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# Bat-eared fox behavioural ecology and the incidence of rabies in the Serengeti National Park

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**ABSTRACT**

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This paper provides a brief introduction into some aspects of bat-eared fox biology and social organization that is important to understanding rabies transmission and disease management in susceptible wildlife species (Macdonald 1980; 1993). A detailed description of the effects of two rabies outbreaks on a population of known individuals in the Serengeti National Park is given. Inter- and intrasexual differences in adult mortality rates are reported and discussed.

## INTRODUCTION

Reliable information on rabies in African wildlife is scarce, not least because of the enormous practical difficulties associated with effective monitoring. In Tanzania, rabies was first reported in 1932/1933 (see Rweyemamu, Loretta, Jacobs & Gorton 1973), but in the Serengeti National Park the disease was not confirmed until 1986 (Maas 1993). However, anecdotal accounts of disease-related mortality in African wild dogs (*Lycaon pictus*) exist from the 1970s (Schaller 1972; Malcolm 1979) and even before that time, Leaky (1969) attributed high fluctuations in the number of bat-eared foxes near his camp in the south of the Park to periodic outbreaks of disease. However, so far wild dogs and bat-eared foxes continue to be the only carnivores in which rabies has been confirmed in the laboratory (Maas 1993; Gascoyne, Laurenson, Burrows, Lelo & Borner, in press).

## TAXONOMY

Bat-eared foxes (*Otocyon megalotis*) are comparatively small nocturnal canids, which live in two disjunct populations in the eastern and southern parts of Africa (Fig. 1). They are the only species in the genus *Otocyon* and are set apart from the rest of the Canidae on the basis of several morphological characteristics associated primarily with the species dentition. Firstly, compared to other canids, bat-eared foxes have between one and four pairs of extra molars. Secondly, a modification of the insertion point of the digastric muscle allows the animals to open and close their jaws up to $5 \times s^{-1}$.

## DIET

Although the ears of bat-eared foxes may also serve a thermoregulatory function, their main purpose, like that of the anatomical features described earlier, seems to lie in facilitating effective prey detection. This is so, because bat-eared foxes, unlike most other canids, rarely prey on vertebrates and primarily feed on insects (Nel 1978; Berry 1980; Smithers 1983). In parts of the southern African population, where wild fruit and berries are available, these may also form a substantial part of the species diet (Smithers 1983; Kuntzsch & Nel 1992).

## SOCIAL ORGANIZATION

In the Serengeti, bat-eared foxes live in stable family groups of one male and up to three related females, all of which raise young (Maas 1993). Here, as well as in many parts of southern Africa, the harvester termite *Hodotermes mossambicus* and dung beetles constitute the most important source of food for bat-eared foxes (Nel 1978; Lamprecht 1979; Malcolm 1986; Maas 1993). In this study, both termites and dung beetles were more abundant in areas inhabited by bat-eared foxes than in those which were not, and local differences in *H. mossambicus* foraging hole density were negatively related to the territory size of bat-eared foxes. *H. mossambicus* foraging hole density was further correlated with a variety of demographic and reproductive variables, such as litter size and female recruitment rate (Maas 1993).

Studies carried out in the southern part of the species distribution range have repeatedly described bat-eared foxes as non-territorial (e.g. Nel 1978; Koop & Velimirov 1982; Mackie & Nel 1989; Lourens & Nel 1990; see also Moehlman 1989). In contrast, Lamprecht's (1979) report that the majority of intergroup encounters in the Serengeti were hostile. Observations made in this study are in accord with Lamprecht's accounts and show that Serengeti bat-eared foxes are territorial; they urine-mark and actively defend specific areas against intruding conspecifics during major parts of the year. Thus, it is suggested that bat-eared foxes are territorial in areas where harvester termites form the most important part of their diet and where harvester termite availability is limited.

