

Social systems and behaviour of the African wild dog *Lycaon pictus* and the spotted hyaena *Crocuta crocuta* with special reference to rabies

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ABSTRACT

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Differences in the social systems and behaviour of two potentially important hosts of rabies, the African wild dog and the spotted hyaena, may lead to differences in the epizootiology of the disease in the two species. Wild dogs are highly social animals in which pack members are in constant physical contact with each other, but in which inter-pack interactions are rare. Spotted hyaenas are more flexible in their social systems and behaviour. Clan members interact less frequently than do wild dogs, but inter-clan contact rates may be high in high density populations. Rabies transmission within wild dog packs should be rapid, but rare between packs. In spotted hyaenas rabies transmission between clan members may partially depend on the social status of the animals involved and between packs on the density of hyaenas in the area.

INTRODUCTION

An important aspect in many outbreaks of rabies is the wildlife management problems they pose (Barnard 1979; Meredith 1982). Macdonald (1980) urged that this kind of problem should be tackled on the basis of a thorough understanding of the behavioural ecology of the species involved. The African wild dog *Lycaon pictus* and the spotted hyaena *Crocuta crocuta* are two of Africa's most widespread large carnivores, although the distribution range of the wild dog has been drastically reduced in recent years (Fanshawe, Frame & Ginsberg 1991). Both species have been implicated in rabies outbreaks (Mills 1990; Burrows 1992). In the case of the wild dog this has had serious consequences for the survival of the species in the Serengeti ecosystem (Burrows 1992). In the case of the spotted hyaena rabies has been men-

tioned as a possible limiting factor for the low density southern Kalahari population (Mills 1990).

In this paper I describe those aspects of the social systems and behaviour of these two species which may be of relevance in the epizootiology of rabies. I then speculate on the manner in which rabies may be transmitted between members of the species. Most of the information for the wild dog is taken from my own studies on this species in the Kruger National Park (KNP). In this species flexibility in social system appears to be limited (Fuller, Kat, Bulger, Maddock, Ginsberg, Burrows, McNutt & Mills 1992a) and the basic principles enumerated here are applicable to most wild dog populations. Spotted hyaenas, on the other hand, have a highly flexible social system (Mills 1990). More attention is given to this flexibility in the discussion of the spotted hyaena.

AFRICAN WILD DOG

Group structure

The African wild dog is a highly social, pack-living animal. Pack size varies from a pair and their latest litter of pups to 50 or more animals of all ages (Fuller *et al.* 1992a). This variation in pack size occurs in all regions, so that within a region pack size varies markedly both between and within packs (Fig. 1). In the KNP the mean size of 26 packs mid-way through the annual breeding cycle was $13,7 \pm 7,1$ (Maddock & Mills 1993).

Packs comprise varying numbers of males and females. The sex ratio in 16 packs in the KNP varied from a male:female ratio of 1:0,3–1:4, with an overall sex ratio of 1:0,9 which is not a significant diversion from parity (Binomial $P = 0,4562$; double-tailed) (Maddock & Mills 1993). Adult pack members are related within but not between the sexes. Pups and yearlings are normally the offspring of the dominant pair.

Much of the fluctuation in pack size is caused through the mid-year birth pulse (Fig. 1) and subsequent high pup mortality, which averaged 74% in the first year in 14 litters. The cause of death of most pups is unknown, but predation by lions *Panthera leo* which accounted for 12 out of 26 known deaths may be the most important factor.

Adult mortality rates are also relatively high, being 35% per year for 40 dogs over one year of age fitted with radio transmitters. No major mortality factor could be identified; lion predation, intra-specific fighting by males and human causes associated with snaring contributed equally to the 11 known cases. Disease was only implicated in the deaths of three pups and no antibodies in the sera of 27 dogs tested for rabies, canine distemper, canine parvovirus and canine ehrlichiosis were found (Van Heerden, unpublished data).

