

Winter activity of bat-eared foxes *Otocyon megalotis* on the Cape West coast

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Diurnal activity budgets of bat-eared foxes *Otocyon megalotis* in winter (June) at the Postberg Nature Reserve, West Coast National Park, were analysed to determine the influence of environmental factors on their activity. Abiotic factors such as effective temperature, wind speed, cloud cover and rainfall have an effect on prey availability and thermoregulation of the foxes and therefore affect their activity rhythm. Low effective temperature and high wind speed result in more resting and less foraging by foxes. The reverse applies at high effective temperature and low wind speed. No foraging occurred during rain, and only for short periods when the sun shone on overcast days. With the start of pair formation in June–July allogrooming, which was not influenced by abiotic factors, increased. Foxes resumed activity from the same resting sites each day.

Tydbesteding aan verskillende aktiwiteite deur bakoorsosse *Otocyon megalotis* bedags gedurende die winter (Junie) in die Postberg Natuurreservaat, Weskus Nasionale Park, is geanaliseer om die invloed van omgewingsfaktore op aktiwiteite te bepaal. Abiotiese faktore soos effektiewe temperatuur, windspoed, wolkbedekking en reënval beïnvloed prooi beskikbaarheid en termoregulering van die vosse, en dus ook hulle aktiwiteitsritme. Lae effektiewe temperatuur en hoë windspoed veroorsaak meer rusperiodes en minder kossoek; die teenoorgestelde geld by hoë effektiewe temperatuur en lae windspoed. Geen kossoek vind plaas as dit reën nie, en slegs vir kort tye as die son deurbreek op bewolkte dae. Gepaardgaande met paarvorming in Junie–Julie is daar 'n toename in wederkerige tooiing, wat nie deur abiotiese faktore beïnvloed word nie. Vosse het elke dag vanaf dieselfde lêplek begin kos soek.

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Bat-eared foxes *Otocyon megalotis* prefer open habitat with a short grass cover but retreat to dense cover when danger threatens (Berry 1978; Lamprecht 1979; Smithers 1983; Malcolm 1986). In East Africa they are normally nocturnal (Lamprecht 1979), but in southern Africa activity gradually shifts from a diurnal regime in winter to a nocturnal regime in summer, when midday temperatures are high (Smithers 1971; Nel & Bester 1983). Bat-eared foxes are considered to be more social than other fox-like canids (Kleiman & Eisenberg 1972). Pair formation, associated with pair bonding behaviour, occurs during June–July and mean group size during 1974–1980 in the Kalahari Gemsbok National Park was 2.72, with a monthly variation of between 2.26 and 4.19 foxes/group (Nel, Mills & van Aarde 1984).

Although changes in activity periods have been documented for bat-eared foxes in southern Africa, no information exists on overall activity budgeting in this species. In fact, as far as canids are concerned, the only data of this kind available are on time-budgeting by coyotes (Bekoff & Wells 1981). The present study investigated the influence of proximate variables such as abiotic factors on activity patterns of free-ranging bat-eared foxes. As vantage points were restricted to the periphery of the study area only daytime observations could be undertaken; consequently a protocol period in winter (June) was selected.

Study area

The Postberg Nature Reserve (33°05'S / 18°E) on the Langebaan peninsula forms an integral part of the West Coast National Park. The 2 700 ha consist of low granite hills interspersed with flats, some of which are fields

cultivated prior to proclamation in 1969. Vegetation is West Coast Strandveld with major communities of *Nenax-Maytenus-Zygophyllum* (Limestone Evergreen Shrubland), *Atriplex-Zygophyllum* and *Pelargonium-Muralia* (Coastal Shelf Dwarf Shrubland) and *Ehrharta-Maurocena* (Hillside Dense Shrubland) (Boucher & Jarman 1977). The vegetation of the old cultivated lands consists mainly of 100 mm high *Atriplex semibaccata*, *Schismus barbatus* and *Penzia pilulifera*, and dense clumps of 1 m high groups of *Exomis microphylla* var. *axyrioides*. Rainfall at Langebaan village across the lagoon averages 253 mm p.a. with the highest rainfall in May and July (Boucher & Jarman 1977). During June 1987 it rained on four days, mist occurred on seven mornings, clearing later in the day, and strong berg winds blew on three days. All observations were made on bat-eared foxes active on an old cultivated land to the south-west of Konstabelkop.

Methods

Data on fox group sizes, activity patterns, and movements were collected by direct observation from a parked vehicle in June 1987, during daylight hours over 18 days, and during all weather conditions. One or more foxes were visible and observed for 151 h over this period; the actual number of 'fox-hours' (observation time × no. of foxes in sight) amounted to 1963. Binoculars (7 × 42) were used to scan the study area at 3-min intervals during a 30 min observation period every hour. Data on group size and position and activity category of each fox were recorded onto magnetic tape and later transcribed. On five days randomly distributed over the study period the last 15 min of each 30 min

observation period were used to record the activities of a focal animal. Activity budgets were calculated as the mean percentage of foxes engaged in each activity category per observation period. Observations were made at distances between 10–300 m.

Temperature (measured with a Brannan dry-bulb thermometer) and wind speed (measured with a Dueta standard anemometer) were used to derive the effective temperatures from the table in Mather (1974: 240). Other weather conditions (cloud cover and precipitation) were also recorded.

