch (m)
Winter (diurnal feeding)	Short grass, <i>Rhigozum</i> shrubs	$\bar{x}$ =8,89 min SD=7,37 min n=22	$\bar{x}$ =25,4 SD=9,08 n=17	$\bar{x}$ =45 SD=31,27 n=19
	Riverbed, short grass	$\bar{x}$ =13 min SD=17,68 min n=10	$\bar{x}$ =70 SD=43,6 n=5	$\bar{x}$ =40 SD=16,04 n=7
Autumn (nocturnal feeding)	Short grass, <i>Rhigozum</i> shrubs	$\bar{x}$ =3,53 min D=2,77 min n=24	$\bar{x}$ =16,3 SD=10,27 n=17	no data
	Riverbed, short grass	1,67 min and 1,92 min	6 20	— —
	<i>Stipagrostis</i> <i>obtusata</i> flats	6 min and 4,12 min	30 25	— —

Feeding behaviour

Table 3 shows the number of feeding bouts per 5 min sampling period, and time per feeding bout of a known male and female bat-eared fox in winter and summer. There was no significant intersexual difference in the number of feeding bouts, winter or summer. However, when the male was accompanied by three cubs in summer his feeding bouts were significantly fewer than that of the female foraging independently. The male had significantly longer feeding bouts than the female in winter; the reverse applied during summer irrespective of whether or not cubs accompanied the male. In summer, when the cubs were still small, there was a great disparity in the total time spent foraging during a night by the male and female. The male guarded the cubs most of the time and foraged only ca. 3-4 h, in contrast to the female that foraged >8 h (see also Nel 1978).

Intrasexual comparison showed that the number of feeding bouts per 5 min period of the male did not vary significantly between sum-

mer and winter ($t=2,08$, $P > 0,05$). In the summer the presence or not of cubs did not affect the number of feeding bouts of the male significantly ($t=1,13$, $P > 0,5$), but compared to winter significantly fewer bouts resulted when the cubs accompanied the male ($t=3,73$, $P < 0,5$). Comparing the mean time per feeding bout of the male in winter and summer showed significant differences, whether or not the male was accompanied by cubs in summer ($t=5,04$ and $4,36$ respectively, $P < 0,05$); longer feeding bout times prevailed in winter. Again, in summer the presence or not of cubs did not affect the feeding bout time of the male significantly ($t=0,51$, $P > 0,05$).

The female had significantly more feeding bouts per 5 min period in winter ($t=3,12$, $P < 0,05$) than in summer. However, when comparing the number of feeding bouts per 5 min period in winter and during the first 4 h of foraging in summer, differences were not significant. Later in the night and up till cessation of feeding at dawn the number of feeding bouts per 5 min period dropped;

Table 3

Number of feeding bouts per 5 min period, and the mean time per feeding bout (seconds) per 5 min period of male and female Otocyon megalotis in the southwestern Kalahari.
Sample size refers to number of 5 min periods

Season (prey)	No. bouts/5 min.		Mean time(s)/feeding bout/5 min period (no. of bouts in parenthesis)	
Winter (termites)	♂ $\bar{x}=22,22$ SD=6,87 n=18	♀ $\bar{x}=28,92$ SD=6,85 n=25	♂ $\bar{x}=7,97$ SD=2,06 n=6 (164)	♀ $\bar{x}=6,27$ SD=1,17 n=15 (438)
	t=1,99, $P > 0,05$		t=2,4, $P < 0,05$	
(larvae)	sexes combined $\bar{x} = 1,95$ SD = 2,05 n = 20			
Summer (mixed)	♂ w. cubs $\bar{x}=12,5$ SD=5,42 n=18	♀ $\bar{x}=19,17$ SD=10,56 n=12	♂ w. cubs $\bar{x}=3,12$ SD=0,57 n=15 (186)	♀ $\bar{x}=4,68$ SD=1,40 n=9 (217)
	t=-2,8, $P < 0,05$		t=3,86, $P < 0,05$	
	♂ w. ♀ cubs $\bar{x}=19,17$ SD=10,56 n=12	♀ $\bar{x}=15,6$ SD=9,96 n=15	♂ w.o. cubs $\bar{x}=2,96$ SD=1,05 n=12 (127)	♀ $\bar{x}=4,68$ SD=1,40 n=9 (217)
	t=0,9, $P > 0,05$		t=-3,22, $P < 0,05$	

significantly more bouts occurred during earlier feeding ($t=4,12$, $P < 0,05$). There was no significant difference in mean time per feeding bout in winter and summer ($t=1,9$, $P > 0,05$). During the early stages of lactation (December) feeding bouts were significantly longer than later (January) when cubs had started to forage ($t=2,96$, $P < 0,5$).

