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The bat-eared fox: a prime candidate for rabies vector?

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ABSTRACT

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Bat-eared foxes, *Otocyon megalotis*, are small (3–5 kg), primarily insectivorous carnivores widespread in the more arid areas of southern and East Africa. For many months of the year they live in nuclear family groups, members of which frequently indulge in affiliative behaviour such as play, allogrooming, and huddling. Physical contact between individuals in any particular group is thus common. In addition, groups are non-territorial and intermingle freely at times when exploiting food-rich patches of clumped prey, e.g. individuals foraging for harvester termites, *Hodotermes mossambicus*.

INTRODUCTION

Field work over many years, in the south-western Kalahari, has indicated that bat-eared-fox density fluctuates, at times markedly (Nel, Mills & Van Aarde 1984; Nel, unpublished data). In this area, changes in rainfall, and therefore available numbers of insects have been implicated (Nel *et al.* 1984). However, other agents may also have been involved. Susceptibility to disease would be enhanced in a population already stressed by reduced food availability. During 1990 to 1992 bat-eared foxes reached a very high density in the Kalahari Gemsbok National Park. This was followed by a dramatic slump in numbers from June 1992 to March 1993 (see below). Breeding failed, with few cubs produced (T. Jackson, personal communication 1993). Mean group size during March 1993 was two, low when considering this is the period when family groups forage together. Dead foxes, and foxes at water troughs "foaming at the mouth", were observed in the park or on neighbouring farms (E.A.N. le Riche, personal communication 1993).

The behaviour and contact rates between healthy free-ranging bat-eared foxes are described below. Although no comparable data for foxes during the incubation period, or showing clinical signs of rabies are available, affiliative behaviours are so common in this species that intra- and intergroup contacts between rabid and non-rabid individuals probably occur frequently. This paper aims to show that the social dynamics of bat-eared foxes, and especially certain behavioural traits, make them prime candidates for rabies vectors. Obviously transmission of rabies in bat-eared foxes can only be accomplished through direct physical contact. The understanding of the epizootiology of rabies would therefore be much improved if data on contact behaviour and contact tempo for this species were available.

MATERIALS AND METHODS

Groups of bat-eared foxes were followed by vehicle in the Kalahari Gemsbok National Park (south-western Kalahari) during the course of an ongoing project on foraging behaviour from 1976 till the present. Low numbers of foxes from 1981 to 1987 precluded worthwhile data being gathered on social interactions. Counts of fox density were conducted in the dry bed of the Nossob River, from Nossob Camp up to Kwang windmill (*c.* 23,5 km) or to Bedinkt windmill (*c.* 38 km). Normally several counts were conducted during a particular visit and the results of these and behavioural data were entered onto standard data sheets, or onto magnetic tapes which were later transcribed.

RESULTS

To place the role of bat-eared foxes as vectors of rabies in perspective, a brief summary of their behavioural ecology is first given. Bat-eared foxes feed predominantly on insect prey (Nel 1978; Nel & Mackie 1990; Skinner & Smithers 1990; Kuntzsch & Nel 1992), a unique trait amongst canids. They forage preferentially in short-grass habitat (Mackie & Nel 1989; Nel 1992) and utilize home ranges varying from 0,37– 1,28 km^2 in the south-eastern Orange Free State (Mackie & Nel 1989) to 0,5–3,0 km^2 in the south-western Kalahari (Nel 1984) and 0,9–2,9 km^2 in the central Karoo (Kuntzsch 1992). Pair formation occurs during June/July and cubs are born from October to December. Before weaning is completed at an age of *c.* 10 weeks (Berry 1978) the male guards the cubs and initiates them into foraging (Nel 1978; Malcolm 1986), while the female forages singly. Thereafter, nuclear family groups forage together until June/July, when such groups split up. Group size at any particular time of year is not fixed, but depends on litter size and mortality, and group composition— mated pairs and non-breeding sibling groups from June/July up till December/January, and family groups from December to July. In the present study area, group size varied from month-to-month with the frequency distribution of group sizes differing significantly between January to July and August to December (Nel *et al.* 1984). A whole suite of communicatory behaviours have been described in this species (Lamprecht 1979; Nel & Bester 1983). In the southern subspecies, *Otocyon m. megalotis*, visual communication is most common, followed by olfactory and tactile communication. Vocalizations are rare (Nel & Bester 1983).

