ASPECTS OF THE ECOLOGY AND BEHAVIOUR OF THE BAT-EARED FOX, *OTOCYON MEGALOTIS* (DESMAREST, 1822), IN THE UPPER LIMPOPO RIVER VALLEY

by

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ABSTRACT

Bat-eared foxes were studied at two different areas in the upper Limpopo valley. Their habitat preferences, denning and feeding behaviour were investigated. Captive foxes were examined to determine growth curves and changes in dentition and pelage. Population densities and activity cycles were determined. Bat-eared fox populations were found to be limited by a number of abiotic and biotic factors and fluctuated in response to these factors.

I thank Estate Late A.V. Lindbergh for the opportunity to carry out this research on Mmabolela Estates, Northern Transvaal and Ian and David Haggie for allowing me to work at Mashatu, Botswana. Also Clive Walker and the Endangered Wildlife Trust for the use of their facilities and vehicle at Mashatu.

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And finally, I thank all the game scouts on Mmabolela, particularly Mr. Selete Sebadi and Mr. Molele Pheseke who assisted me throughout the study.

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INTRODUCTION

The bat-eared fox Otocyon megalotis is at present classified under its own subfamily the Otocyoninae. However, there is anatomical (Guilday, 1962) and behavioural (Kleinman, 1967) evidence to suggest that Otocyon is closely related to the grey fox genus Urocyon and the raccoon dog genus Nycteroides.

Three subspecies of Otocyon megalotis are recognised by Coetzee (1967). The southern form (O. m. megalotis) is found throughout the semi-arid regions of southern Africa. The northern form O. m. virgatus) is found from Tanzania northwards to southern Sudan with a third form (O. m. canescens) in Ethiopia and Somalia.

STUDY AREAS

The study was done on two areas (Fig.1). The main study was centered on a private nature reserve, Mmabolela Estates, in the far northwestern Transvaal bushveld, bordering on the Limpopo River ($22^{o}38'$ S; $22^{o}16'$ E), but specimens were collected as far as 30 km around Mmabolela.

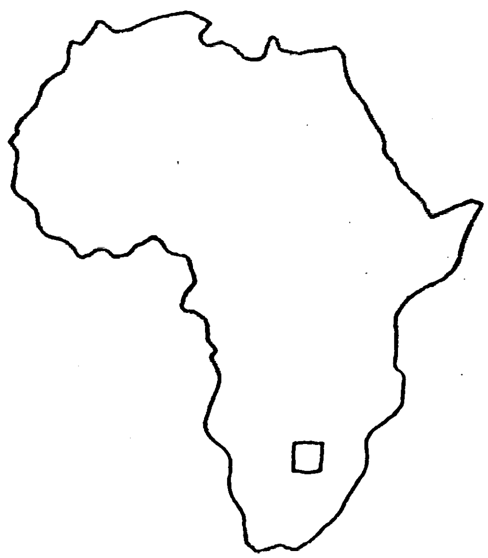
Mmabolela comprises an area of 5 371 ha with a mean annual rainfall of 300 mm (Range: 125 - 700 mm).

The main soil type is Hutton form, Shorrocks series, but also includes Hutton series and form Mispah, Muden series.

Acocks (1953) classifies this veld type broadly as Arid Sweet Bushfeld divided further into *Grewia flava* veld and dwarf *Commiphora* veld. The veld type is characterised by scrub savanna with a sparse herbaceous grass layer. The more common plant species include :

Acacia erubescens	*Commiphora pyracanthoides*	*Enneapogon cenchroides*
Acacia mellifera	*Grewia* spp.	*Pannicum maximum*
Acacia nigrescens		*Aristida* spp.
Acacia tortilis		*Eragrostis rigidior*
Boscia albitrunca		*Eragrostis superba*
Terminalia prunioides		

During the latter part of this project, a second study area was visited at the confluence of the Shashi and Limpopo Rivers in the Mashatu Game Reserve (22^{o} 10' S; 29^{o} 15' E) in Botswana (Fig. 1). This area lies some 90 km east of Mmabolela and attention here was concentrated on a narrow strip of land between the Limpopo riverine gallery bush and *Colophospermum mopane* woodland.



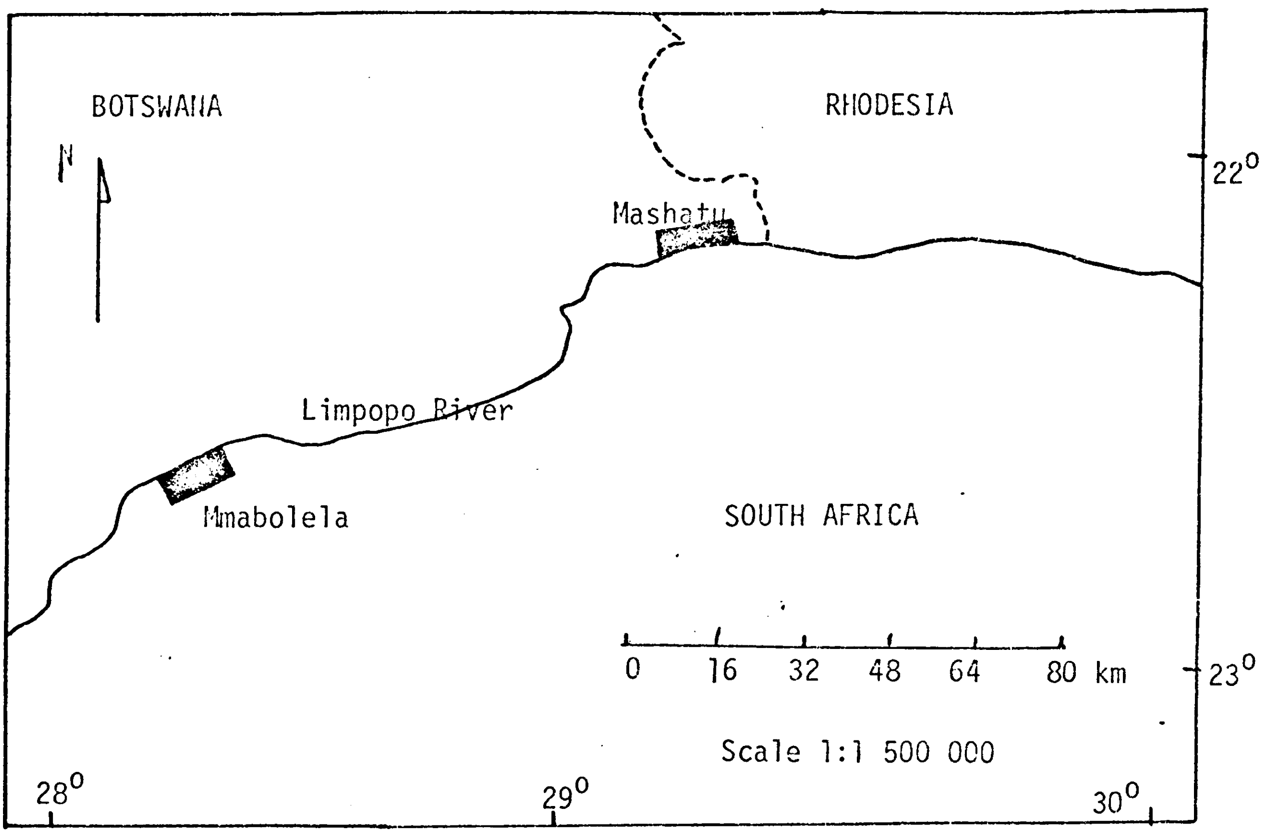


Figure 1. Location of the study areas, Mmabolela Estates in Northern Transvaal, South Africa and Mashatu in Botswana, in the Upper Limpopo River Valley

The soil type here is mainly form Mispah, Muden series, and consists of calcareous soils. The mean annual rainfall is 250 mm, the increased aridity giving rise to an open veld type with sparsely scattered trees and shrubs mainly comprising Boscia albitrunca, Boscia foetida, Sesamothamnus lugardii and Acacia newbrownii. Grass, when present, was sparse and annual herbs were plentiful.

The low rainfall and high game concentrations on this area resulted in a bare and downgraded veld type.

MATERIALS AND METHODS

CAPTURE

Attempts to entice bat-eared foxes into baited traps proved futile. Dogs were used to try and run down foxes but this also proved unsuccessful, as foxes had no difficulty in evading the dogs. Finally dens were located during the breeding season and the occupants excavated. In this manner it was possible to obtain juvenile foxes but adults always vacated the den at our approach and could therefore not be captured alive. Of 12 dens excavated, six were found to be occupied and contained a total of 13 pups (Range 1 - 4).

All juveniles excavated from dens were tagged and marked. This was done by puncturing two holes about 20 mm apart in both ears and a numbered tag fixed in these holes with a coloured rectangle of plastic approximately 30 x 50 mm in size. A differently coloured plastic strip was used for each ear, thus giving a number of combinations for later identification (Fig. 17).

Captive foxes were kept in a pen measuring 20 x 40 m and containing natural bush. The pen was constructed of wire mesh 1,4 m high and buried 0,9 m below ground level to ensure that the animals did not burrow out.

GROWTH

Throughout the study period foxes killed by vehicles on roads through the Mmabolela study area were collected and standard body measurements recorded. Of 19 individuals, 13 juveniles excavated from dens were similarly measured. Seven captive foxes were initially measured and weighed bi-weekly, but the period between measurements increased with age.

The standard measurements used were the following :

Total length from nose tip to end of the terminal vertebra of the tail.
Tail length from the base of the tail to the end of the terminal vertebra of the tail.
Hindfoot length from the heel to the end of the longest claw.
Ear length from the ear notch to the tip of the cartilage of the ear.
Mass was recorded on a balance calibrated in units of 10 gm and with a 3 kg capacity; thereafter on a spring balance graduated in 100 gm units.

In addition to the above measurements, captive foxes were examined to determine development in dentition and pelage. Similarly, mortalities were examined for moult.

STOMACH ANALYSES

The stomachs of 21 road mortalities collected were removed and preserved in 10 per cent formaldehyde solution. Of these 18 were later examined volumetrically after Bothma (1966 a). The contents were identified and separated into their respective classes and the volume of each class determined separately. These results are expressed as a percentage occurrence of each class in Table 5 i.e. the number of stomachs out of 18 in which each class was recorded.

ACTIVITY STUDIES

These studies commenced in 1975 on Mmabolela. However, over 1 000 km were driven without seeing one bat-eared fox, so it was decided to move to Mashatu in Botswana where foxes appeared more plentiful.

A drive varying between 7,6 and 10,0 km was then driven when possible at hourly intervals throughout the night on four nights and the number of foxes, group size and composition were recorded. Two operators with spotlights each covered one side of the vehicle. The maximum effective distance of the light beam was about 100 m either side of the road.

DENSITY DETERMINATION

For the Mmabolela study area, a Lincoln index was used for determining the size of the bat-eared fox population, i.e. :-

$$N = n \frac{M}{m}$$

N = Population size

n = Total number of sightings

M = Number of marked foxes

m = Number of sightings of marked foxes

Sightings were used for only one year after releasing and marking foxes in determining the population size over Mmabolela, and thus the density per square kilometre.

For Mashatu population data collected on activity studies were used to determine the population size. The distance travelled per drive was recorded and assuming all foxes 100 m either side of the vehicle were seen, this gave an area as follows :

$$\text{Area (km}^2) = \frac{\text{Distance driven (m)} \times 200}{1\,000 \times 1\,000}$$

Hence the density per square kilometre could be determined.

SIGHTING DATA

Sight records of Mmabolela (Table 11) are divided into calendar years i.e. from the 1st January one year to 31st December of that year.

In Table 12 sight records have been divided into a twelve month period from 1st April to 31st March. This allows a better comparison with annual rainfall which occurs mainly during the spring and summer months (September to March inclusive). Data for the Kruger National Park (Table 13) are also divided into the same annual periods.

RESULTS AND DISCUSSION

HABITAT PREFERENCE

Although found generally in dry savanna country, in this study the bat-eared fox definitely shows a preference for more open, bare areas as found by Shortridge (1934) and Smithers (1971). This was particularly so for calcareous soils that by their nature tend to have a sparse ground cover as a result of their susceptibility to trampling and overgrazing, and is illustrated by calcareous pans with which foxes are often associated (Smithers, 1971; Parris, 1976). Further evidence for their preference for bare, open areas is the frequency with which foxes are encountered on gravel roads.

The preference for short grass to bare areas shown by the bat-eared fox is related to feeding and its further association with calcareous soil for denning.