Discussion

From the study, the indications are that the foraging behaviour of bat-eared foxes is related to their near catholic diet. Although primarily insects are eaten, usage probably depends on availability. Harvester termites occur year round in fox droppings, but are utilized more heavily in winter in the study

area (Nel 1978) as well as elsewhere (Mackie 1988), when their daytime above-ground activity increases (Nel & Hewitt 1969; Nel 1970).

The distribution of prey (clumped or dispersed), has a marked influence on the foraging pattern and the distance covered during a foraging period. Switching between clumped and dispersed prey can occur during a foraging period, depending on habitat type foraged in and presumably prey type availability; e.g. no digging for larvae was ever noted in the riverbed with its short grass cover but lack of shrubs.

No data are available on the energy content or nutrient value of the prey utilized in the study area. Published data for other areas suggest

that differences between termites and e.g. beetles would be slight (Redford & Dorea 1984; Van der Westhuizen, Hewitt & Van der Linde 1985) with figures of ca. 21-22 kJ⁻¹ average energy value and 15-20 % protein and 5-10 % fat pertaining, for individual insects in general or *Hodotermes mossambicus*.

If these figures indeed hold true then battered foxes do not have an optimal diet in the sense of selecting food with the highest energy (or nutrient) value as predicted by optimal foraging theory (see reviews by Krebs & McCleery 1984; Pyke 1984; Schoener 1987 and references therein) but rather that the optimal diet reflects the highest prey profitability, in this case resulting from optimal ingestion rate which occurs when feeding on clumped prey, such as termites. Feeding on larvae yields one prey item per feeding bout (irrespective of the length of the feeding bout, which includes digging for the prey item) whereas feeding on termites yields ca. 1 termite/s (Mackie 1988). Observations on utilization of particular patches indicate that their renewal time (Waser 1981) is probably not less than 24 h, but that >30 patches can be utilized during a particular day, even if no dispersed (single) prey items are utilized.

This kind of optimal diet could then account for the lack of territoriality, and mingling of groups (up to 15 individuals from 4 groups in 0.5 km²) when feeding on presumably productive patches, as no defence of resources is necessary (see also Waser 1981).

Data on patch feeding showed that no correlation existed between patch size and time spent in a patch, or between time in a patch and time (or distance) to next patch. There are no known methods of censusing termites, thus the correlation between number of termites and patch usage remains unknown. It is therefore difficult to test whether or not the marginal value theorem applies; the data indicate, however, that the "decision" to leave a patch is seldom "reconsidered" by immedi-

ately returning to the same patch. The observed foraging and feeding behaviour thus to some extent, and *a posteriori*, bears out that predicted in a qualitative fashion if the battered foxes were feeding optimally. Patch location, in this case distribution of termite colonies, is fixed and can be learnt and remembered.

The occurrence of enough termites to make exploitation of a particular patch profitable would be unknown, but are tested for; there are also enough other potential patches to visit and exploit. Habitat selection while foraging would afford the possibility of encountering many or few patches, many or few other dispersed prey items and thus perhaps other nutritional substances not available in patch (i.e. termite) prey.

Also, feeding bout duration and number of feeding bouts remain fairly constant, except for the negative influence of cubs, or the dictates of maximum energy acquisition by lactating females.

Perhaps, even though selection for optimal foraging functions on the individual level, some measure of optimal foraging of especially a pair can also operate in this species of strict monogamy and intensive bi-parental care. The high degree of sociality, lack of territoriality and overlap in home ranges in this canid also suggests an evolutionary adaptation to feeding on clumped prey resources, occurring in patches.

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