Home-range size and utilization

Home-range size and utilization were determined by initially recording the location of each individual or group at 30-min intervals and later plotting these onto tracing paper overlying a map of the study area. The size of daily diurnal home ranges was then determined with the Newmain image analyser computer programme by tracing the outermost localities on the plotted range on a digital tablet (minimum range method of Riney (1982)). The study area was divided, through topographical features, into a conceptual grid of 50 × 50 m cells, which was drawn and superimposed on a map of the study area. The number of times each cell was utilized by a group or individual was determined by noting animals as present or absent during each scan. Habitat selection and foraging patterns were also derived from these data. To determine the effect of weather conditions on home-range size and utilization, data from a protocol of two clear and two overcast days, each with an effective temperature corresponding to the average for June 1987, were used.

Activity budgets

Observed behaviour was allocated to four main categories namely rest, groom, walk and forage (see clarification of terms below). Data for each day were analysed by expressing the number of individuals in each behaviour category during each scan as a percentage of the total number of individuals in sight. Mean values of the percentage of individuals in each behaviour category were plotted against time of day, the effective temperature range and wind speed range. These were tested to see whether there was any significant correlation between effective temperature, wind speed, cloud cover or rainfall and activities of the bat-eared foxes. Occasional bouts of play, aggression, urination, defaecation and marking were merely noted and included in the walking category of the activity.

Foraging behaviour was further subdivided into rest, social, search and feed, while searching was broken down into stand, walk and trot (see clarification of terms below). These data were analysed as percentage of time spent per 15 min in each subdivision of foraging. The average time spent in each activity at the commencement, peak and termination of the day's foraging was again correlated with environmental variables, to determine their influence.

The significance of correlations between effective

temperature, windspeed and time spent in each major activity was tested using the (NWA) STAT-PAK 3.1 computer program. Regression was used to test the significance of correlations between foraging sub-categories, effective temperature and wind speed. The significance level was set at 1% ($p < 0,01$). One-way analysis of variance (f-distribution) was conducted using the Epistat computer programme with a significance level set at 1%; $F > 8,29$; $p < 0,01$.

Incidental data on communication, body postures and general behaviour were also recorded, and will be mentioned where appropriate.

Clarification of terms

Effective temperature

The ambient temperature and wind speed combined to reflect the actual temperature the animal is subjected to (Mather 1974: 238–242).

Precipitation

Rain and fog.

Cloud cover

Clear: less than 50% cloud cover, and sunshine on most of the study area.

Overcast: more than 50% cloud cover, and shade on the whole study area.

Activity

Four major categories of activity were recognized:

Rest: bat-eared foxes sleeping, or scanning the surroundings from a lying down or sitting up position during active periods.

Groom: grooming (one individual) or allogrooming (two or more individuals) while lying down, sitting or standing.

Walk: travelling by means of walking, trotting or running and for physiological needs (urinating or defaecating). Occurrence of play, marking and agonistic behaviour were also included in this category.

Forage: bat-eared foxes actively moving in and between feeding patches to search for prey items. This was recognized by the distinct foraging posture where the head is held forward, muzzle close to the ground, ears directed forward and downwards. When 'active periods/hour' are referred to, grooming, walking and foraging are included as a whole.

Foraging was subdivided according to time spent in each of four categories, which were defined as follows:
Rest: either sitting or lying down sporadically while foraging.

Social: time spent allogrooming or sporadically grooming during foraging. Play, urination, defaecating, marking and agonistic behaviour while foraging, were also included here.

Feeding: actual bouts of ingesting and chewing of food, with ears pulled back from forward position and muzzle

close to the ground (see Nel & Bester (1983) for further details of body postures).

Search: actual attempt to locate the position of prey items by sniffing, digging with front paws and listening. The ears are held forward, or pulled downwards and sideways and the head can either be held forward with muzzle close to the ground or in the upright position (Nel & Bester 1983).

Searching for prey was further subdivided into:

Stand: standing and looking forward or turning the body during searching for prey.

Walk: walking while searching for prey.

Trot: trotting while in search of prey items.

Results

Group sizes

Four pairs and two groups of three animals frequented the study area, to give a mean group size of 2,3. Usually only 13 foxes were visible at any one time, the other one being obscured by the vegetation. Occasionally a third individual from another group socialized with one of the pairs. Group cohesion relaxed and individuals foraged on their own when more than one group utilized the same food patch.

General activity

Foxes soon habituated to the vehicle and approached it closely (< 20 m). Activity commenced between 09h00 and 11h30 and ceased between 15h00 and 19h00, but varied according to weather conditions. Table 1 shows the hours spent being active, foraging or resting for the 18 days, and Table 2 the prevailing weather conditions and the time of day at the peak of resting and foraging

Table 1 The mean number of hours spent per day on resting, being active and foraging during winter days by bat-eared foxes (*Otocyon megalotis*) in the Postberg Nature Reserve, during 1 963 'fox-hours' of observation. Data is arranged according to clear (S) and overcast (O) days

Days (n)	Weather (O/S)	'Fox-hours'	Rest	Activity	Forage
12	S	1 560	5,96	7,58	4,83
6	O	403	7,17	6,5	1,67

Table 2 The prevailing diurnal effective temperature and wind speed ranges at the peak of rest and activity of bat-eared foxes (*Otocyon megalotis*) during winter (June 1987) in the Postberg Nature Reserve

Activity	Time of day	Eff. temp. range (°C)	Windspeed range (m/s)
Rest	10:30 and 17:30	-1,50- 3,50	8,00-1,50
Forage	14:30	25,00-27,00	0,50-1,50

for the same period.