The study area at Mashatu primarily consisted of these bare soil types (Figs. 2 and 3) which would account for the high number of foxes found there. On Mmabolela, these areas only covered portions of the study area (Figs. 4 and 5). It is probable that foxes spend periods of time in what must be considered marginal habitat where the herbaceous layer is either too dense and/or too long to be considered prime habitat.

The considered prime fox habitat of bare, open scrub as found around pans and on calcareous soils is largely a result of overgrazing and trampling by high concentrations of both large and small herbivores as has been shown by Parris (1976). It is, therefore probable that with

Figure 2. Typical open veld with a short sparse ground cover as found at Mashatu, Botswana

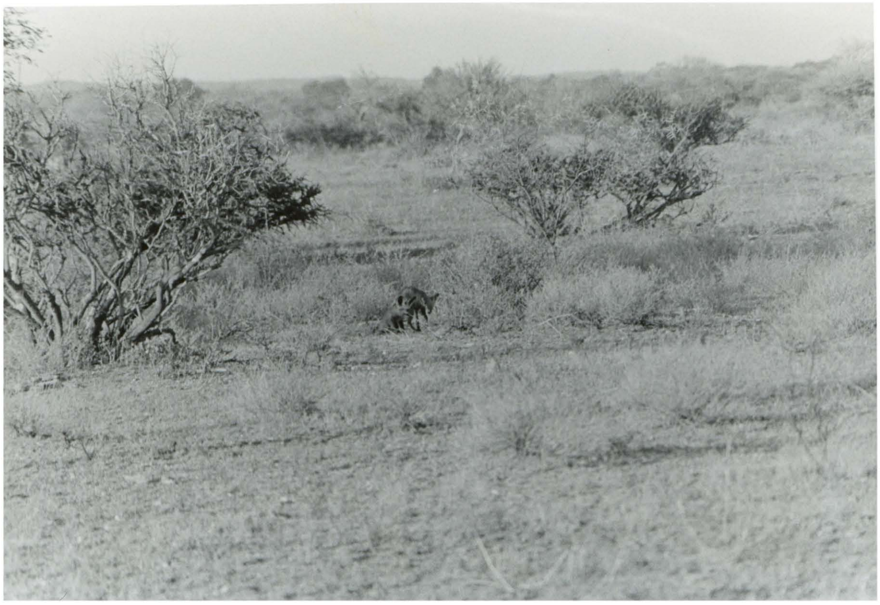
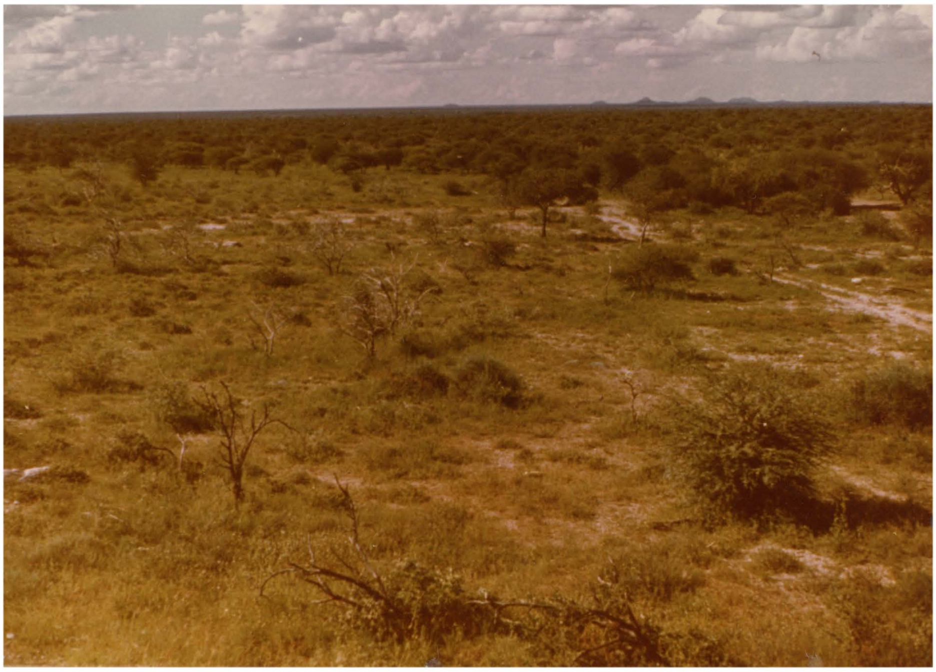
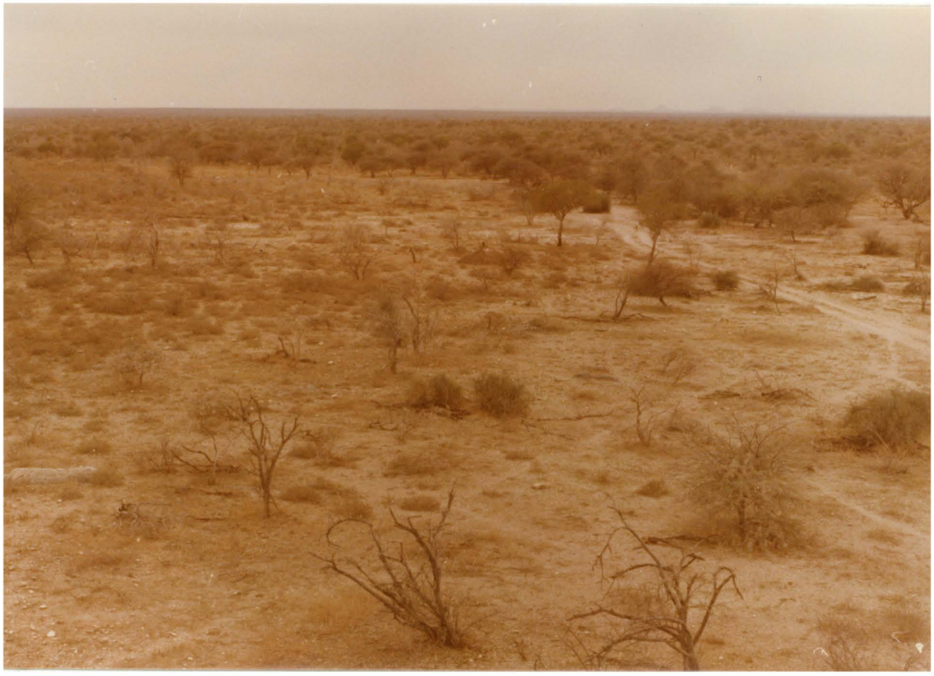


Figure 3. A pair of bat-ear foxes, Otocyon megalotis moving off to shelter at first light at Mashatu, Botswana, during December, 1976



(a)



(b)

Figure 4. Typical veld type on calcareous soils on Mmabolela Estates, Northern Transvaal. Photograph (a) shows the vegetation after above normal annual rainfall and photograph (b) the same vegetation during drought conditions

(a)

(b)

Figure 5. Typical open veld type on red soils on Mmabolela Estates, Northern Transvaal. Photograph (a) shows the vegetation after above normal annual rainfall and photograph (b) shows the same vegetation during drought conditions

climate, i.e. low rainfall, these high herbivore concentrations play a decisive role in the distribution of foxes, but this will be discussed in more detail later.

Although in the present study, foxes were always recorded within 2 - 3 km of open water, Smithers (1971) states that they are found in the Kalahari where open water is only available for limited periods. Certainly captive foxes drank freely when water was available. Hendrichs (1972) studied bat-eared foxes in the Serengeti, East Africa and noted that they were dependent on water there.

PELAGE

At birth the pelage of a bat-eared fox consists of a soft, woolly undercoat without guard hairs (Fig. 6). Up until the development of guard hairs, which Smithers (1971) says appear at four to five weeks of age, the general body colour is a pale grey-brown. Pups taken at dens in the present study indicate that guard hairs may appear from an age of three weeks onwards. The distal parts of the limbs are grey-black in colour, as is the muzzle, the back of the ears and the terminal two-thirds of the tail dorsally, the entire distal third of the tail being black. The top and the back of the head have a darker buffy-brown colour than the body, with the face tending to be greyer than the body.

From the age of five weeks and with the development of the guard hairs, the fox takes on a greyer appearance. The guard hairs in the main are black with a white band centrally, although they may be entirely black. The increasing mixtures of black and white as the guard hairs develop gives the fox its greyer colour.

Figure 6. Two young bat-eared foxes, *Otocyon megalotis*, at three weeks of age, illustrating soft undercoat without guard hairs

From five weeks on the reddish brown dorso-median band is evident and with the development of black guard hairs this forms a dark band behind the shoulder at the age of some 12 weeks (Fig. 7). With the further development of guard hairs this dark band continues forward to reach the base of the head at the age of about 18 weeks. The dorso-median band is broken between the shoulders and Kleinman (1966) is of the opinion that a scent gland exists at this hair break and that this explains the unique rolling behaviour of Otocyon.

From 12 - 20 weeks of age, the general body colour becomes increasingly grey-black with the development of guard hairs. In some individuals the dorsal band is less pronounced, the guard hairs having less black and thus the band being much the same colour as the rest of the body.

The distal parts of the body take on an increasing blackness with age, and in the limbs the blackness fades up the leg to merge with the body colour. The ears become more reddish-brown with age and in many animals, the face becomes paler grey. This was particularly evident in captive females. The top of the head between the ears also is a darker grey than the body. The muzzle remains dark, the hair being darker behind and below the eye.

With increasing age, from 6 - 20 weeks, the undercoat loses its reddish brown colour and takes on a more greyish-brown colour but tending to be more red at the base of the ears and on the throat. The belly becomes paler, almost whitish in the adult pelage (Fig. 8).

Kleinman (1967) has proposed that the black dorso-median band on the tail plays an important part in tail postures as found in the foxes.

Figure 7. Bat-eared fox, Otocyon megalotis, showing pelage at 12 weeks of age

Figure 8. Bat-eared fox, Otocyon megalotis, showing full development of pelage

Similarly she suggests that the black facial mask has developed in association with conspecific grooming found in Otocyon.

Moulting was found to occur during the summer months and this agrees with Smithers (1971) who recorded moulting in all months from August to March, the pelages being in their prime from April to July. Smithers (1971) states that moulting takes eight weeks to complete and that the guard hairs moult first, followed by the under-hair and that moulting was assisted by grooming. With the absence of guard hairs in the moult, the adult takes on the appearance described for juveniles.

An entirely melanistic male bat-eared fox was reported by a farmer near Mmabolela, in a litter of six excavated from a den. However, this animal died shortly afterwards.

GROWTH

Three males judged to be three weeks old when taken, were measured periodically to an age of 118 days. Subsequently one of these individuals which had escaped, was killed by a vehicle at the age of 247 days. These data were used for determining growth curves and as a standard for age determination of 10 other juveniles measured. It was found that the ear length and hindfoot length gave curves with the smallest range between readings and these data were treated statistically with the aid of a computer.

Since the range in measurements for the three individual foxes was so small, it was decided to use the mean of the three readings on a specific date to determine the best fit with recognised growth curve formulae.

With ear length the best fit was found against a Gompertz curve where

$$y = ab^{c^t}$$

y = mean ear length

t = age in days

a = upper bound in ear length

b = potential increase in ear length

c = rate of growth

thus giving the computerised value of y as

$$y = 126{,}0855\ (0{,}0228)^{(0{,}9495)^t}$$

Hindfoot length was treated in a similar manner and a logistical curve gave the best fit where

$$y = \frac{a}{1+bc^t}$$

y = hindfoot length

t = age in days

a = upper band in hindfoot length

b = potential increase in hindfoot length

c = rate of growth

thus giving

$$y = \frac{147{,}8103}{1 + 3{,}1975\ (0{,}9610)^t}$$

RESULTS AND DISCUSSION OF GROWTH DATA

The mean measurements of three captive males are recorded in Appendix 1. The measurements of these individuals at maturity are greater than those of adult foxes collected in the field (Appendix 2) and can possibly be attributed to the higher plane of nutrition of captive animals compared to those in the wild. The results of wild foxes (Appendix 2) indicate that other than the males being slightly heavier, there is no significant difference in body measurements for the different foxes. This is contrary to what Smithers (1971) found when comparing 25 males and 29 females taken in Botswana. In this case the females tended to be larger and heavier than the males.

With reference to Figs. 9 and 10 the theoretical growth curves are given. The crosses are actual measurements recorded.

It can be seen that in Fig. 9, the Gompertz curve fitted extremely well to the actual recorded measurements for ear length. The logistical curve for hindfoot length, although not giving as good a fit, was statistically acceptable. In both cases age determination at less than 20 days and greater than 120 days must be taken with caution and reliable ages should only be gauged up to an age of three months.