Bat-eared fox cubs rely on maternal milk for a period of approximately 12 weeks. However, after the cubs are about two weeks old, male bat-eared foxes take over parental duties such as guarding, grooming, play and anti-predator defence and after about five weeks, when the cubs are old enough to venture on short foraging trips, they are also accompanied by their father. Nel (1978) has shown that this form of paternal care is energetically costly, since males were found to have smaller ranges and spend less time feeding when accompanied by cubs. In contrast, the female's involvement with the cubs during the weeks of lactation is almost exclusively restricted to nursing. Because of their unorthodox diet bat-eared foxes are subject to a different set of foraging constraints than carnivores which feed on larger prey. For insect eaters, the collection of a sufficient quantity of very small food items does not only depend on overall availability but is also directly dependent on available foraging time. The importance of time as a potentially limiting factor during foraging is intensified during nutritional bottlenecks, which can occur as a result of a reduction in availability (e.g. a drought), an increase in physiological requirements (e.g. during reproduction) or a combination of both. The unusually high degree of male parental care observed in bat-eared foxes allows lactating females to maximise their foraging time so as to cover both their own nutritional demands as well as those of their growing cubs.

## RABIES MORTALITY IN SERENGETI BAT-EARED FOXES

Between 1986 and 1989, 90% (N = 94) of the mortality suffered by a population of known individuals was caused by disease (Fig. 2 a–c). In contrast, the proportion of animals which were killed by predation or road accidents was negligible (6%). During the four years of this study (1986–1989), two separate disease outbreaks affected the population—the first in 1987 and the second in 1988. Both outbreaks were of short duration and lasted only for approximately seven weeks in 1987 and five weeks in 1988. All of three animals, which had been submitted for postmortem examination shortly after they had died were diagnosed as rabid. (The number of necropsied individuals is regrettably small due to the difficulties associated with finding the dead animals and finding them before decomposition has made postmortem examination impossible.) Thus, it was assumed that other animals which disappeared shortly after they were observed to show signs of rabies had died of the same cause.

The majority of infected animals developed the paralytic form of rabies and did not show any furious signs. Instead, an initial stiffness and lack of coordination in the animals hind limbs progressively developed into complete ataxia. At the same time, the animals grew increasingly weak and sometimes suffered violent convulsions and cramp-like seizures, which affected their entire body and during which they frequently cried out. Other symptoms included conjunctival and scleral congestion, accompanied by varying degrees of discharge mainly from the animals' eyes. Increased salivation was not observed. Some individuals developed an almost 'obsessive' tendency to pick up food items and carry them around in their jaws. Infected animals soon became too weak to forage and usually died within a week after first showing signs of altered behaviour. Animals which showed signs of restlessness were actively avoided by other group members and although this was true also for several animals suffering the terminal stages of paralytic rabies, most individuals with paralytic rabies received increased amounts of grooming and contact behaviour.

Looking at the study population as a whole, it was found that approximately 20% of all males and cubs (N = 19 and N = 234 respectively) and about 60% of all females (N = 48) were affected by the disease. Data presented in Fig. 2 show that during the four years of the study, rabies was the major cause of death in both adult and juvenile bat-eared foxes. However, a comparison of proportional adult mortality revealed that in both years the proportion of females which fell victim to the disease was significantly larger than the proportion of males. Further examination of the data showed that in both groups of adults fewer animals died during the 1987 outbreak than during that of the subsequent year. In contrast, the proportion of cubs which died from rabies was the same in both years. Translated into probability ratios, the data on male and female rabies-related mortality suggest that in years in which rabies outbreaks occurred, females were at least 11 times more likely to die than males (Maas 1993).

## DISCUSSION

### Differences in susceptibility?

Although some continue to consider rabies an inevitably fatal disease, the outcome of rabies infections is believed to depend on multiple factors such as virus strain and pathogenicity, the dose of infectivity, host susceptibility and route of exposure (see Baer 1991). Today ample evidence (reviewed by Martin 1989) exists for physiological mechanisms by which exposure to stressors can increase the susceptibility of individuals to infectious diseases (Fowler 1986; Workman & La Via 1987; Jeppesen 1988; Wemelsfelder 1990). Evidence which indicates a possible link between immunocompetence and susceptibility to rabies has also been accumulating (Wiktor *et al.* 1980, cited by King & Turner 1993; Sriwanthana, Hemachuda, Griffen, Manusathit, Tweardy & Phanuphak 1989; see also Fekadu 1991). In 1975, Winkler reported that stress and physical condition can influence the length of the incubation period in foxes. McLean (1975) argued that in raccoons, latent rabies infections may be reactivated by stress (see also Johnston & Beauregard 1969), although this view is increasingly disputed.