Very few intra- or intergroup agonistic encounters were noted during foraging or feeding. As the foxes feed on prey occurring in clumps, e.g. harvester termites, *Hodotermes mossambicus* or *Microhodotermes viator*, and on temporarily depleted, or widely dispersed and therefore even more unpredictable prey, e.g. crickets, beetles or grubs, defence of this resource is uneconomical. Territoriality, in the southern subspecies at least, is therefore absent. Food patches are shared not only by members of a particular group, but also by those of different groups, leading to feeding aggregation of 15 or more foxes in an area of < 0,5 km^2 (Nel 1978). Similarly, dens housing cubs can be clumped: during December 1976, five dens and a total of 19 foxes occurred in < 0,5 km^2 in the Nossob river-bed just south of Nossob Camp, with a further two dens (nine foxes) in an adjoining 500 m strip. Movements of adults between dens were noted (see also Malcolm 1986).

Direct physical contact between individuals is common. During April (autumn) and June to August (winter) at least two, often all, members of groups encountered when resting or sleeping huddled together. Allo (mutual) grooming is more prevalent during summer months, when cubs are present, than during winter. During a total of 26 h 34 min of observations allogrooming occurred 15 times; face (mouth) licking took place during nine of these episodes. By contrast, during 25 h 37 min of observations in winter only three instances of allogrooming were recorded, including one bout of face-licking lasting 3 min 30 s.

Numbers of foxes also vary within and between years, e.g. along a particular 6,3 km stretch of the Nossob River south of the Nossob Camp, 71 foxes were counted in April 1991, but only 32 in July (i.e. *c.* 11,3 and 5,1 fox/km of river-bed). Over a 26 km stretch of riverbed (including the 6,3 of above), 170 foxes were counted in April 1991, but only 19 in March 1993 (i.e. 6,5 *vs* 0,7 fox/km of river-bed). In preferred short-grass habitat in the south-eastern Orange Free State, fox densities also varied: 0,75 foxes/km^2 in 1986, 0,99/km^2 in 1987 and 0,68/km^2 in 1988 (Mackie & Nel 1989). In the central Karoo, densities were 1,11 and 1,67 foxes/km^2 (September 1988 and February 1989, Karoo National Park), and 1,05 and 2,97/km^2 (September 1988 and April 1989, on farmland) (Kuntzsch 1992). Bat-eared foxes normally have one litter/year; litter size varies from 4–6 (Skinner & Smithers 1990).

DISCUSSION

A prerequisite for the persistence of rabies in a fox-population, or for it to spread, is physical contact between individuals. The contact rate, in a behavioural sense, is the frequency per given time period of some kind of physical contact, not necessarily violent, between individuals. In the sense of rabies persistence, the contact rate for a population signifies the average number of susceptible individuals infected by each diseased animal; this must ≥ 1,0 for rabies to remain enzootic (Bailey 1975; May 1983, cited by Ginsberg & Macdonald 1990). Aggressive interactions, between apparently healthy foxes, are very rare and have only been noted once, in a feeding context, and once between an adult male accompanying cubs and another adult of unknown sex. Interspecific physical contacts with other canids have only been observed during summer when black-backed jackals, *Canis mesomelas*, have been attacked, bitten, and driven away when approaching dens with cubs, too closely. Adults from other neighbouring dens can also participate in such attacks. Amicable contact between group members, on the other hand, is very common and densities can approach 1/km^2—a high figure for a carnivore. If rabies can be spread through salivary interchange in nature—oral infection of some foxes have been reported (Howell

1982)—the high frequency of oro-oral contact between adults, and especially between adults and cubs in summer would provide an ideal route for the transmission of the virus. In addition to this behavioural trait, other species attributes such as huddling, living in family groups for 5–7 months, overlapping home ranges of groups and intermingling of members of several groups on feeding patches, suggests the possibility, indeed probability, of frequent close approach and even physical contact between individuals. Furthermore, the transmission risk increases exponentially with increasing fox density; the risk of an infected individual spreading rabies would thus be enhanced during periods, in areas, with high fox densities. Clearly thus, from a behavioural and ecological point of view, bat-eared foxes would be an ideal vector for the transmission of rabies.

One is tempted to implicate rabies as the agent causing the precipitous decline in bat-eared fox numbers at intervals. This could be due also to a food shortage (Nel *et al*. 1984) or other diseases, e.g. canine distemper (Meredith 1982). However, as Meredith (1982) and Thomson & Meredith (1993) pointed out, the incidence of rabies in bat-eared foxes is increasing. These foxes are so widespread in southern Africa that any control programme probably has little chance of success; in addition, their feeding habits would make the use of oral vaccines administered through bait problematical.

To understand the epizootiology of rabies in a particular species and to suggest possible ways of controlling its spread or even eradicating it, the biology of the particular species should be known (Macdonald 1980). What is known about the biology of bat-eared foxes, and especially their socio-ecology, can at this stage to a limited extent help in predicting the epizootiology of an outbreak at a particular location. Clearly, much more needs to be known in order for efficacious counter-measures to be devised.

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