Smithers (1966 a) found that a captive bat-eared fox attained maximum ear length at 109 days and maximum hindfoot length at 111 days which compares favourably with the curves in this study.

Total body length and tail length were found to have a wide range at specific ages. Although this probably reflects the natural difference in these measurements at a given age, the range is compounded by the difficulty in measuring these lengths, particularly in live animals.

Table 1 gives age determination predictions from measurements of 13 juvenile foxes (either excavated from either dens or taken as a result of road mortalities) based on the known-age growth curves (Figs. 9 and 10). Age determination from either ear length or hindfoot length in many

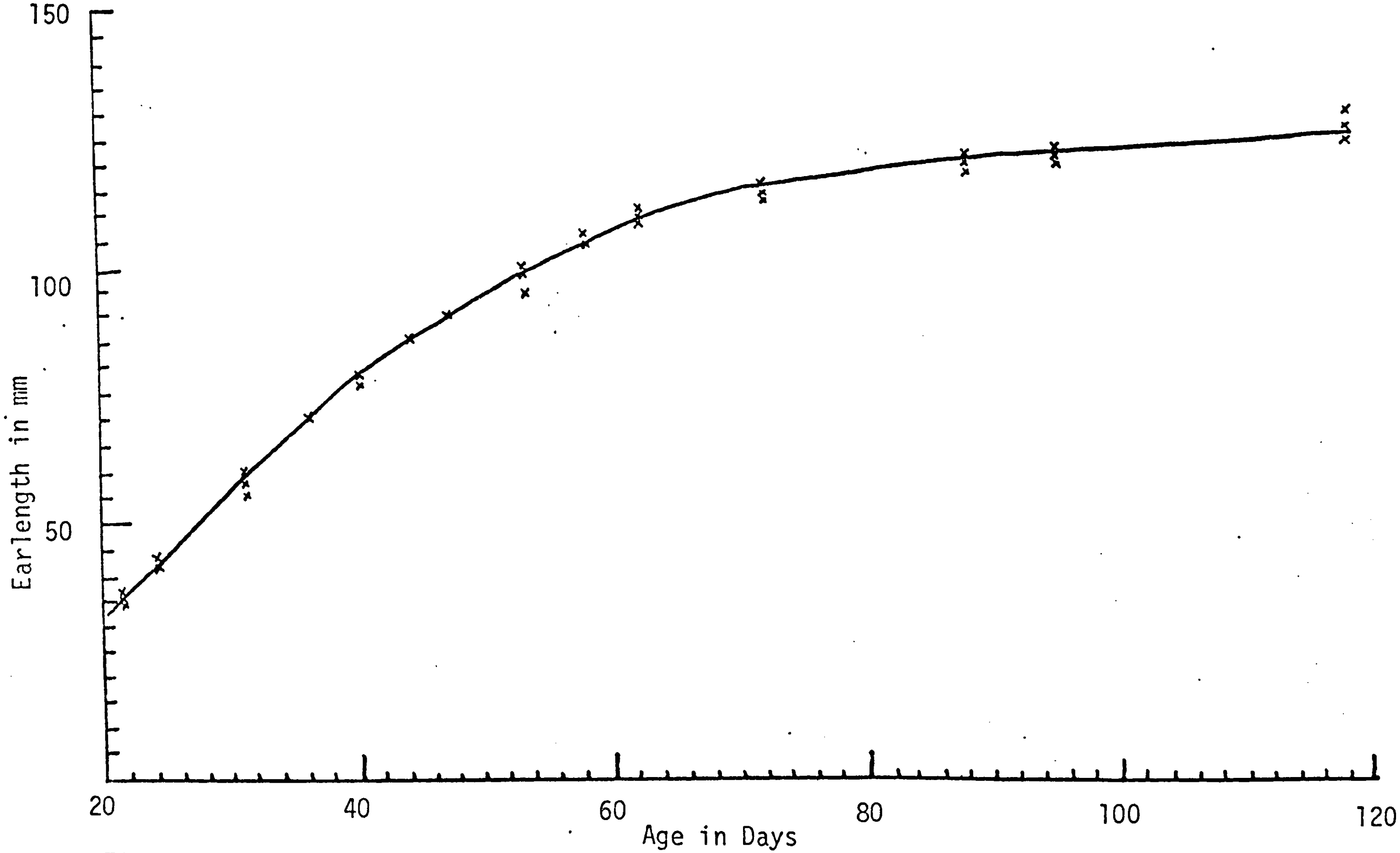


Figure 9. Growth curve for Otocyon megalotis earlength (mm) against age (days) based on three males collected on Mmabolela Estates, Northern Transvaal in October, 1974. The crosses represent actual recorded earlengths and the curve was fitted by computer using a Gompertz formula

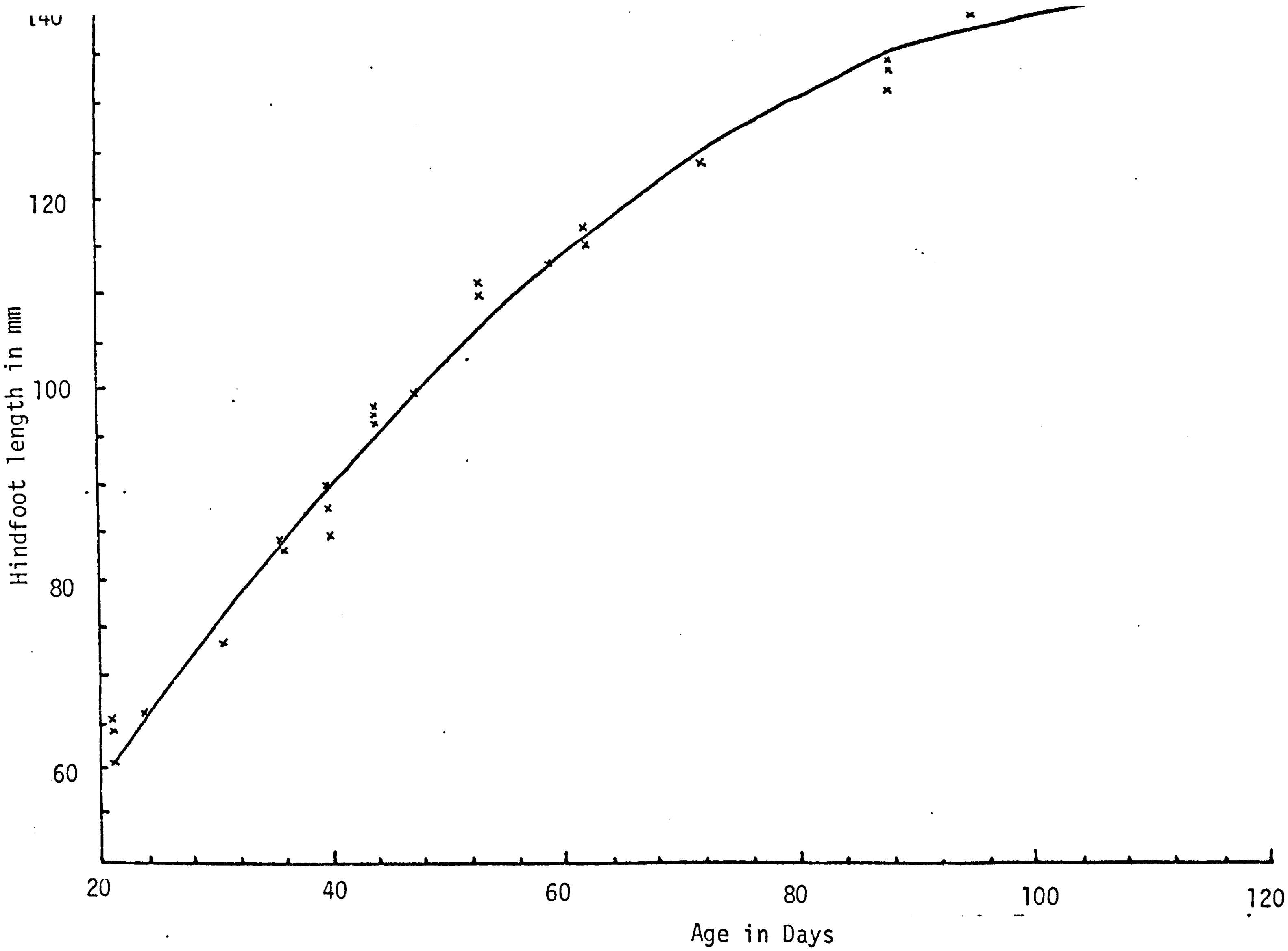


Figure 10. Growth curve for <u>Otocyon</u> <u>megalotis</u> hindfoot length (mm) against age (days) based on three males collected on Mmabolela Estates, Northern Transvaal in October, 1974. The crosses represent actual recorded hindfoot lengths and the curve was fitted by computer using a Logistic formula.

Table 1 : Age determination (days) of <u>Otocyon megalotis</u> as based on body measurements (mm) of 13 juveniles excavated from their dens on Mmabolela Estates, Northern Transvaal, during 1974. Brackets indicate litter mates

Date measured	Sex	Ear length	Hindfoot length	Age estimate from ear length	Age estimate from hindfoot length	Birth date from ear length	Birth date from hindfoot length
13 November	Male	76	90	39	40	6 October	5 October
13 November	Female	77	90	39	40	6 October	5 October
13 November	Male	59	77	31	32	14 October	13 October
13 November	Male	58	78	31	32	14 October	13 October
13 November	Female	64	80	33	34	12 October	11 October
13 November	Female	79	96	41	45	4 October	30 September
18 November	Male	67	83	35	36	15 October	14 October
18 November	Male	61	75	32	30	18 October	20 October
18 November	Male	70	83	36	36	14 October	14 October
18 November	Female	72	84	37	37	13 October	13 October
13 December	Female	104	120	58	67	17 October	8 October
13 December	Male	107	120	60	67	15 October	8 October
25 December	Female	119	132	84	83	3 October	4 October

cases gave a birthdate within a day or on the same day. Similarly individuals from the same litter were of comparable size in spite of sex differences. It was evident that with increasing age there was wider discrepancy between the two methods of age determination.

A notable feature of this table is the narrow period during which foxes are born. Births all occurred during the first three weeks of October, with a peak during the second week of that month.

DENTITION

The dentition of Otocyon is unique among the Canidae in that it has more than three functional lower molars and is the only modern canid with three upper molars (Guilday, 1962).

The most common dentition formula is :

I 3/3 C 1/1 P 4/4 M 3/4 = 46

There may be an extra molar in each half of the upper and the lower jaw, giving a maximum of 50 teeth.

Guilday (1962) states that the dentition of Otocyon is the most bunodont of any living fox, and the evolution of increasing crushing surface at the expense of the carnassials may lie in its omnivorous diet. Normally this would be a disadvantageous mutation, but the opposite is true for Otocyon as it allows it to exploit better the environmental niche of a desert omnivore.

Anatomically the skull of Otocyon has a close resemblance to that of the North American grey-fox Urocyon and the racoon dog Nycteroides (Guilday, 1962).

Ewer (1973) notes that the high-cusped teeth of *Otocyon* and their interlocking favour a quick chopping movement, rather than mastication. Thus, rapid chewing is a further adaptation to *Otocyon's* insectivorous diet.

Six captive bat-eared foxes were examined periodically for eruption of permanent teeth up until the age of 17 weeks. Without actually tranquilising the animals, this was extremely difficult. Table 2 gives an indication of the apparent tooth eruption pattern. However, even in individuals from the same litter, there was considerable variation in tooth eruption and Table 2 should only be used as a guide rather than being conclusive.

It appears that the first permanent tooth, PM_I erupts at about the age of eight weeks and eruption of all teeth is probably concluded at some seven months of age when the foxes are physically mature.

Although skulls were collected during the course of the study, no known-aged specimens were obtainable, as all captive animals escaped.

FEEDING BEHAVIOUR

Activities of foxes are mainly concerned with foraging for food. The animal moves with its head down and ears extended forwards and its nose close to the ground. Olfactory and auditory senses play the main role in prey location, but movement of the prey species is quickly noticed. Once the subterranean prey has been located, the fox holds its nose close to the ground and slightly backwards and the ears almost touch the ground above the prey. With the forepaws

Table 2 : Age in weeks at eruption of permanent teeth of *Otocyon megalotis*, based on data from three captive male foxes collected at an estimated age of three weeks on Mmabolela Estates, Northern Transvaal, in October, 1974. Dash indicates no data.