Rain and / or mist suppressed activity; foraging only commenced when it had cleared in the mornings. Foraging also ceased during strong winds. On three occasions, foxes resumed foraging at dusk after resting for a few hours during and after overcast periods, strong wind or rain. During overcast conditions, mist or rain, resting sites were only left to urinate and defaecate, less than 20 m away. On clear days, however, these activities occurred anywhere in the home range, and up to 60 m from resting sites when leaving them in the morning. When it was overcast or rainy, individuals also huddled together, and grooming and allogrooming was less than on clear days.

Bat-eared foxes were located at the same resting sites every morning when observations commenced. Three dens were newly dug as evidenced by fresh soil. On four occasions, at approximately midday, foxes were seen briefly scraping soil from dens after emerging for the first time. On three occasions pairs were involved; on the other a group of three individuals. On all occasions turns were taken at digging, with the non-diggers being passive onlookers or busy grooming. Resting sites used when activity ceased for the day usually differed from where the same group was found the next morning, indicating some nocturnal movements.

Foxes left resting sites singly or as a group. Where three individuals rested together, one occasionally remained behind for some time when the others commenced foraging. Grooming and allogrooming occurred in every group observed. Resting, grooming and allogrooming occurred sporadically during foraging, while grooming also occurred for a short period after the termination of foraging, before the animals rested. Allogrooming occurred mostly between pairs, while grooming with a third individual was common in larger groups. Single individuals sometimes switched groups.

Agonistic behaviour was observed three times, when a third individual snapped at or muzzled in on a grooming pair, but was rebuffed and chased away. On one occasion all the foxes congregated on a 50 × 30 m area. Twirling runs, charging and rolling over were interrupted by loud snarls, short barks and yaps. No injuries were observed.

Utilization and size of diurnal home range

Average daily diurnal home-range size for the whole study period was 0,34 km². On overcast days ($n = 6$) the average size was 0,27 km² and on clear days ($n = 12$) 0,41 km². Home ranges of groups overlapped extensively. The borders of the home range of each group remained essentially static, and no particular shape of the home range could be derived from the limited data protocol. On three occasions, during play with a bontebok (*Damaliscus dorcas dorcas*), individual foxes temporarily left their usual range.

Movements within and between foraging patches, to urinate, defaecate, mark or play and to and from resting sites, determined the pattern of utilization of the home range. Movements within foraging patches seemed to

Table 3 The utilization of home range by bat-eared foxes (*Otocyon megalotis*) in the Postberg Nature Reserve. Prevailing weather conditions (effective temperature, wind speed and clear (S) and overcast (O) days) are indicated. The number of groups and hours active and foraging, as well as the number of times a specific 50 × 50 m cell in the home range was used for foraging are indicated

Weather (O/S)	Eff. temp °C (\bar{x})	Wind m/s (\bar{x})	Groups (No.)	Active hours	Foraging hours	Total number 50 × 50 m cells utilized					
						1×	2×	3×	4×	5×	
S	11,50	1,43	5	7	3,5	79	47	19	8	1	4
S	15,40	1,54	6	7,5	4,5	84	52	20	8	4	0
O	9,02	3,14	6	5	2,5	43	36	6	1	0	0
O	7,32	4,34	11	6,5	1,5	40	29	11	0	0	0

occur according to prey items, and movement for urination, defaecation and marking occurred haphazardly throughout the home range. The effect of wind direction on movements was not determined. Foxes were not seen to re-utilize particular 50 × 50 m cells on a particular day for foraging, but could cross them during other activities (Table 3). During lower effective temperature and strong wind foraging was desultory. This resulted in a smaller home range for those particular days, than on sunny days.

Activity budgets

Diurnal rhythm

Figures 1, 2 and 3 respectively illustrate total diurnal activity for 18 days in June, activity on clear days and activity on overcast days.

Rest. A bimodal diurnal resting pattern occurred (Figure 1). The first peak in the morning (10h30) followed a period of extensive grooming and occurred before foraging commenced for the day. The second (17h30) was after termination of foraging, which was followed by a short period of grooming. On clear days less resting occurred during foraging (Figure 2), while resting was common throughout the day on overcast days (Figure 3).

Forage. This was the obverse of resting. A unimodal diurnal foraging pattern prevailed with a peak at 14h30, despite variations in prevailing effective temperature, wind speed and cloud cover. Some foraging by one or two individuals before the others started occurred, but such individuals ceased foraging after a short while and only started again when the others commenced foraging. The average time for commencement of foraging by most foxes on clear days ($n = 12$) was 12h00, while foraging terminated at 17h30, giving an effective foraging period per day of 5 h 30 min. A slow decline in the number of individuals foraging later in the day and a high percentage of the total number of individuals in the study area foraging were also noted on clear days (Figure 2). On overcast days foraging only occurred during periods of sunshine but only a low percentage of the total number of individuals then foraged at any one time. An increase in foraging intensity and number of individuals foraging occurred after the sky cleared late in the afternoons.