An important factor in pack dynamics of wild dogs is emigration and immigration. Over a three year pe-

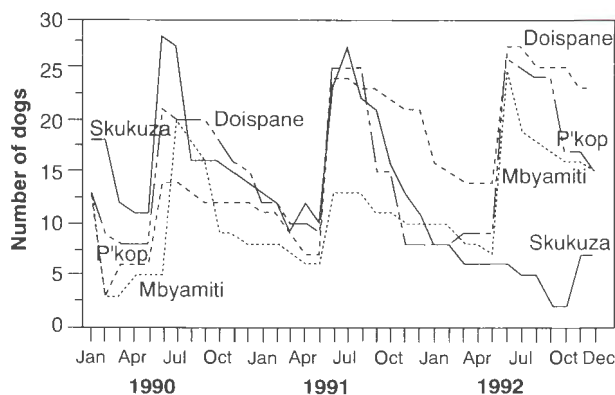


FIG. 1. The number of African wild dogs/month in four packs from the Kruger National Park, 1990–1992

riod 0,7 emigration events/pack/year took place in eight packs in the KNP, with a mean of 2,3 dogs emigrating/emigration event. Wild dogs emigrate in same-sex groups. In the KNP males have been observed to emigrate more frequently and in larger groups than females. Dispersal distances are usually quite short; 14 (67%) of 21 dispersing groups observed have moved between packs within the southern district of the KNP (see Maddock & Mills 1993), involving distances of less than 50 km. Some, however, are extensive; two males dispersed over 250 km from their natal pack, before forming a new pack with three females (Fuller, Mills, Borner, Laurenson & Kat 1992b). Dispersing dogs may quickly attract mates from established packs once these are located. On two occasions single females were seen in the presence of new males within one day of disappearing from their natal pack.

Social behaviour

The members of a wild dog pack spend nearly all their time in close proximity to each other. When resting they frequently lie together so that they are in bodily contact, although pups and adults usually lie under separate trees. Prior to moving off from a resting place, or when pack members have been separated, the members of a pack indulge in a conspicuous greeting ceremony (Kuhme 1965; Schaller 1972). This entails dogs gambolling about uttering a chattering sound and coming together to muzzle and lick each other around the mouth.

During the mating season competition between males for females may be severe, particularly in packs with several adult males. During this time males may inflict severe injuries on each other with biting being directed at the face and head. Normally only the top ranking (alpha) male and female breed, although at 9 (43%) of 21 dens observed in the KNP a second female bred. In only two of these did the lower ranking female's pups survive beyond one month. Wild dogs are seasonal breeders, 37 (93%) of 40 litters being born between 20 May and 6 July in the KNP.

Non-breeding animals contribute to the welfare of pups by feeding them regurgitated meat at the den and by acting as guards when pack members are out hunting (Malcom & Marten 1982).

Home range and movements

Wild dogs occupy large home ranges which vary in size, not only between areas, but seasonally (Fuller *et al.* 1992a). During the 10–12 weeks denning period a pack in the KNP occupied a range of 81 km², whereas for the rest of the year the same pack ranged over an area of 885 km² (Gorman, Mills & French 1992). The mean home range size for four packs studied in the KNP was 545 km² (Gorman *et al.* 1992).

There may be considerable overlap in the home ranges of different packs, but this is largely negated by differences in temporal usage (Mills & Gorman, unpublished data). It is rare for established packs to meet up with each other and when this happens the larger pack chases off the smaller pack (Frame, Malcolm, Frame & Van Lawick 1979). Physical contact between established packs has not been observed.

SPOTTED HYAENA

Group structure

Like the African wild dog the spotted hyaena is a highly social carnivore living in clans which vary in size from 5–80 individuals (Mills 1990). Spotted hyaena group sizes vary more markedly from area to area than do wild dog pack sizes, depending on the dispersion pattern of the food. For example, in the southern Kalahari mean spotted hyaena clan size was eight (Mills 1990), whereas in the Ngorongoro Crater it was 56 (Kruuk 1972).

Females outnumber males in the clans. For example, in the southern Kalahari the male:female sex ratio of clan-living hyaenas was 0,4:1 (Binomial $P = 0,039$; single-tailed).