Jaw	Incisors			Canines	Premolars				Molars			
	1	2	3	1	1	2	3	4	1	2	3	4
Upper	8,5	9,0	9,5	11,0	8,0	16,5	-	-	9,0	11,5	17,0	-
Lower	8,5	9,5	11,0	11,0	8,0	17,0	-	-	9,0	16,5	17,0	-

and claws striking the ground alternatively, the fox rapidly excavates a hole until the prey has been unearthed. The prey is then usually well masticated, particularly large insects, but stomach analyses show that fruit and carrion may be swallowed in large lumps. Mastication possibly assists in killing an insect before it is swallowed.

Captive bat-eared foxes were initially fed on a mixture of equal portions of Pronutro, Epol dog meal and milk. Later on meat, liver, bones and birds were included in the diet, as well as insects attracted to a light in their pen. The foxes readily took meat and would squabble amongst each other for possession of the feeding dish. Should a fox manage to obtain a large piece of meat that it was unable to swallow, it would retreat to a secluded part of the pen where it might finish its meal undisturbed. Although birds were usually plucked prior to feeding, should the foxes be presented with a bird with feathers, they would tear it apart and would eat the feathers as well. As with other canids the foxes would periodically eat green grass growing in the pen.

Captive animals were initially fed five times a day up until the age of four weeks, but this was gradually reduced to twice a day, in the morning and in the evening, from the age of about six weeks. At the age of six to seven weeks the daily intake of food by the foxes was recorded and the mean intake of 20,4 per cent of body mass per day was found (Table 3).

Table 3 : Daily mean food intake (gm) of Otocyon megalotis compared with mean fox mass (gm) for captive foxes on Mmabolela Estates, Northern Transvaal, in 1974.

Date	Estimated fox age in weeks	Number of foxes	Total fox mass	Mean fox mass	Total food intake	Mean food intake	Intake as a percentage of body mass
23 November	6,0	8	7 135	891,8	1 315	164,3	18,4
24 November	6,0	7	7 795	1 113,5	1 885	269,2	21,1
29 November	6,5	7	8 395	1 199,2	1 703	243,2	20,1
1 December	7,0	7	9 840	1 405,7	2 180	311,4	22,1
Total	-	29	33 165	-	7 083	-	-
Mean	-	-	-	1 152,5	-	247,0	20,4

STOMACH ANALYSES

During the course of the study, 21 stomachs were collected. Of these, three were empty and the remaining 18 were analysed volumetrically according to the technique of Bothma (1966 a). These results are summarised in Table 4.

A mean stomach content of 76,9 cc was found with a range of 5 - 280 cc. This mean compares well with that of Bothma (1966 b) of 65,1 cc (n=4), but is lower than that of Bothma (1971) of 148 cc (n=2) and higher than the 56,4 cc (n=2) found by Viljoen and Davis (1973). These differences in volumes of stomach contents is probably related to when the animal was collected. In this study it was found that road mortalities early in the evening had a smaller stomach content than those collected late at night or early morning. As found by other workers, Insecta, mainly termites, *Hodotermes mossambicus*, comprise the major part of the diet. In one case, the entire stomach content of 280 cc was made up of this species. A notable feature of this study is the high percentage of fruits (33,0 per cent) which was recorded in seven of the 18 stomachs. Of these seven, berries of *Grewia* spp. were recorded in two stomachs and groundnuts, *Arachis* sp. in five, one of which also contained portions of watermelon, *Citrullus* sp. These crops are cultivated around the study area and would account for their presence in the diet.

The occurrence of Aves is unrecorded by other workers in stomach analyses, although many authors state that foxes take nestlings (Astley-Maberly, 1967; Dorst and Dandelot, 1970; Shortridge, 1934). In two stomachs nestlings were found but the bird was unidentifiable. Leakey (1969, *In*: Bueler, 1974) states that foxes rob falcons of pigeons

Table 4 : Analysis of contents by volume (cc) of 18 stomachs of Otocyon megalotis collected on and around Mmabolela Estates Northern Transvaal, from 1974 to 1977 (T indicates a food trace)

Year and day collected		Total volume	Insecta	Arachnida	Grass	Fruit	Amphibia	Reptilia	Aves	Carrion	Larvae
1974	25 March	87	10	-	-	77	-	-	-	-	-
	25 March	150	24	-	-	126	-	-	-	-	-
	25 March	148	7	3	-	138	-	-	-	-	-
	28 March	5	5	-	-	-	-	-	-	-	-
	11 April	38	29	-	T	-	-	-	-	-	9
	14 May	90	64	-	5	15	-	-	-	-	6
	17 May	115	30	-	-	67	-	-	-	-	18
	13 December	9	8	-	T	-	-	-	-	-	1
	13 December	12	5	-	-	-	6	-	-	-	1
	25 December	65	40	24	T	-	-	1	-	-	-
	25 December	50	47	3	-	-	-	-	-	-	-
1975	07 February	280	280	-	-	T	-	-	-	-	-
	14 March	18	12	-	-	-	-	-	6	-	-
	14 March	22	19	T	-	-	-	-	3	-	-
	07 June	30	T	-	-	-	-	-	-	30	-
	02 October	170	156	-	14	-	-	-	-	-	-
	13 October	50	40	4	6	-	-	-	-	-	-
1977	16 April	45	10	-	-	35	-	-	-	-	-
Total		1 384	786	34	25	458	6	1	9	30	35
Mean		76,9	-	-	-	-	-	-	-	-	-
Percentage of total volume		-	56,8	2,5	1,8	33,0	0,4	0,1	0,7	2,2	2,5

caught by them. Corn crickets, Acanthoproctus sp., were recorded in five stomachs, and have also been recorded by Bothma (1966 b) in spite of them being distasteful due to a protecting fluid given off when alarmed.

Carrion was only found in the contents of one stomach and would appear to be a minor constituent of the diet, although it has also been recorded by Bothma (1971) and Schaller (1972). The high occurrence of dry grass is probably associated with the intake of harvester termites from their nests. Small stones were also recorded in two stomachs which were also probably taken in while consuming the prey species. The Arachnids found in four stomachs were all sunspiders (Solifugae). The reptile recorded in one stomach appeared to be a blind snake, Typhlops sp. A partially eaten snake of the same genus was found in one of the fox dens during excavation. Smithers (1971) has also recorded snakes in stomachs of bat-eared foxes collected by him. A single specimen of rain frog (Breviceps sp.) was found in one stomach, amphibia being also recorded by Bothma (1971).

Table 5 gives the frequency of occurrence of the different prey species, and this compares well with that found by Smithers (1971). A notable exception is the absence of Muridae in this study whereas Smithers (1971) found them to occur in 12 of the 50 (24,0 per cent) of stomachs examined.

It is apparent that Otocyon has a wide and variable diet with a high preference for Isoptera, Coleoptera and their larvae, although in the study population, plant material would also seem to be a major dietary constituent. Occurrence of food items in stomach contents is probably more related to seasonal availability and opportunity rather than a particular preference for any single prey species, with the exception of the harvester termite, which is associated with degraded veld types.

Table 5 : Percentage occurrence of different food types from 18 stomachs of Otocyon megalotis collected on and around Mmabolela Estates, Northern Transvaal from March, 1974 to April, 1977

Food item	Number of occurrences	Percentage occurrence
Isoptera	12	66
Coleoptera	10	55
Fruits	7	39
Coleoptera larvae	6	33
Grass	6	33
Orthoptera	5	28
Arachnida	5	28
Aves	2	11
Odonata	1	6
Amphibia	1	6
Reptilia	1	6
Carrion	1	6

BEHAVIOUR

VOICE

A number of alarm calls were identified. Adults use an abrupt snorting growl to warn the juveniles when the den is threatened, and the pups immediately take refuge in the den. Should the pups either venture too far from the den or try and follow their parents, a soft growl is used. A longer rapid chattering growl is given by both adult and juvenile foxes when threatened viz. cornered or being chased. A loud chank-chank bark was heard during the period when a female was in oestrus and is probably used to attract other foxes. A similar call was reported by Mills (*pers. comm.*) when 11 foxes chased and mobbed a leopard that had tried to catch a fox.

When juveniles either become separated from each other, or when in strange surroundings they use a mournful distress call. This call is a continuous staccato whistle descending in scale (not unlike the call of a Burchell's coucal, *Centropus superciliosis*, but higher.) Pups taken from dens used this call continually for the first few days in captivity, until they had settled down.

During grooming or when tickled, foxes were often heard to give a low continuous whine presumably indicating pleasure. Smithers (1971) notes that a similar noise accompanied submissive postures. Pups greeting adults often used a soft whimper.

M.G.L. Mills. Kalahari Gemsbok National Park, via Upington.

POSTURES

Juveniles greeted adults returning to the den by nuzzling the adult around the neck and on the underparts of the body, probably in an attempt to suckle. During suckling the tail was wagged from side to side.

Mutual grooming appears well developed in foxes and was often observed in captive animals during early evening and after feeding. Kleinman (1967) is of the opinion that facial markings in the bat-eared fox are specifically related to allogrooming.

An offensive aggressive posture was characterised by the animal standing, ears held erect, but slightly backwards and the tail held straight up. This posture was particularly seen during feeding and individuals would snap at each other's cheeks and try to bump others away from the dish with their bodies.

A defensive aggressive posture was similar but the tail was held high in an inverted 'u' position. This posture was always used when the fox was being chased. Kleinman (1967) relates this tail position to the black dorsal stripe on the tail, which expresses dominance. The only other species of the Canidae to adopt such a tail position is the raccoon dog (Kleinman, 1967). When chased the fox flicks its curved tail from side to side and Smithers (1966 a) is of the opinion that this confuses the attacker.

Fear was characterised by the animal crouching, mouth agape, ears back and flat on the head and growling. The hairs along the back were raised and a pungent smell was often given off.

Play behaviour was found to be well developed in juvenile foxes. This was particularly observed in captive animals after feeding. The foxes would gallop back and forth in their pen, tackling one another, and turning to avoid being caught. Von Ketelhodt (1966. In : Ewer, 1973) believes that play behaviour is related to the development of escape behaviour. Although the fox's reduced dentition does not favour fighting, Smithers (1971) observed strong protective behaviour by parents towards young and between pairs.

All captive animals used only one corner of the pen for defaecating. Similarly near dens scats were often found in a confined area. Urination in juvenile captive foxes appeared to be random. Smithers (1971) states that juveniles show no marking behaviour for the first four months, although adults marked their terrain regularly. Kleinman (1966) records that female foxes only mark during pro-oestrus and oestrus, and males mark more frequently during this period, although she does not say how much more.

There are no known published data on the home range of bat-eared foxes. It appears from this study that outside the breeding season they are almost nomadic, wandering over large areas. This is possibly due to the decreased availability of food during the winter months. When the marked captive animals escaped during this study they immediately split up. Although one female remained near the pen for a week or so, she was subsequently seen on three occasions during the next two weeks up to a kilometre away from the pen, before finally disappearing. Of the other marked animals, a male was killed four kilometres south of the pen five days after escaping. Another was recorded some five kilometres northwest from this male six weeks after escape. Thus it would appear that the foxes dispersed over a wide area, considering that these two individuals gave a dispersal area of approximately 8 km^2.

The reason for the gregariousness of the bat-eared fox remains obscure. Foxes appear to form loose packs in remote areas (Mills, pers. comm.). It is apparent that family units come together particularly during foraging periods, to give the appearance of a pack, but the unit remains stable within the association. The value of these associations may be related to a particular prey species occurring over a small area and the foxes are brought together in their search for food. The value of a 'pack' with regard to predators is also important and Mills (pers. comm.) has observed such a pack driving off a leopard which one or two individuals would be unable to do.

DENNING

It appears that the bat-eared fox only makes use of dens for breeding and does not inhabit them permanently. Although dens may be visited outside the breeding season these visits seem to be incidental except in adverse weather conditions when a den or burrow may be used for shelter. However, under normal weather conditions, occupied dens were found only while the pups were being reared from September to January.

From the beginning of July, for a period of four to six weeks, foxes were heard barking and chattering from sunset onwards in both study areas. On one occasion after dark, two foxes were seen fighting while accompanied by these vocalisations.

If the gestation period of 60-75 days (Bekoff, 1975; Rosenberg, 1971; Smithers, 1971) is correct, these vocalisations would coincide with the female coming into pre-oestrus and oestrus. It seems probable that foxes, particularly males, are vocalistic during this period to either attract a female or to ward off other males, or both. This may explain the fighting that was observed.