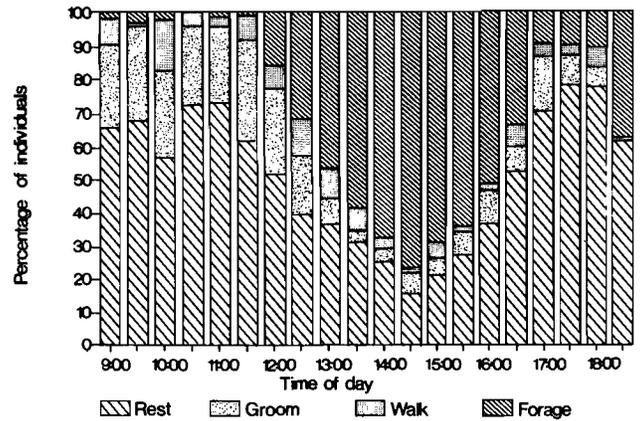


Figure 1 Diurnal activity budget of bat-eared foxes *Otocyon megalotis* in Postberg Nature Reserve in relation to time of day. Data is expressed as the percentage of individuals in a certain activity category at a certain time of day during June 1987. Values have been standardized for the number of foxes observable during each 30 min observation period.

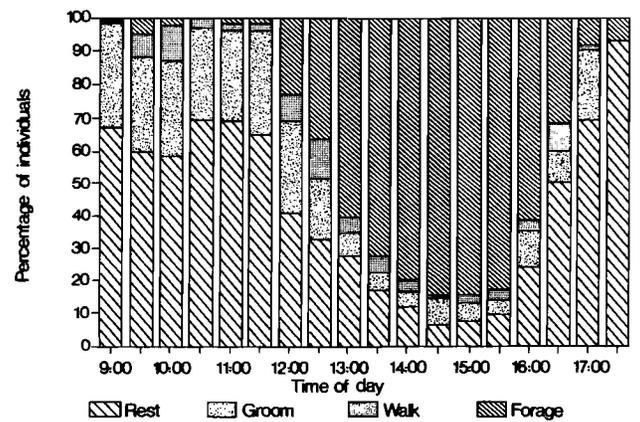


Figure 2 Diurnal activity of bat-eared foxes *Otocyon megalotis* in Postberg Nature Reserve in relation to time of day on a clear winter's day.

Groom. A peak in diurnal grooming occurred after waking up and prior to commencement of foraging in the morning. A second peak occurred after foraging ceased and before sleeping. Short bouts of grooming and allo-

grooming interrupted foraging (Figure 1). Proportionally more grooming than foraging occurred on overcast days than on clear days, but less in relation to resting (Figures 2 & 3).

Walk. Most direct movements occurred when travelling within and between feeding patches and for urinating, defaecating and marking. Minimal walking (without intervals of actual feeding) occurred during foraging (Figure 1). On overcast days walking only occurred early in the morning and late in the afternoon in order to urinate and defaecate.

Effect of effective temperature and wind speed

Distinct differences in the amount of time spent on specific activities were found when related to the effective temperature and wind speed.

Rest. When effective temperature increased, resting decreased (Figure 4); a significant negative correlation between effective temperature and resting at a range of 1,5–27°C ($r^2 = 0,85$; $p < 0,001$; $d.f. = 56$) resulted.

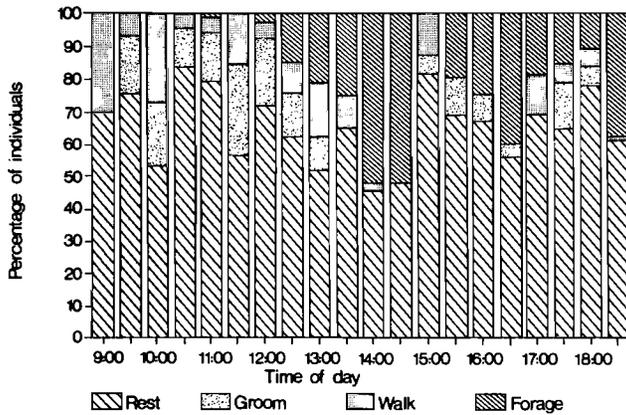


Figure 3 Diurnal activity of bat-eared foxes *Otocyon megalotis* in Postberg Nature Reserve in relation to time of day on an overcast winter's day.

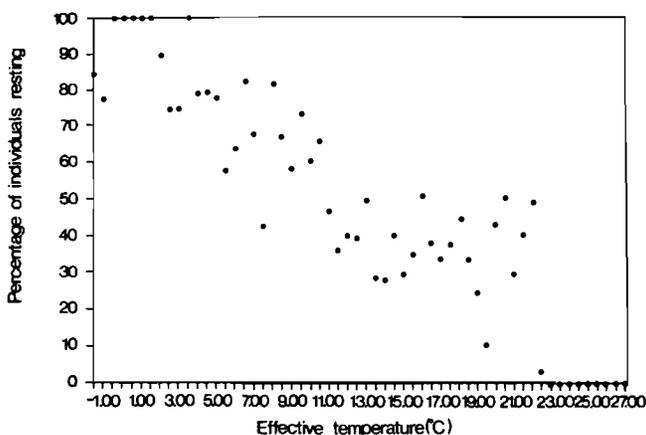


Figure 4 The effect of diurnal effective temperature on resting activity of bat-eared foxes *Otocyon megalotis* during June 1987. Data is expressed as the mean percentage of individuals resting at the effective temperature.