Spotted hyaena clans do not fluctuate to the extent of wild dog packs (Fig. 2). There is no seasonal birth pulse and mortality rates tend to be lower than in wild dogs. In the southern Kalahari 75 % of cubs born survived to 15 months (Mills 1990) and adult mortality rates were less than 10 % per annum (Mills, unpublished data).

Most females spend their lives in their natal packs, but all males eventually leave to become nomadic or to become immigrant males in a new pack (Henschel & Skinner 1986; Mills 1990). In one pack studied in the southern Kalahari there were on average 1,6 emigration events/year over a five year period.

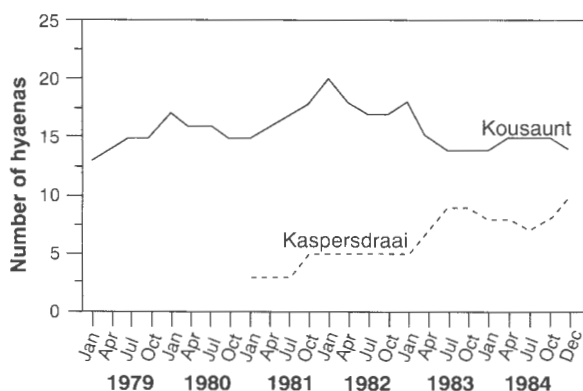


FIG. 2 The number of spotted hyaenas/three month period in two clans from the southern Kalahari, 1979–1984

Unlike wild dogs, spotted hyaena dispersers are usually solitary, but they may cover large distances (Mills 1990).

Social behaviour

Spotted hyaenas are more flexible in their social behaviour than are wild dogs. Rarely do all the members of a clan come together at one time. Sub-groups form and break up and an individual may be on its own on one day, with a group of three the next and with six different hyaenas on a third day. When the members of a clan meet up they often perform a ritualised meeting ceremony where mutual sniffing and licking of the sexual organs takes place (Kruuk 1972). A well established dominance hierarchy exists within spotted hyaena clans (Frank 1986; Mills 1990). High ranking animals participate more fully in clan activities such as the meeting ceremony and are more likely to be in a group than on their own (Mills 1990).

All females produce cubs. Litter size is only one or two and births are aseasonal (Lindeque & Skinner 1982; Mills 1990). Females den communally and suckle their cubs for about 12 months. The den is the social centre of a spotted hyaena clan and a place where members often interact with each other. Although they den communally spotted hyaenas do not co-operate in feeding young. Until the cubs are old enough to join pack members foraging, at about nine months of age, they rely almost exclusively on their mother's milk for sustenance (Mills 1990).

Home range and movements

Spotted hyaenas exhibit more territorial behaviour than do African wild dogs. They scent-mark their home ranges (Kruuk 1972; Mills & Gorman 1987), particularly around boundaries (Henschel & Skinner 1991). They also physically defend their areas against neighbouring clans (Kruuk 1972), although if possible this is avoided and territorial defence is carried out through vocal and other displays as well (Mills 1990; East & Hofer 1991; Henschel & Skinner 1991).

As with clan sizes, territory sizes in spotted hyaenas vary greatly from region to region, again because of differences in food dispersion (Mills 1990). In the Ngorongoro Crater clans of up to 80 spotted hyaenas occupy territories of 30–40 km² and inter-territorial clashes are frequent (Kruuk 1972). In the southern Kalahari ranges of up to 1 776 km² occupied by nine adults have been reported (Mills 1990) and hyaenas from neighbouring clans rarely come into contact with each other. Hofer & East (1993a) describe an unusual commuting system for spotted hyaenas on the Serengeti plains. Here clans occupy small territories of about 55 km², but during times of food shortage within the territory the residents commute long

distances to feeding grounds of migratory prey. Residents clash with commuters on kills in their territories, but ignore commuters "in transit" (Hofer & East 1993b).

RABIES TRANSMISSION

Rabies virus is generally transmitted by the bite of an infected animal, as it is present in the saliva (Kaplan 1977). The virus may also be transmitted through the transfer of saliva to intact mucous membranes of the lips of animals (Hassel 1982), for example by an infected animal licking another on the lips.