It would, therefore, appear that pairing takes place during July and early August. Once this has occurred, a pair will then seek a suitable site for a den and usually excavate their own.

During the study period, 19 occupied breeding dens were found. Of these, 13 (68,4 per cent) were in calcareous soil types and the remainder in a red sandy soil type. Of the 19 dens, 12 (63,2 per cent) were excavated by the foxes themselves, and of the other seven, six (85,7 per cent) were old antbear (Orycteropus afer) burrows. In one case an old springhair (Pedetes capensis) warren was used. The dens excavated by the foxes themselves were with one exception, in calcareous soils, and there appears to be a definite preference for this soil type.

Fox excavated dens were characterised by being shallow, usually between 40 - 50 cm deep, having from three to seven entrances/exits (Fig. 11) inter-connected with a number of chambers which were large enough to accommodate the entire fox family. Invariably the den was dug around or under a small bush, a metre or so high. This is important in concealing the den from predators and in strengthening the den from collapsing due to the retaining action of the roots of the bush. The

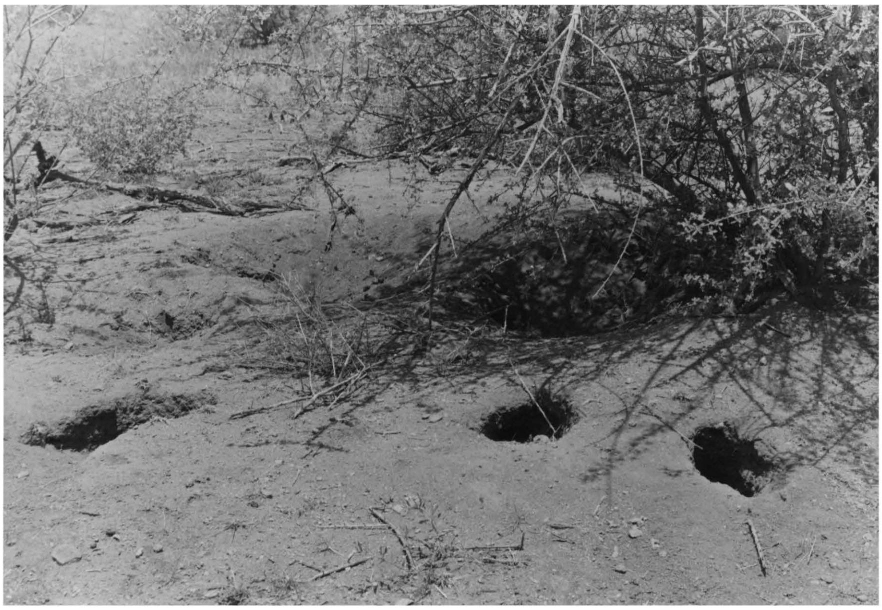


Figure 11. Typical fox excavated den on Mmabolela Estates, Northern Transvaal, showing location under a bush and several entrances/exits

bush also provided shade and cover for the foxes in which to lie up when not in the den itself (Fig. 12).

At two of the seven dens (28,6 per cent) used by foxes that were not excavated by themselves, both parents were seen. Both these dens were known to have only been occupied as a result of the original den having been disturbed. In the one case, the pups were moved into an abandoned antbear hole 130 m distant, in the other, into a springhare warren some 90 m away. The remaining five dens were all in old antbear holes and without exception, only one parent was seen at each of these dens in spite of several days of observation. In each case, the fox appeared to be the mother of the pups (Fig. 13).

If it was indeed so, that only one parent, the female was raising the young there, then this would further suggest that pairing and mating takes place prior to den establishment and that the male plays a vital role in initiating or digging the fox's own den. In cases where holes excavated by other animals were used, the male may have been killed between mating and den establishment. If a den had been established, it may have been attacked by some predator killing the male and some of the pups, resulting in the female abandoning her own primary den for a secondary one. There is some evidence of this latter assumption in that at all five dens under discussion, the most young observed per den was two, while in two instances only one pup was seen. In contrast, at nine dens excavated by the foxes, the number of pups varied from one to six, with a mean of 3,55.

Once the den has been established in September, both parents remain at the den during the day usually lying under the den bush rather than in the den itself, in a shallow excavation especially made for this

Figure 12. Typical fox excavated den site here occupied by both parents and a number of juveniles, as found on Mashatu, Botswana

'Figure 13. Old antbear hole being used as a secondary den by one adult bat-eared fox, _Otocyon megalotis_ with its single juvenile, on Mmabolela Estates, Northern Transvaal, in 1975 purpose. The adult foxes only leave the den precincts at night to forage. This pattern continues after the pups are born and up until the den is vacated.

The pups first come out of the den at an age of about two weeks, but remain at or near the entrances. As they get older they may venture a few metres from the den itself. The parents keep a constant watch on the pups and should they venture too far, a growl from one of the parents warns them to return to the den. Should the den be threatened or disturbed, the adult foxes will give a short, sharp growl and the pups immediately take refuge in the den.

Once the pups are more mobile, at the age of approximately four weeks, they will accompany one or both of the parents on foraging trips away from the den at night. With increasing age these excursions cover greater and greater distances away from the den. Prior to foraging in the evening, the pups become increasingly restless and play among themselves or with their parents.

Den occupation lasts until the pups are approximately 12 weeks old in late December to early January, and this spans a period of four months. When the pups are 12 - 15 weeks old, the family will leave the den to forage and may not return for several days. Visits to the den now gradually become more and more infrequent until they may only be incidental or are made when climatic conditions are unfavourable.

Captive pups from about the age of five weeks onwards were found to excavate small burrows and even at this young age proved to be prodigious diggers. These pups up until the age of eight weeks, displayed a certain insecurity in the absence of a den. Thereafter they showed no inclination to burrow and excavate shallow depressions under bushes where they sheltered (Fig. 14). During a three-day period of cold rainy weather, these captive foxes again excavated a den in spite of having spent several weeks before that in the pen without having attempted to dig a burrow. This confirms field observations that dens are only used for breeding or when unfavourable weather conditions prevail. Similar results have also been found for the red fox, Vulpes vulpes, in that they prefer to lie above ground, but will occupy burrows following prolonged rainfall (Lloyd, 1975).

There is no evidence to suggest that den establishment is related to territoriality as dens of different pairs were found within 100 m of each other. Lawick-Goodall and Lawick-Goodall (1970) report an instance of two female foxes sharing the same den and that the five pups fed from both mothers. Bueler (1974) states that several burrows may be found close together and Kruuk (1972) records that foxes often have dens remarkably close to those of the spotted hyaena, Crocuta crocuta.

In three cases, two or more different families were found at dens within 300 m of each other. This would largely seem to be the result of a suitable soil type being present for den sites. Only one of the 19 dens (5,2 per cent) was found to be used on two consecutive breeding seasons and it would seem that in this case, the den was a secondary den in that only one parent and two young were seen there.

The sensitivity of foxes to den disturbance cannot be over-emphasised. Without exception, it was found that if the den site was disturbed or visited too frequently, the den would be abandoned. In some cases

Figure 14. Typical excavation made by <u>Otocyon megalotis</u> for sheltering during the day on Mmabolela Estates, Northern Transvaal in 1974

two visits to the den was sufficient to make the foxes move to a new site. This made den observations extremely difficult and it was not possible to approach a den closer than 50 m lest the occupants become alarmed.

Occupied dens were characterised by fresh spoor around the den and by small excavations usually made by the pups while looking for insects (Fig. 15). From observations on both captive and wild foxes, it would seem that the dens are constantly extended and dug at during occupation, as freshly dug earth was often found at the entrances to dens.

Structurally the dens were quite stable and in only two cases out of 24 (8,3 per cent) were dens in red soil found to have collapsed. This would only occur during extended wet periods and may be a factor in juvenile mortality. The porous nature of calcareous soils prevents a den from collapsing easily and may be another factor for preference for this soil type as a denning site.

REPRODUCTION

The breeding season for the southern form of the bat-eared fox, O. megalotis, is more restricted than that of the northern varieties due to the more marked seasonal changes here than at the equator. In this study, pups were only found to be born during the first three weeks in October.

Breeding pairs only raise one litter per year. Smithers (1971) states that a captive female comes into oestrus for the first time at 18 months

Figure 15. Typical Otocyon megalotis den showing excavations made by pups around den, on Mmabolela Estates, Northern Transvaal during 1974

of age. However, personal field observations suggest that foxes may come into oestrus in their first year of life, as non-breeding sub-adults were not seen during the breeding season. Further evidence for this is that foxes reach physical maturity at the age of seven months and that family units break up at this age. Sightings during June and July are usually of single or paired animals. If the foxes at the age of seven to eight months were not going to breed until the following year there seems to be no advantage in litter dispersion at this age. Field observations furthermore suggest that females come into oestrus in July. During this period pairing takes place accompanied by frequent vocalisation and possible fighting between males. Smithers (1971) found that captive females come into oestrus in August.

From sightings in the Northern Transvaal, there is some evidence that the pair bond may continue outside the breeding season. This has also been suggested by Hendrichs (1972) studying foxes in the Serengeti and by Nel (pers. comm.) for the Kalahari Gemsbok National Park.

Litter sizes recorded in this study varied to a maximum of six (Table 6). From 12 dens at which the young were counted, the mean was found to be 3,00 (Range 1 - 6). At six (50,0 per cent) of these dens, the sex of each pup was determined and a ratio of 1,20 males per female was found. Sightings of family groups in Mmabolela gave a mean litter size of 3,33 (n=21) while that at Mashatu was 2,93 (n=29). A mean of 3,09 per litter was found for both areas. This gives an annual productivity of 54 per cent. Smithers (1971) found a mean of 2,2 (n=13) from observations in Botswana. The higher mean recorded in the present study areas can possibly be attributed to the small number of predators there.

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Table 6 : Litter size data for *Otocyon megalotis* from Mmabolela Estates, Northern Transvaal and Mashatu, Eastern Botswana from February 1974 to August 1977

Sightings	Total number of juveniles	Number of litters	Range	Mean litter size
Mmabolela field sightings	70	21	1 - 5	3,33
Mashatu field sightings	85	29	1 - 4	2,93
Den sightings at both study areas	36	12	1 - 6	3,00
Total	191	62	1-6	-
Mean	-	-	-	3,09

Weaning probably takes place from the age of 10 weeks onwards and from mid-December sightings of juveniles without any adults were common. The nursery groups of young from the same litter remain together until physical maturity at seven months of age. Only three separate sightings of more than two individuals were recorded after April during this study. One of these was a family group of six sighted on Mmabolela during July, 1975 and the other two were of three individuals each at Mashatu during June, 1976 and August, 1976.

From Table 7 it can be seen that at the onset of breeding in October, group size comprising parents and juveniles is high (7,00). Smithers (1971) found a mean of five foetuses per litter (n=8) from gravid females taken in the field and observations of litters at birth of captive females. In these captive litters the female never raised more than four young, which would seem to be the optimum number. In this study, family groups of six were common and on one occasion a group of seven was observed.

Due to pup mortality during the first few weeks of life, the group size for November drops to 4,0 and then remains relatively stable until and including February. The ensuing decline in group size is probably the effect of pups leaving adults and forming nursery herds during March and April. As already mentioned, at physical maturity at seven months (May), nursery herds break up into solitary individuals. The group size increases again during July when pairing takes place. The low recordings for August and September can be attributed to one of the pair, probably the female, remaining at the den during late gestation and parturition.

Table 7 : Mean group size of sightings of *Otocyon megalotis* for different months on Mmabolela and Mashatu study areas in the Upper Limpopo Valley from February, 1974 to August, 1977

Month	Number of foxes	Number of groups	Mean group size
February	17	4	4,25
March	12	4	3,00
April	14	4	3,50
May	5	4	1,25
June	42	24	1,75
July	16	7	2,29
August	37	20	1,85
September	2	2	1,00
October	7	1	7,00
November	44	11	4,00
December	222	66	3,60
Total	418	147	-
Mean	-	-	3,04

Table 8 : Sightings (x) per kilometre of *Otocyon megalotis* based on road censuses at Mashatu, Botswana during 1976

Day	Age group		Foxes	Total distance in kilometres	Sighting per kilometre
	Adult	Juvenile			
19 June	x	-	42	60,8	0,69
17 August	x	-	34	102,3	0,33
28 December	x	x	59	27,0	2,18
29 December	x	x	93	50,0	1,86
Total	-	-	228	240,1	-
Mean	-	-	-	-	1,26

Adult females found dead in March, although having enlarged mammae, had ceased lactating, supporting the hypothesis that juveniles are weaned by February. It is probable that juveniles from the age of 10 - 12 weeks onwards leave their parents for short periods prior to forming their own separate group, as family units were recorded up until and including February.