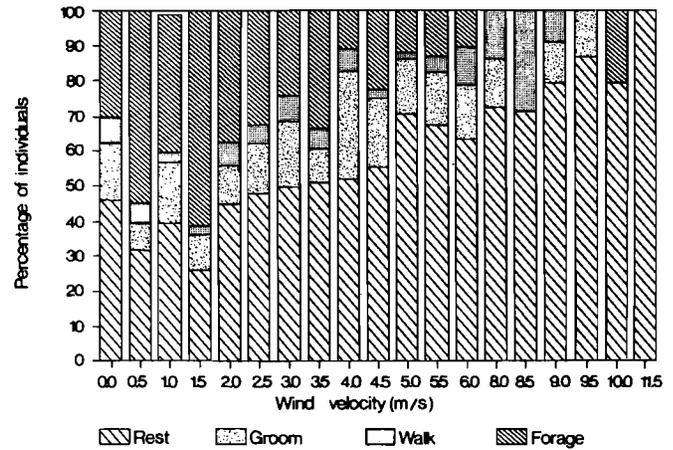


Figure 5 The effect of windspeed on diurnal activity budgeting of bat-eared foxes *Otocyon megalotis* during June 1987. Data is expressed as the mean percentage of individuals engaged in each activity.

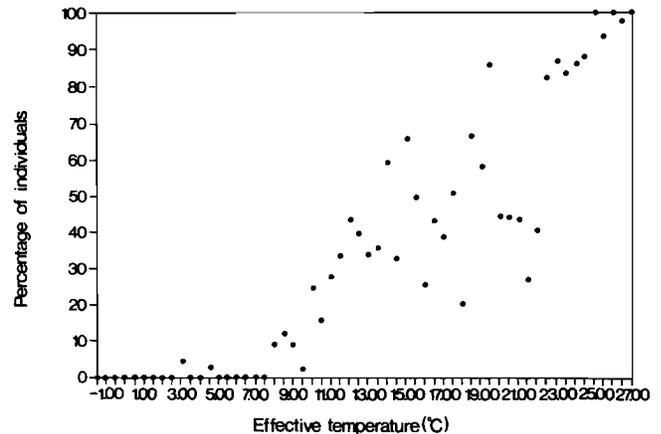


Figure 6 The relationship between effective temperature and percentage of bat-eared foxes *Otocyon megalotis* foraging during June 1987 in the Postberg Nature Reserve.

Figure 5 shows that with increasing wind speed the percentage of foxes resting increased; this is significant at a wind speed of 0–11,5 m/s ($r^2 = 0,89$; $p < 0,001$; $d.f. = 18$).

Forage. The percentage of foxes actively foraging increased significantly with increasing effective temperature ($r^2 = 0,82$; $p < 0,001$; $d.f. = 56$) (Figure 6). Figure 5 also shows that as windspeed increased, the percentage of total number of individuals foraging decreased. This relationship is significant ($r^2 = 0,68$; $p < 0,01$; $d.f. = 18$).

Groom. Time spent grooming was not significantly influenced by the reigning effective temperature ($r^2 = 0,04$; $p > 0,01$; $d.f. = 56$) or wind speed ($r^2 = 0,30$; $p = 0,02$; $d.f. = 18$).

Walk. There was no significant correlation between walking and effective temperature or between walking and wind speed ($r^2 = 0,01$; $p > 0,01$; $d.f. = 18$). Walk-

ing appeared to be linked to foraging and physiological needs only.

Analysis of variance indicated that (with 99% certainty) a highly significant linear relationship between effective temperature and resting ($F > 78,29$; $d.f._1 = 1$; $d.f._2 = 18$; $p < 0,01$), and effective temperature and foraging ($F > 8,29$; $d.f._1 = 1$; $d.f._2 = 18$; $p < 0,01$) prevailed. No significant linear relationship was found between effective temperature and grooming ($F < 3,01$; $d.f._1 = 1$; $d.f._2 = 18$, $p > 0,01$) or walking ($F < 3,01$; $d.f._1 = 1$; $d.f._2 = 18$; $p > 0,01$). A highly significant linear relationship also existed between windspeed and resting ($F > 8,29$; $d.f._1 = 3$; $d.f._2 = 16$; $p < 0,01$) and foraging ($F > 8,29$; $d.f._1 = 3$; $d.f._2 = 16$; $p < 0,01$). A non-significant relationship occurred between windspeed and grooming ($F < 4,41$; $d.f._1 = 3$; $d.f._2 = 16$; $p > 0,01$), and windspeed and walking ($F < 4,41$; $d.f._1 = 3$; $d.f._2 = 16$; $p > 0,01$).

Foraging budgets

Foraging time budgets are illustrated in Figure 7, with the time spent on the subdivisions of searching (walking, standing and trotting) in Figure 8. Figure 9 shows the subdivision of foraging time during twenty 15-min periods at commencement, peak (when the greatest number of foxes are foraging), and towards termination (when time spent by foxes to forage declined) of foraging during the 18 days of this study. At commencement of foraging, early in the day, the greatest percentage of time was spent resting and on social activities. Percentage of time spent on actual feeding bouts was greatest at the peak of foraging, while the most time spent searching for prey items was near the end of foraging. Standing still while searching for prey occurred mostly near the termination of the day's foraging. Walking and trotting while searching for prey items mostly occurred at commencement of foraging. Walking was equally distributed throughout the day, with trotting occurring mostly at the