The 1987 epidemic of this study took place at a time when the cubs were almost fully grown, while the 1988 outbreak reached the population in November, when females were in mid-lactation. Furthermore, rainfall in November and thus insect availability was exceptionally low in 1988. November usually marks the early part of the rainy season and brings with it a dramatic increase in insect availability. After four months of dry season during which food supplies become increasingly scarce, the animals are at a nutritional low, a fact which is reflected in their poor physical condition during this time of year. Thus, a delay in the onset of the rainy season signifies a nutritional dilemma at a time when, as a consequence of lactation and the cost of parental care, nutritional demands on adults are greatest. This is particularly relevant since compared to other canids for which this information is available, the cost of lactation is high in bat-eared foxes (Maas 1993). [Other species concerned are: domestic dog, coyote, dhole, red fox, grey fox (see Oftedal 1984; Oftedal & Gittleman 1989)]. Other aspects of the species' reproductive biology provide further evidence for the nutritional challenge faced by bat-eared fox females during the time of lactation. Thus, in years of food scarcity during the time of lactation a reduction of litter size is accompanied by a female biased offspring sex ratio (Maas 1993). Whether this reduction in offspring numbers is a consequence of maternal infanticide, pre-natal adjustments of litter size or simply the result of early cub mortality is unknown.

It is therefore possible that poor physical condition, aggravated by reduced availability of food and water was associated with higher mortality rates in lactating females in 1988. Restricted access to food, due to lack of rainfall, would also affect male bat-eared foxes and hence may explain the difference in male mortality rates between the two years. Data which are perhaps related to this phenomenon have been presented by McLean (1975), who reported a female bias in the occurrence of rabies serum neutralising antibodies in raccoons. Furthermore, female bats tend to be over-represented in rabies samples submitted for examination in the United States (Rupprecht, personal communication). As far as the differential mortality rates between lactating and non-lactating females are concerned, it was found that in some ungulates females undergo a period of postpartum immunosuppression. However, the question of whether the observed phenomena indicate inter- or intrasexual differences in susceptibility which are related to differences in condition, cannot be resolved until data on the presence of rabies neutralizing antibodies, physical condition and immune systems are available.

### Differences in exposure

Differences in exposure rather than susceptibility may provide an alternative explanation for the observed intra- and intersexual differences in disease-related mortality. It has been suggested that rabies transmission may take place during social grooming in wild dogs (Gascoyne, personal communication). However, in bat-eared foxes, disease transmission through grooming cannot explain the observed differences in male and female mortality rates, since males are more active groomers than females (Maas 1993). Moreover, intra- and intergroup aggression is rare in bat-eared foxes and both territorial and antipredator defence are almost exclusively performed by males. Hence, increased exposure of females through intra- or interspecific antagonistic encounters is an unlikely explanation for the observed phenomena. However, rabies may be transmitted from one female to another during communal suckling. In family groups with more than one breeding female, females always suckle each other's cubs communally. It is thus possible that disease transmission via maternal milk occurs between nursing mothers to their cubs (see Constantine 1967; Afshar & Bahmanyar 1979). Infected cubs may then pass the disease on to other females through abrasions on the females' teats. Whether or not, however, this hypothesis reflects reality cannot be decided without further research.

In most areas where rabies epidemics occur, one species is predominantly involved in maintaining the disease, while other—so called "spill-over species"—are less frequently affected. In the Serengeti National Park, rabies so far has been found only in bat-eared foxes and wild dogs (Gascoyne *et al*., in press). The disease is also present among the domestic dog population which inhabits areas surrounding the Park (Gascoyne King, Laurenson, Borner, Schildger & Barrat 1993). It is unlikely, however, that these three carnivore species will remain the only ones implicated in the transmission of rabies in the Serengeti ecosystem, once further studies are undertaken. The problem of disease-related mortality in Serengeti carnivores is further complicated by the recent occurrence of distemper in the Kenyan Masai Mara Game Reserve (Alexander, personal communication), which is situated to the north of the Park and is part of the same ecosystem. In the field it is difficult to distinguish between canine rabies without laboratory confirmation. Thus, the problem of disease-related mortality in Serengeti carnivores may be even more complex than it at first appears (Macdonald 1993; Gascoyne *et al*. 1993). Yet, the currently available information on the prevalence of rabies in the local wild dog population as well as the results of the present study, emphasise the urgent need for more information on both the spectrum and the scale of rabies infection in Serengeti carnivores. This information is necessary in order to identify the relative roles which wildlife species and domestic animals play in the transmission and maintenance of rabies in the area, both in view of its conservation implications (Macdonald 1993) and in terms of minimising human exposure.

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