ACTIVITY STUDIES

FIELD OBSERVATIONS

In the two study areas foxes were almost entirely nocturnal, and were only seen during the day if they were disturbed from where they were resting. Smithers (1971) found that in Botswana the foxes were only diurnal in remote areas, while Hendrichs (1972) found them to be nocturnal.

Activity studies at night were started in 1975 on Mmabolela but later moved to Mashatu. Road census data are summarised in Table 8. From the limited activity data available, it appears that considering all foxes outside the breeding season, the number of groups per kilometre is more or less the same for the first three periods (0,28; 0,30; 0,28) but drops off for the last period (0,15), (Table 9). There was no significant difference between these results (t = 3,39, df = 2). Considering the number of foxes per kilometre, there is a decrease in activity in the third period and a further decrease in the final period. The drop in the final period is probably related to the moon rising on the one night during the final drive of this period.

Table 9 : Activity studies of *Otocyon megalotis* giving the number and composition of foxes seen per kilometre on a road census, and analysed per three hourly periods from 19h00 to 07h00 at Mashatu, Botswana in June and August 1976.

Item	Period				Total	Mean
	19h00-22h00	22h00-01h00	01h00-04h00	04h00-07h00		
Number of groups	14	13	10	5	42	-
Foxes	26	23	15	12	76	-
Mean group size	1,86	1,76	1,50	2,40	-	1,88
Kilometres driven	50,70	43,10	35,50	33,80	163,10	-
Groups per kilometre	0,28	0,30	0,28	0,15	-	0,25
Foxes per kilometre	0,51	0,53	0,42	0,35	-	0,45

If one excludes this result the number of foxes per kilometre rises from 0,15 to 0,30 which makes these results comparable to those for the first three periods. Thus it appears that the foxes are almost equally active throughtou the night, but that they show a slight decrease in activity in the third period. However, there was a marked decline in activity after the moon rose.

Hendrichs (1972) also recorded that foxes are active throughout the night with peak periods from 18h00 - 22h00 and 05h00 - 07h00.

If one considers the results for juveniles, during the breeding season (Table 10) it would appear that they are more active during the first half of the night. This is confirmed by observations on juveniles at their dens rather than foraging during the second period and the high number of adults per juvenile for the third period (2,50) compared with those of the first two periods (0,75 and 0,65). In the final period, the juveniles again became relatively more active (0,42). The percentage activity of adults indicate that both parents are more likely to forage with the juveniles early on in the evening whereas in the third period the pups are left at the den while the parents forage on their own. In the final period, one of the parents may accompany the juveniles while foraging. These activity results are summarised in Fig. 16.

Sightings of adults per kilometre indicate that adults spend more time foraging when they have pups (0,81 per km) compared with other times outside the breeding season (0,45 per km). Similarly the size and number of groups per kilometre is higher in the breeding season than at other times.

Table 10 : Activity studies of Otocyon megalotis giving number and composition of foxes seen on a road census and analysed per three hourly periods from 19h00 to 07h00 at Mashatu, Botswana during December, 1976.

Item	Period				Total	Mean
	19h00-22h00	22h00-01h00	01h00-04h00	04h00-07h00		
Number of groups	20	17	7	5	49	-
Adults	30	20	10	5	65	-
Juveniles	40	31	4	12	87	-
Total foxes	70	51	14	17	152	-
Mean group size	3,50	3,00	2,00	3,40	-	2,97
Adults per juvenile	0,75	0,65	2,50	0,42	-	1,08
Kilometres driven	33,50	23,50	10,00	10,00	77	-
Groups per kilometre	0,60	0,72	0,70	0,50	-	0,63
Adults per kilometre	0,90	0,85	1,00	0,50	-	0,81
Juveniles per kilometre	1,19	1,32	0,40	1,20	-	1,03
Total foxes per kilometre	2,09	2,17	1,40	1,70	-	1,84
Percentage activity of adults	42,86	39,21	71,42	29,41	-	45,72

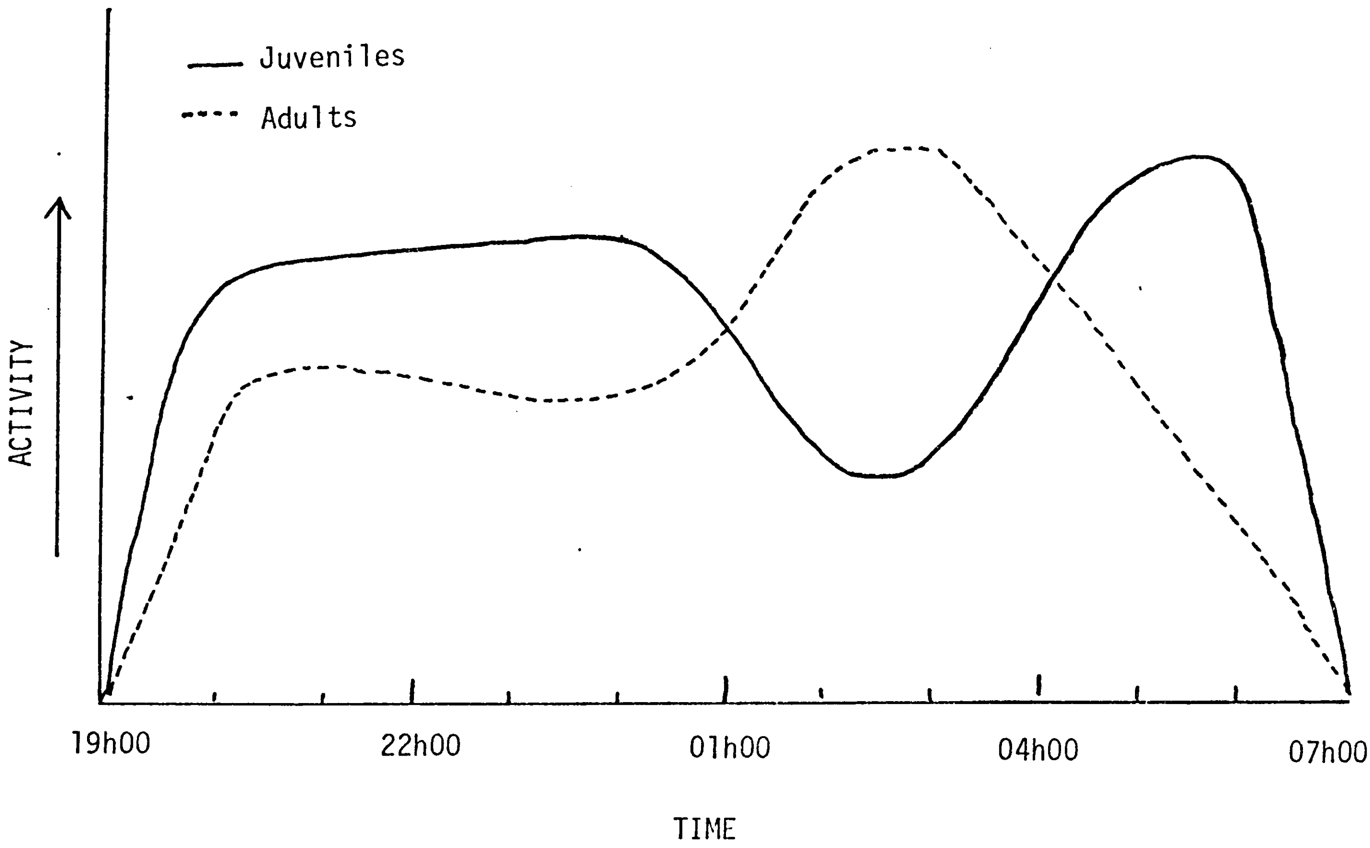

Figure 16. Stylised activity diagram for adult and juvenile bat-eared foxes, *Otocyon megalotis*, at Mashatu, Botswana, during December, 1976

During the early part of the day while still cool, the pups remain at the entrance of the den, the parents resting some distance away. During the heat of the day the juveniles seek shelter in the den itself, and only emerge when it becomes cooler in the late afternoon, where they remain until evening.

PEN OBSERVATIONS

Six foxes were kept in a pen of 20 x 40 m with natural bush. Captive foxes showed a similar activity pattern to those observed in the field, i.e. they spent the daylight hours resting and only became active towards evening. When young, these foxes showed more activity during the early part of the night and just before sunrise, but as they became older they spent more time being active at night.

Prior to the evening feed, they became restless and would play with one another as well as groom themselves or each other. After feeding, playing increased and foraging around the pen commenced and much time would be spent excavating their burrow. Activity continued throughout the night with intermittent periods of rest.

Captive foxes were probably less active than their wild counterparts due to artificial feeding and more time was spent grooming and playing, as opposed to foraging, than observed in wild foxes.

POPULATION DENSITIES

At the start of the study a number of different capture methods were tried; i.e. trapping and running down foxes with dogs and excavating dens, but these proved unsuccessful because foxes were not permanently resident at dens as was thought at first. At the slightest disturbance, adults would vacate the den and it was never possible to approach the den before the adults ran away.

During the breeding season of October to November 1974, 14 juveniles were excavated from their dens. Six of these were marked with coloured ear tags (Fig. 17) and released, and the remaining eight were held captive, six of which were marked and kept for some seven months before they escaped. Of the 12 marked and released individuals, there were only four subsequent resightings from a total of 113 sightings (juveniles excluded) up until the end of 1975. Although there were insufficient resightings to be meaningful, this gave an estimate of 452 for the population over an area of 7 900 ha., or 5,72 foxes/km^2. At Mashatu, analysis of foxes sighted per km (Table 10) gave a density of 9,20 foxes/km^2 in the breeding season, and 2,25 foxes/km^2 outside the breeding season (Table 9). This would indicate a wide dispersion of young animals. Hendrichs (1972) found a density of 0,3 to 1,0 foxes/km^2 in the Serengeti which is considerably lower than those found in this study. This is possibly due to the habitat having a better grass cover which is less favourable for the foxes. Also the large number of predators may limit population size in this area.

MORTALITIES

PREDATION

The only evidence of predation found during this study was a single incidence of fox hair in leopard faeces. Mills (1977) has seen leopard actively hunting bat-eared foxes in the Kalahari Gemsbok National Park and Shortrige (1934) states that leopards take many

Figure 17. Captive Otocyon megalotis showing coloured plastic ear tags used for identifying individual foxes on Mmabolela Estates, Northern Transvaal in 1974

foxes. Bothma (*pers.comm.*) recorded two separate leopard kills of foxes in the Kalahari Gemsbok Park.

All three species of hyaena have been recorded to kill and feed on bat-eared foxes, i.e. striped hyaena, *Hyaena hyaena* (Kruuk, 1972), spotted hyaena, *Crocuta crocuta* (Kruuk, 1972) and brown hyaena, *Hyaena brunnea* (Mills, 1977). In the above brown hyaena study, only one of 11 attempts to catch and kill foxes was successful in spite of some attempts at excavating the foxes from their dens. Schaller (1972) recorded adult black-backed jackals, *Canis mesomelas* catching young bat-eared foxes.

A number of authors (Astley Maberly, 1967; Bueler, 1974 and Dorst and Dandelot, 1970) state that large raptors take foxes. In areas where foxes are nocturnal, diurnal raptors probably take few foxes, particularly adults. However, it seems more probable that the larger nocturnal raptors, such as the giant eagle owl, *Bubo lacteur*, may take juveniles at night.

Pythons, *Python sebae*, were on two occasions seen to enter springhare. warrens and catch and kill a springhare and would possibly also be able to take foxes during denning.

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JUVENILE MORTALITY AND DISEASE

There appears to be a high mortality of juvenile foxes prior to weaning, particularly during the first two weeks after birth. During this study only one den investigated was found to have pups younger than one week and these numbered six juveniles. Smithers (1971) recorded a mean of five for four litters at birth. This indicates that litter size at birth ranges from four to six, yet field observations of young pups gave a mean litter size of 3,1 (Table 6). Smithers (1971) reports a captive female eating some of her young in three consecutive litters. In this study in addition to three live pups, the remains of a partially eaten pup were found in the den of a wild fox during excavation. Whether this is canabalism on the part of the parents or juveniles or both, is uncertain. Competition for food amongst individuals of the litter may account for these early mortalities. A difference in size of individuals of the same litter was found in some dens that were excavated. Weaker members of the litter possibly starve or become so weak that they are more susceptible to disease and die. Under damp circumstances this disease factor would be aggravated.