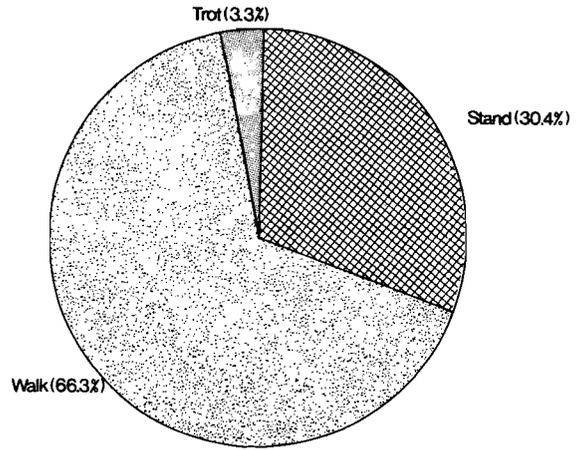


Figure 8 Division of searching time during foraging by bat-eared foxes *Otocyon megalotis* in June 1987. Data are expressed as percentage of total time spent on each subdivision.

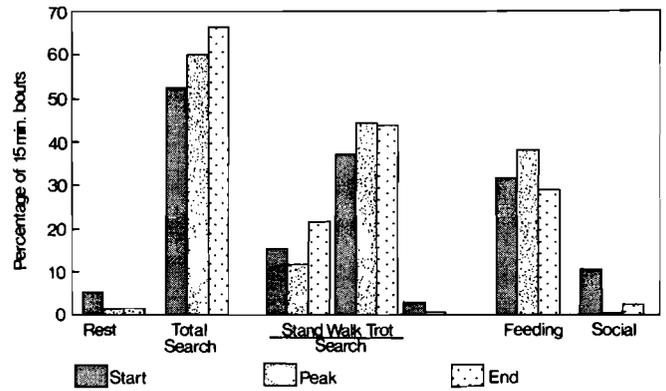


Figure 9 Division of foraging time (rest, feeding and social) at the start, peak, and end of foraging by bat-eared foxes during winter in the Postberg Nature Reserve. Subdivisions of search (stand, walk, trot) are given. Data are expressed as percentage of time per 15 min observation period.

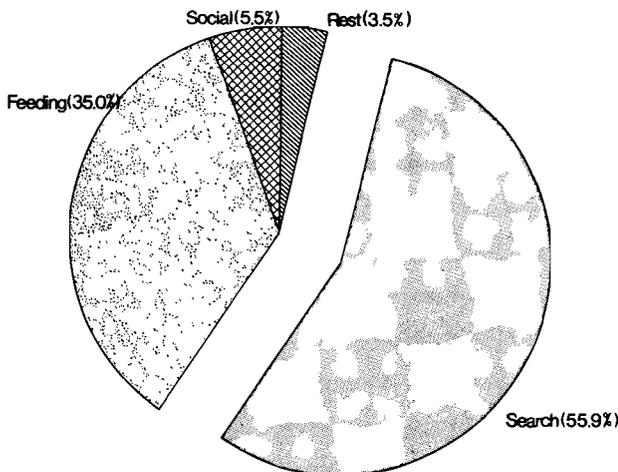


Figure 7 Division of diurnal foraging time by bat-eared foxes *Otocyon megalotis* in June 1987 in the Postberg Nature Reserve. Data is expressed as the percentage of time spent in each category of foraging during 15 min observation periods.

peak of foraging. On average 35% of the 15 min observation periods was spent on actual feeding. Feeding bouts were recognized by the position of the ears, these being flipped back from the forward-pointing position when actually feeding (ingesting), with the muzzle near the ground (see Nel & Bester 1983). Limited data on the number of feeding bouts/15 min, the mean duration and the range of bouts at the start, peak and termination of foraging, are given in Table 4. Most bouts occurred at the peak of foraging while individual bouts were shortest towards the end of the foraging period each day, probably as saturation point of feeding was approached.

Effective temperature had no significant influence on resting during foraging ($r^2 = 0,41$; $p > 0,01$; $d.f. = 17$), or time spent searching ($r^2 = 0,25$; $p > 0,01$; $d.f. = 17$). No significant correlation was found between effective temperature and percentage of time spent on social activities during foraging ($p > 0,01$). Wind speed apparently also had no significant effect on division of

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Table 4 Number and duration of feeding bouts of bat-eared foxes (*Otocyon megalotis*) at commencement, peak and terminal phases of diurnal foraging during June 1987

Stage of foraging	Mean		S.D.	Range (s)
	No./15 min	duration (s)		
Commence	8,80	17,91	3,69	4,00–40,20
Peak	12,10	14,79	7,90	2,20–32,10
Terminal	9,50	11,88	2,50	2,25–28,25

foraging time by bat-eared foxes. The average effective temperature at commencement of foraging was 13,13°C (*S.D.* = 4,14), and the average wind speed was 2,72 m/s. The average effective temperature at termination of foraging was again 13,13°C (*S.D.* = 4,76) with an average wind speed of 1,38 m/s.

Bat-eared foxes left resting sites without preliminary scouting for possible predators. Group members tended to stay between 5 and 50 m of each other when foraging, but sometimes foraged close together (< 1 m), or far apart (\geq 100 m). Foraging in patches was the main foraging pattern observed. At the peak of foraging a number of groups could aggregate on a single food patch and feed in a radius of 15 m. More than one aggregation sometimes formed at the same time. The duration of these aggregations of foxes varied between 15 and 90 min (\bar{x} = 37,6 min). The areas the aggregations foraged in varied from 20 × 20 m to 150 × 200 m (\bar{x} = 55 × 70 m).