How might the contrasting social systems and behaviour patterns of the two species influence their vulnerability to the rabies virus? Two aspects need to be addressed; the manner in which the virus is transmitted to a species and the manner in which it is transmitted within the species.

If the virus can only be transmitted through saliva, interspecific contact is essential for the transfer of the virus between species. The social behaviour of a species does not seem to be an important consideration here. Although African wild dogs in the Serengeti may obtain the virus through contact with domestic dogs on the periphery of the ecosystem (Gascoyne, personal communication), rabies is often spread by wildlife, usually with one dominant vector species in an area (Barnard 1979; Macdonald 1980; Meredith 1982). The dominant vector may be important in determining which species are infected. For example, jackals, which frequently interact with hyaenas around carcasses, are more likely to bite hyaenas than are mongooses. Also the susceptibility of different species to the particular rabies virus is an important consideration (Macdonald 1980), but is not discussed here.

If an African wild dog contracts rabies it is likely that the entire pack will become infected by the virus. Their highly integrated social system lends itself to this. If the rabid dog becomes aggressive the other pack members will be in close proximity and vulnerable to being bitten. Moreover, when a wild dog exhibits unusual behaviour, it immediately attracts the attention of other members of the pack, which may lick the infected animal around the mouth as shown in the television documentary "Running for their Lives" (BBC, Bristol).

Transmission from one pack to another would not seem to be a major concern in the African wild dog. Packs so rarely come into contact with each other that the chances of this happening when at least one member of a pack is infectious must be low. This has also been suggested to be the case for rabies transmission amongst wolves (Chapman 1978). Even the so-called furiously rabid stage, where animals may cover large distances (Macdonald 1980), does

not seem to be an important means of intraspecific infection in a species living at such a low density as the African wild dog. The fact that rabies transmission between pack members is probably mainly effected through mouth to mouth contact, suggests that the incubation period (time between infection and the development of clinical signs) is short. Emigration and new pack formation involving an infectious rabid dog, therefore, must be highly unusual. If the demise of the wild dog on the Serengeti plains is due to rabies it suggests that each pack was infected separately with rabies virus.

The possible transmission of the disease through a spotted hyaena clan in the southern Kalahari has been documented by Mills (1990). This was a small clan comprising only four adults. In larger clans the social status of the infected animal may be important in determining whether the virus will spread through the clan. A high ranking member will interact more frequently with other clan members than a low ranking one and, therefore, may be more likely to be infected and to transmit rabies. The behaviour of a low ranking animal that has contracted rabies may change so that it becomes more aggressive and, therefore, more likely to interact with other members of the clan. However, the chances of a low ranking animal being bitten by a rabid high ranking animal may be small, because of avoidance of the dominant animal by the submissive one. Low ranking animals may, however, be more likely to be bitten by another species and thereby introduce the virus into the species. For example, they are more likely to scavenge on the periphery, or on the last remains of a carcass, when jackals become far bolder.

The semi-permanent nature of spotted hyaena dens enhances their vulnerability to rabies transmission. A rabies carrier visiting a den is likely to contact other clan members as reported in Mills (1990).

In high density spotted hyaena areas, contact rates between clans may be frequent, consequently rabies transmission between clans would be expected to be high. If rabies entered the Ngorongoro spotted hyaena population it may be devastating. In a rabies outbreak in the low density spotted hyaena population in the southern Kalahari a clan was eradicated and the disease apparently spread no further amongst spotted hyaenas. However, in a later outbreak in a higher density spotted hyaena region of the southern Kalahari, the disease appeared to spread to several clans, without decimating any of them (Mills 1990). It must be added that the behaviour of animals that contract rabies may also vary; sometimes they may seek a familiar area, at other times they may become abnormally wide-ranging.

The social systems of carnivores are clearly important determinants in the epizootiology of rabies and other infectious diseases. The flexibility and variation

in social systems, however, can cause differences in frequencies of encounters between individuals and hence in potentially different contact rates for rabies (Macdonald & Bacon 1982). This, together with the complexities of the virus itself, complicates the understanding and study of rabies transmission in free ranging carnivores.

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