In particularly wet conditions, den collapse may also be a mortality factor. Although no occupied fox dens were found collapsed, porcupines were found killed in their dens on two occasions due to den collapse onto the occupants.

ROAD MORTALITIES

One of the major causes of fox mortality in the Mmabolela study areas was road casualties. The preference of bat-eared foxes to forage over bare areas attracts them to gravel roads. These animals are dazzled by vehicle lights and tend to run in the headlight beam and are easily killed. On one occasion on Mmabolela a family group of one adult and four juveniles was found to have been killed by one vehicle.

A further mortality factor is that the bat-eared fox is considered a jackal-type animal and is associated by farmers with damage to domestic stock. It is therefore intentionally run down by vehicles on the road. In many instances, the driver is probably unable to distinguish between the bat-eared fox and the black-backed jackal which is common in the area.

LIMITING FACTORS AFFECTING DISTRIBUTION

Coetzee (1967) gives the distribution of O. megalotis as throughout the semi-arid areas of southern Africa, including the southwestern Transvaal and the western border areas of Rhodesia. Smithers (1966 b) gave their distribution in Rhodesia as only in the Wankie area and in the extreme southwest corner. Recent sightings suggest a wider distribution for the northern Transvaal (Rautenbach, In litt.) and an eastern extension in both Rhodesia (Smithers, 1971) and the northern Transvaal (Pienaar, 1970), and Moçambizue (Smithers and Lobão Tello, 1975).

HABITAT REQUIREMENTS

From this study it is apparent that the bat-eared fox has specific habitat requirements. These are a short-grass open veld type, and suitable soil material for denning. Of these two factors, a short sparse herbaceous layer with bare patches is more important.

In southern Africa one or more factors give rise to the above specific habitat conditions.

J.L. Rautenbach . Transvaal Museum, Pretoria.

Rainfall

The fox requires an annual rainfall regime of neither too much nor too little rain. In practice, the optimum fox habitat is found between the isohyets of 200 and 300 mm. When the rainfall exceeds 300 mm, the grass cover becomes too tall and dense for ideal fox habitat. Below 200 mm annual rainfall the converse occurs and the veld is possibly unable to support sufficient insect life for the foxes.

Grazing pressure

Herbivore utilisation can modify the veld type sufficiently to produce optimum fox habitat. Heavy utilisation by the larger ungulates not only crops the herbaceous layer to keep it short, but the trampling effect leads to open bare patches within the veld. The small herbivores, particularly the harvester termites, also play an important role in producing the downgraded veld condition favoured by the foxes.

Soil type

Within low rainfall areas are soils that give rise to a particularly sweet and palatable veld type. This in turn leads to greater herbivore pressure and the resultant grazing and trampling effect which produces the optimum bat-eared fox habitat. Further, a soil type that provides suitable denning material is favoured by the foxes. This requires a soil type that is neither too hard nor too soft. A hard but crumbly soil is ideal.

Calcareous soils have both the above characteristics.

An example of a habitat type that meets all the above requirements is the pan edge of the salt pans of the central Kalahari (Botswana). Therefore it is not surprising that bat-eared foxes are primarily associated with the Kalahari pans. Fig. 18 diagrammatically summarises the biotic and abiotic factors giving rise to certain habitat types.

There are a number of reasons why the foxes have such specific habitat requirements. They are :

Vegetation and density

The bat-eared fox is a small mammal, standing some 300 mm at the shoulder. It preys mainly on insects and their larvae which are primarily found by audio-location. As has already been described (Feeding behaviour) the fox locates its prey by holding its ears close to the ground (Fig. 19). In tall, dense grass the fox would be unable to correctly position its ears to find its prey accurately. Also, should it locate an insect, it would be difficult for it to catch it in dense grass if it were above ground, and even more so should the fox have to dig for its prey through the grass tuft and roots. Thus only in a short, sparse vegetation (Fig. 2) can the fox feed effectively.

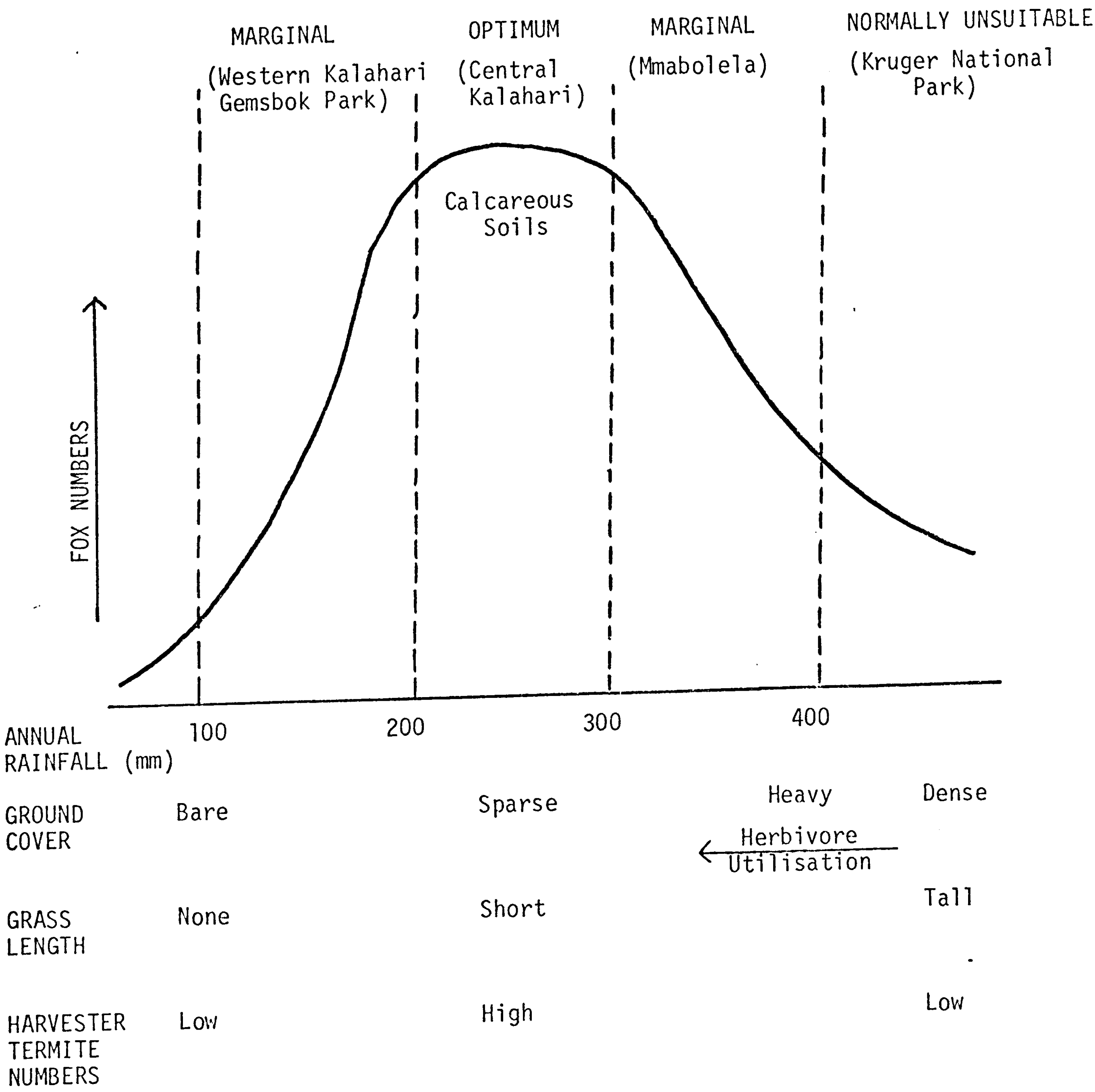

Figure 18. Diagrammatic representation of how abiotic and biotic factors affect bat-eared fox numbers

Figure 19. Position of ears of Otocyon megalotis, when locating food

These specific habitat requirements of the foxes are well illustrated by looking at a typical Kalahari pan. The pan edge zone lies between the pan bank and the pan floor. A study of the pan edge (Parris, 1976) has revealed that this zone has the lowest percentage ground cover, and shortest perennial grasses and shrubs when compared with the other two zones. It is in this pan edge zone that foxes are most commonly found. Thus even over a short distance of a few hundred metres the foxes exhibit a preference for areas that meet their specific habitat requirements (Parris, pers. comm.). Similarly within Mmabolela, foxes were found to be most common on areas of sparse short grass. These were usually on calcareous soils (Fig. 5(b)).

Prey preferences

Stomach analyses in this study indicate that harvester termites are the main dietary constituent of bat-eared foxes and all workers agree that foxes have a decided preference for the harvester termite. Harvester termites have long been associated with downgraded veld types. Recent work at the Matopos Research Station has shown that in the harvester termite, Hodotermes mossambicus, population size is inversely related to seasonal rainfall (Bisset and Macdonald, 1974) i.e. termite populations are low during seasons of high rainfall, and increase dramatically during periods of drought. Further, optimum habitat requirements for the termites are found on areas of low basal cover at the edge zone of bare ground and vigorous veld (Bisset and Macdonald, 1974).

That termites form the major part of foxes' diet indicates that these two species are closely associated. Parris (1976) found that termite

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Pietersburg

activity was most evident in the edge zone of Kalahari pans where foxes were also most commonly encountered. It is also apparent that like that of termites, bat-eared fox population size is inversely related to rainfall (Population fluctuations). Therefore it is more than coincidence that the habitat requirements of the bat-eared fox are almost identical to those of the harvester termite.

Denning soils

The preference for a particular soil type is also related to denning. The fox being a prodigious digger can excavate dens in very hard soils. A soil normally too hard for a would-be predator, e.g. brown hyaena, to effectively dig them out is of important survival value. Calcareous soils provide ideal material for denning. These soils are composed of hard lumps of calcrete within the calcareous soil which is generally powdery. This provides a very solid yet comfortable den. On both Mmabolela and Mashatu the highest number of fox sightings were recorded on calcareous soils in spite of other soil types having the same short sparce basal cover.

POPULATION FLUCTUATIONS IN THE STUDY AREAS

Mmabolela Estates population changes

The study commenced in February 1974, and observations were continued on Mmabolela for four consecutive years. Table 11 summarises the sightings on Mmabolela for the calendar years 1974 to 1977. All sightings averaged 7,18 foxes per months(excluding den observations) in 1974, fell to 3,25 per month in 1975 and to only 0,08 per month in 1976. The number of dens found and the road mortalities recorded during this period declined similarly although sightings per den found

Table 11 : All sightings, including those at dens and road mortalities, of *Otocyon megalotis* on Mmabolela Estates, Northern Transvaal from February, 1974 to August, 1977

Year	Mean monthly fox sightings	Mean number of dens found per month	Mean monthly road mortalities	Mean number of foxes per den found	Mean number of foxes sighted per known road death
1974	7,18	0,54	1,45	13,29	4,95
1975	3,25	0,25	0,75	13,00	4,30
1976	0,08	0,00	0,00	0,00	0,00
1977	1,50	0,00	0,37	0,00	4,00

Table 12 : All sightings and known road mortalities of <u>Otocyon megalotis</u> recorded on Mmabolela Estates, Northern Transvaal, from February 1974 to August 1977, showing inverse relationship with rainfall (mm)

Period : April to March	Mean number of mortalities per month	Mean number of groups per month	Mean number of foxes per month	Rainfall of previous period
1973/74	3,50	3,50	11,00	126
1974/75	1,00	2,08	8,00	487
1975/76	0,50	1,33	3,20	563
1976/77	0,00	0,08	0,08	708
1977/78	0,60	0,60	2,40	337

13,2 (1974) and 13,0 (1975) and sightings per road mortality 4,9 (1974), 4,3 (1975) and 4,0 (1977) remained virtually constant indicating that these factors (dens and mortalities) were density dependent to some degree. Correlation index of 0,99 for both dens and mortalities was found (t = 9,92, df = 2). No evidence of natural mortalities was found in the field. From a single sighting in 1976, foxes again became evident in the first eight months of 1977, for which data is available. In this period 12 sightings were recorded and three road mortalities were found. Thus it appears that the population reached a low during 1976 and is once again increasing.

Bueler (1974) reports that similar peaks and declines occur in fox populations in northern Tanzania and suggests that disease, possibly distemper, may be the responsible factor.