Discussion

Proximate factors such as social organization, food availability, and environmental conditions influence various aspects of the activity patterns of bat-eared foxes. The size and utilization of the home range, their foraging strategies, and activity budgeting were apparently determined by environmental conditions which directly influenced prey availability and thermoregulation. The shift from a general diurnal activity regime in winter to a nocturnal regime in summer also occurs in other areas (Smithers 1971; Nel 1978; Mackie 1988), and can probably be ascribed to prevailing temperatures. During our study diurnal activity occurred between -1 and 27°C. Mean maximum and minimum temperatures in the area are 14,6°C and 8,7°C (July), and 21°C and 13,2°C in February; while absolute winter and summer maxima are 30,6°C and 29,0°C.

Size and utilization of home range

The foraging patterns of the foxes probably determine the size and utilization of their home range. The smaller home range on overcast days, as compared with clear days, probably results from lower temperatures negatively affecting prey activity and availability. This resulted in temporarily less activity and more resting by foxes which often huddled together, as also observed during cold winter nights in the Kalahari and Namib deserts

(Nel unpubl. data). Foraging only during the short periods of sunshine on overcast days further emphasizes this phenomenon. Waser (1980, 1981) emphasized the role of prey availability and prey replenishment in foraging patterns of small carnivores. In our study area bat-eared foxes feed primarily on harvester termites *Microhodotermes viator*, a clumped, time-depleted prey base. In a study subsequent to ours Smit (1989) found that these termites, in our study site, quickly (< 2 min) reacted to disturbance of foraging workers and retreated underground; renewal of this prey source (i.e. workers emerging from the same foraging port) took at least 24 h. Thus revisiting the same area (50 × 50 m cell in this case) would clearly be pointless from a foraging point of view.

General activity and activity budgeting

Some nocturnal activity occurred, as evidenced by the different resting sites used at the end of one day and the start of the next. These movements of unknown extent and duration could be to supplement food acquired during diurnal foraging, especially on overcast days when prey was scarce. The commencement of, peaks in, cessation, and budgeting of various activities can thus be related to environmental factors. The time of day, prey availability, thermoregulatory and metabolic needs (in relation to the success during foraging caused by the environmental factors) also influenced activity budgeting.

The influence of effective temperature and wind speed on resting and foraging patterns can be related to the following. (i) Bat-eared foxes have been found to depend primarily on auditory and olfactory means in locating prey (Nel & Bester 1983). High wind speed and rain hinder this, as the rustling of prey is masked by background noise. (ii) At high wind speed and low temperature foxes rest or groom in dens or sheltered by vegetation, for thermoregulatory purposes. (iii) *Microhodotermes viator* was the main prey item (MacDonald & Nel 1986), and, like the closely related *Hodotermes mossambicus* is active by day during winter, and at night during summer. Low temperatures inhibit the activity of these termites. Considering this, the energy expended to forage when few prey (termite and other insects) are available can exceed the energy gain. This could also explain the presence of occasional early morning foragers which soon ceased foraging only to recommence later in the day.

Peaks of rest and foraging remain constant despite weather conditions, on clear and overcast days. In winter, peak time of activity (and probably prey availability) coincided with peak diurnal temperature. The extended peak of foraging on clear days can thus be linked to the availability of prey for longer periods. Temperature, directly or through prey availability, thus seems to be the overriding factor determining resting and foraging activity.

More grooming would be expected during June–July than at other times of the year, as Nel (1978), Lamprecht (1979), Nel & Bester (1983) and Smithers (1983) found that during June–July pair formation, associated with pair bonding, takes place. Agonistic behaviour during

allogrooming, overt aggression, and single individuals moving between groups are further correlates of pair or sibling group formation. Sharing of dens and resting sites, setting off in pairs or threes to forage, and occasional single individuals, agrees with the findings by Nel (1978), Lamprecht (1979) and Malcolm (1986).

Foraging strategies

An initial part of the foraging route, starting from the same resting spot each morning, remained constant for a few days in succession, as also noted by Nel (1978).

Bat-eared foxes are opportunistic feeders. Scats or stomach contents analysed by Bothma (1966), Smithers (1971), Nel (1978), Berry (1981), and MacDonald & Nel (1986) show that insects, on the basis of percentage occurrence in faecal droppings, formed the main prey component. At Postberg this comprised, besides the harvester termites *Microhodotermes viator*, Coleoptera and Formicidae (MacDonald & Nel 1986). Ascertaining their prey when foraging could be determined most accurately when foxes were feeding on termites, owing to their distinct behaviour of casting around in a food patch, while extensive digging during foraging occurred probably in pursuit of underground larvae of Coleoptera.

Time budgeting during foraging resulted from prey availability and an opportunistic foraging strategy. The high percentage of time spent resting and socializing just after becoming active may be due to prey not being abundant early in the day, when temperature is lower than later on. At the start of foraging in the late morning food patches are intact and foxes feed unselectively because of hunger. Feeding bouts last long, and the least time is spent searching for specific prey items. As the day progresses and the peak of foraging is reached the number of feeding bouts increase while their duration decreases, probably owing to termites and other prey seeking refuge when disturbed (Lamprecht 1979), and / or more selective foraging, or variation in termite foraging party size. Towards the end of the day's foraging, the fewer and shorter feeding bouts and more time spent at searching for prey might be the consequence of the foxes becoming satiated, and being more selective in prey acceptance (Lacher, Willig & Mares 1982).