It has been shown that rainfall is one of the major factors affecting habitat requirements of bat-eared foxes. A study of the rainfall on Mmabolela during the period of this study (Table 12) shows exceptionally high rainfall for the years 1973 - 1976, particularly during the 1975/76 season, when more than twice the mean annual rainfall was recorded. Thus as rainfall increased so the fox population decreased. This inverse relationship was confirmed when during 1976/77 with the lower rainfall an increase in sightings was recorded. A correlation index of sightings with rainfall gave a value of 0,76 (t = 2,0, df = 3).

In practice Mmabolela can be classified as marginal fox habitat having a mean annual rainfall of between 300 - 400 mm. In the nine years prior to 1973 below average rainfall fell, resulting in a sparser, more suitable veld type for the foxes (Fig. 4(b)). This led to an increase in fox numbers. From 1973 to 1976, above average rainfall was recorded, which resulted in a denser, taller grass layer which was unsuitable for the foxes (Fig. 4(a)), whose numbers declined.

Stevens (pers.comm.) noted a similar decrease in fox sightings at Mashatu in 1973 - 1974. Although no quantitative data are available, it is apparent that even in prime habitat, population fluctuations may occur.

Population changes in the Kalahari Gemsbok National Park

In the Kalahari Gemsbok National Park, Nel (pers. comm.) has noted that under high rainfall conditions, fox numbers increase. A study of the rainfall here shows that the 200 mm isohyet runs through the middle of the park from northwest to southeast. Thus in years of higher than average rainfall, marginal areas normally too dry (below 200 mm rain) should become relatively more suitable, allowing for an increase in fox numbers. An increase in herbage under above normal rainfall may also tend to concentrate the foxes in the Nossob River bed (more favourable habitat) resulting in an apparent population increase.

Recent range extensions

Smithers (1971) records a progressive eastwards range extension in fox sightings in northwestern and southwestern Rhodesia. The latter extension is associated with their subsequent appearance in the Kruger National Park (Pienaar, 1970). These extensions occurred during the period 1965 to 1970. It is well documented that the summer rainfall regions of southern Africa suffered a severe drought during the mid 1960's (Tyson and Dyer, 1975). Smithers (1971) noted

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that the drought was "unprecedented in the annals of the territory" (Botswana). Below normal rainfall was recorded over summer rainfall regions up until 1972 (Dyer, 1977).

Thus it was during this dry period that the range extension of bat-eared foxes took place. It has already been described above how and why this would happen under low rainfall conditions.

As had occurred on Mmabolela, what was previously marginal fox habitat became prime habitat in the dry years. Similarly, what was unsuitable fox habitat under normal rainfall years, became marginal under low rainfall allowing a further range extension.

The survey of Botswana was carried out during these drought years (Smithers, 1971) and in view of this, the apparent wide fox distribution, particularly in northern Botswana, may have been only temporary. This area enjoys a relatively high rainfall, 500 - 600 mm, and the habitat requirements of foxes are met as a result of the high ungulate populations which maintain a marginal fox habitat through grazing and trampling pressure. This would also account for the establishment of foxes in the Wankie National Park of Rhodesia.

That these extensions may only be temporary, is confirmed by the sight records in the Kruger National Park (Joubert, In litt.). Here fox sightings have followed the same decline as found on Mmabolela (Table 13). Unfortunately, due to the present security situation in Rhodesia, reliable sight records for different years are difficult to obtain.

Dr. S.C. Joubert. Kruger National Park, Skukuza.

Table 13 : Field sightings of *Otocyon megalotis* in the Kruger National Park, South Africa, from 1966 to 1976 (Joubert, *In litt.*)

Period : April to March	Sightings	
	Number of groups	Number of foxes
1966/67	1	6
1967/68	1	2
1968/69	1	6
1969/70	4	10
1970/71	1	1
1971/72	1	3
1972/73	7	12
1973/74	1	1
1974/75	1	1
1975/76	0	0

Pienaar (1970) says it is unlikely that sightings of bat-eared foxes have been overlooked during the past 60 years of the Kruger National Park's existence. Why is it then that only in relatively recent times has the fox extended its range? There is no evidence to suggest that there has been a decline in rainfall over southern Africa during the last 90 years, for which records are available (Tyson, Dyer and Mametse, 1975).

Dyer (1977) has shown that a drought equal to, if not mere severe, than that of the late 1960's occurred in the early 1930's. It is possible that a temporary extension in fox range occurred during this period but that due to the lack of observers in the field, it was overlooked. This may be the case in the Kruger National Park as Tinley (pers. comm.) notes that previous sightings just east of the park in Moçambique have been reported by early hunters, whereas foxes were only scientifically recorded in this area in the late 1960's. Pienaar (1970) comments that their recent range extension is remarkable under the barriers of human settlement and cultivation. It may well be these very factors which have enabled the foxes to migrate and which increased the probability of sighting foxes as they extended their range.

Agricultural practices and development in rural areas (e.g. roads) have increased substantially in the last 30 years. The clearing of land has provided micro-habitats for foxes and the gravel roads have provided access to these habitats. Furthermore, whereas game previously wandered over large expanses of southern Africa, they have been confined to smaller and smaller areas in recent years. This confinement has led to overgrazing and trampling which has created more suitable habitat for

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foxes. This could explain why the foxes have only extended their range in recent years and not during previous periods of apparent suitable climatic conditions. The effect of man-made modifications to the environment is confirmed by the high incidence of foxes on gravel roads and their first appearance in the Victoria Falls area was at the aerodrome (Smithers, 1971).

Optimum fox habitat is to be found in the Kalahari pan system and at Mashatu in Botswana. Under conditions of below average seasonal rainfall, adjoining marginal areas become more suitable for foxes. The longer these climatic conditions persist the greater the area that becomes marginal. Under conditions of above average seasonal rainfall the converse applies.

Thus fox population size and distribution is limited by suitability of the habitat. Modifications of this habitat, primarily with changes in rainfall result in foxes either moving into or out of marginal habitats. Within these habitats under favourable climatic conditions so fox numbers increase and vice versa.

MANAGEMENT

Management practices that would favour bat-eared foxes would be the provision of downgraded habitats. This is in contrast to management systems for most other species, which encourage a vigorous grassland. Likewise, harvester termites, the prime food source of foxes are considered detrimental to good veld management and are often killed by poisoning.

Since rainfall is the main factor affecting fox habitat, there is little man can do to alter this. Fox distribution and numbers will naturally change in response to changes in seasonal rainfall. The effect of herbivore utilisation cannot be overlooked, this being particularly so in the Mashatu Game Reserve and Kalahari pan system of Botswana. The removal or decrease of this factor will adversely affect fox populations.

Although man is unable to modify habitat suitability for foxes on a large scale, there are numerous localised situations that would favour bat-eared foxes. Introduction should be into areas of sparse grassland with bare patches, preferably where calcareous soils are present, although this is not essential. Suitable habitats for introductions are around waterholes where high concentrations of game are to be found, agricultural lands and gravel airstrips. Burning would temporarily provide favourable bat-eared fox habitat. The Bushman in the Kalahari make use of this practice for this very purpose (Parris, per. comm.).

CONCLUSION

In conclusion, it can be said that the bat-eared fox is specialised to a mainly insectivorous diet, showing a high preference for termites. It also has specific habitat requirements in southern Africa, namely short grass with a low basal cover and areas of bare ground. These habitat requirements are found primarily in regions with an annual rainfall of 200 - 300 mm and marginally in areas of mean annual rainfall between 150 - 200 mm and 300 - 400 mm. Furthermore heavy herbivore utilisation helps to maintain a downgraded veld type suitable for foxes. These factors occurring on calcareous soils produce optimum habitat in this region as found in the Kalahari pans of central and southwestern Botswana.

When changes in rainfall and/or grazing pressure occur in areas adjoining optimum fox habitat, foxes either move into the area under favourable conditions or out of the area under unfavourable conditions. The foxes's response to these changes seems to occur over a short period of time.

Thus the bat-eared fox is part of the complicated ecological web and a change in one or more of the abiotic (rainfall) or biotic (herbivore utilisation, termite populations) factors will result in a change in the bat-eared fox population.

SUMMARY

The bat-eared fox Otocyon megalotis is found throughout the semi-arid regions of southern Africa. Bat-eared foxes were studied at two areas in the Upper Limpopo Valley. Pelage, growth and dentition were examined in wild and captive foxes. Growth curves for foxes up until the age of 120 days, and the age at eruption of the permanent teeth were determined. Feeding behaviour and food preferences were studied. It was found that insects and other larvae were the main dietary constituent although in this study, stomach analyses revealed a high proportion of plant material in the diet. Foxes were only found to den during the breeding season and showed a preference for denning in calcareous soils. Births were found to occur over a period of three weeks and pups weaned from an age of 12 weeks onwards. Litter mates remained together up until the age of seven months. Group composition was determined for different months of the year. Activity studies were done during and outside the breeding season and fox densities were determined for both study areas. Foxes have specific habitat requirements which are influenced by rainfall, grazing pressure and soil type: changes in one or more of these factors result in a change in fox populations. Recent range extensions in southern Africa was reviewed in view of the effect of these biotic and abiotic factors.

OPSOMMING

Die bakoorjakkals, Otocyon megalotis, kom in die half dorre gedeeltes van suidelike Afrika voor. Hierdie jakkalse was in twee gebiede van die Boonste Limpopovallei bestudeer. Verharing, groei en tandverwisseling is in jakkalse in hul natuurlike staat, sovel as diê in aanhouding ondersoek. Groeikurwes vir jakkalse tot en met die ouderdom van 120 dae, en tot die verskyning van permanente tande was vasgestel. Voedingsgewoontes en voedsel voorkeur was bestudeer. Daar is gevind dat insekte en ander larwes die hoofbestandeel van die diët is, alhoewel ook 'n groot hoeveelheid plante materiaal in die maag gevind is met ontleding in hierdie studie. Jakkalse het alleenlik in die broeiseisoen van gate gebruik gemaak en het toe kalkagtige grond verkies. Geboortes vind gewoonlik oor 'n tydperk van drie weke plaas en die kleintjies word gespeen vanaf 'n ouderdom van twaalf weke. Werpsels het bymekaar gebly tot en met sewe maande vanaf geboorte. Groep samestellings was gedurende verskillende maande van die jaar vasgestel. Aktiwiteit studies was gedurende die broeiseisoen en daarna gedoen asook bevolkingsdigtheid van die jakkalse in albei gebiede. Jakkalse het spesifieke woonarea-behoeftes wat beïnvloed word deur reënval, tipe grond en veranderings in weidingsomstandighede. Een of meer van hierdie faktore beïnvloed die populasie van die jakkalse. Onlangse uitbreiding van gebiede in suidelike Afrika was gesin in die lig van die invloed van biotiese en abiotiese faktore.

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APPENDIX I : Mean body measurements (lengths in mm and mass in gm) for <u>Otocyon megalotis</u> based on data of three male foxes collected on Mmabolela Estates, Northern Transvaal in October, 1974. The 247-day data are based on a single male fox only

Age in days	Ear length	Hindfoot length	Tail length	Total length	Mass
21	35	65	114	393	390
24	44	66	136	422	445
31	58	73	151	453	592
36	71	84	167	533	722
40	77	87	182	553	780
44	86	97	204	571	953
47	91	98	210	601	1 063
53	98	110	234	630	1 343
58	107	112	271	668	1 430
62	110	116	280	730	1 650
72	114	124	293	740	2 122
88	119	133	339	838	2 900
95	121	140	354	845	3 134
118	127	143	371	923	3 767
247	140	145	370	930	4 600

APPENDIX II. Body measurements (lengths in mm and mass in gm) of *Otocyon megalotis* adults taken from road mortalities on and around Mmabolela Estates, Northern Transvaal from February 1974 to August 1977.

SEX	MEASUREMENT				
	Ear length	Hindfoot length	Tail length	Total length	Mass (gm)
Males	123	148	276	793	4 000
	120	140	270	759	3 600
	115	156	310	858	4 500
	125	138	265	785	4 000
	130	145	300	850	4 600
	140	145	310	870	4 600
	120	146	305	782	3 950
	133	147	305	840	3 000
Total	1 006	1 165	2 341	6 537	32 250
Mean	125,7	145,6	292,6	817,1	4 031
Females	121	141	309	774	2 500
	131	144	312	855	4 100
	123	140	310	873	3 900
	126	150	312	802	4 000
	124	142	301	770	4 100
	131	135	265	777	3 500
	126	140	270	790	3 900
	125	145	290	820	3 800
	120	145	300	800	3 200
	120	145	295	810	3 400
	136	148	300	775	-
Total	1 383	1 575	3 264	8 846	40 400
Mean	125,7	143,1	296,7	804,1	3 640