The influence of effective temperature and wind speed on the percentage of time spent resting and searching for prey at commencement, peak and termination of foraging is again due to prey availability, thermoregulatory needs, the satisfaction of hunger and the consequent selectivity with which prey are sought. The phenomenon that foraging occurred only when the sun shone for short periods on overcast days can also be linked to thermoregulation and prey availability.

Bat-eared foxes appear to make use of the advantages of communal foraging such as detecting predators and extracting of more food from patches of e.g. harvester termites, which is time-depleted. If a foraging partner is a pair mate or offspring, their communal foraging is even more advantageous (Lamprecht 1979). The aggregations formed at the peak of foraging in this study are believed

to be for similar reasons; no advantage would accrue to different groups or individuals in defending a territory, if a major prey source (termites) are time-depleted not only through feeding, but also through disturbances (Waser 1981). Communal foraging by several groups has also been recorded by Nel (1978), Koop & Velimirov (1982) and Malcolm (1986) in other parts of Africa.

The strategy of foraging, time budgeting while foraging and choice of prey by bat-eared foxes in this and other studies thus seems to be dictated by prey availability, which is influenced by effective temperature, wind speed and general weather conditions.

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References

- BEKOFF, M. & WELLS, M.C. 1981. Behavioural budgeting by wild coyotes: the influence of food resources and social organization. *Anim. Behav.* 29: 794–801.
- BERRY, M.P.S. 1978. Aspects of the ecology and behaviour of the bat-eared fox, (*Otocyon megalotis* Desmarest, 1822) in the Upper Limpopo Valley. Unpubl. M.Sc. Thesis, University of Pretoria.
- BERRY, M.P.S. 1981. Stomach contents of bat-eared foxes, *Otocyon megalotis*, from the northern Transvaal. *S. Afr. J. Wildl. Res.* 11: 28–30.
- BOTHMA, J. du P. 1966. Notes on the stomach contents of certain Carnivora (Mammalia) from the Kalahari Gemsbok Park. *Koedoe* 9: 37–39.
- BOUCHER, C. & JARMAN, M.L. 1977. The vegetation of the Langebaan area, South Africa. *Trans. roy. Soc. S. Afr.* 42: 241–272.
- KLEIMAN, D.G. & EISENBERG, J. 1972. Comparisons of canid and felid social systems from an evolutionary perspective. *Anim. Behav.* 21: 637–659.
- KOOP, K. & VELIMIROV, B. 1982. Field observations on activity and feeding of bat-eared foxes (*Otocyon megalotis*) at Nxai Pan, Botswana. *Afr. J. Ecol.* 20: 23–27.
- LACHER, T.E., Jr., WILLIG, M.R. & MARES, M.A. 1982. Food preference as a function of resource abundance with multiple prey types: an experimental analysis of optimal foraging theory. *Am. Nat.* 120: 297–316.
- LAMPRECHT, J. 1979. Field observations on the behaviour and social system of the bat-eared fox (*Otocyon megalotis* Desmarest). *Z. Tierpsychol.* 99: 260–284.
- MACDONALD, J.T. & NEL, J.A.J. 1986. Comparative diets of sympatric small carnivores. *S. Afr. J. Wildl. Res.* 16: 115–129.

- MACKIE, A.J. 1988. Bat-eared foxes *Otocyon megalotis* as predators on harvester termites *Hodotermes mossambicus* in the Orange Free State. Unpubl. M.Sc. thesis, Univ. of Stellenbosch.
- MALCOLM, J.R. 1986. Socio-ecology of bat-eared foxes (*Otocyon megalotis*). *J. Zool., Lond.* 208: 457-467.
- MATHER, J. 1974. Climatology: fundamentals and applications. McGraw-Hill, New York.
- NEL, J.A.J. 1978. Notes on the food and foraging behavior of the bat-eared fox *Otocyon megalotis*. *Bull. Carnegie Mus. Nat. Hist.* 6: 132-137.
- NEL, J.A.J. & BESTER, M.H. 1983. Communication in the southern bat-eared fox *Otocyon m. megalotis* (Desmarest, 1822). *Z. Säugetierk.* 48: 277-290.
- NEL, J.A.J., MILLS, M.G.L. & VAN AARDE, R.J. 1984. Fluctuating group size in bat-eared foxes (*Otocyon m. megalotis*) in the south-western Kalahari. *J. Zool., Lond.* 48: 294-298.
- RINEY, T. 1982. Study and management of large mammals. Wiley Interscience Publ., New York.
- SMIT, B.S. 1989. Insect availability and renewal rate in two habitats. Unpubl. B.Sc. Honours project, Univ. of Stellenbosch.
- SMITHERS, R.H.N. 1971. The mammals of Botswana. *Mus. mem. 4, Nat. Mus. Rhodesia.*
- SMITHERS, R.H.N. 1983. The mammals of the southern African subregion. Univ. of Pretoria, Pretoria.
- WASER, P.M. 1980. Small nocturnal carnivores: ecological studies in the Serengeti. *Afr. J. Ecol.* 18: 167-185.
- WASER, P.M. 1981. Sociality or territorial defense? The influence of resource renewal. *Behav. Ecol. Sociobiol.* 8: 231-237.