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Free-ranging domestic dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: threats of competition and disease to large wild carnivores

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Abstract

Domestic dogs (*Canis familiaris*) arrived in Zimbabwe ca. 1000 years ago. Numbers of free-ranging dogs have reached unprecedented levels in communal lands (agro-pastoralist rural areas), and interact with large wild carnivores along boundaries with wildlife reserves as predators and prey. This study examined a population of 236 dogs in a 33-km^2 section of Gokwe Communal Land (GCL) bordering the Sengwa Wildlife Research Area (SWRA) in north-western Zimbabwe in 1995–1996. Dogs were found up to 6 km within the SWRA, and were the most common carnivore on the GCL–SWRA boundary. Observations of 16 radio-collared dogs showed that they were inefficient predators. Only 20 kills were recorded amongst the remaining dog population, of which three were wild ungulates. Dogs were unsuccessful predators due to their small group size (mean 1.7) and body mass (mean 14.7 kg), and the abundance of alternative food. It is therefore unlikely that they compete with large carnivores for wild prey. However, leopards (*Panthera pardus*), lions (*P. leo*) and spotted hyaenas (*Crocuta crocuta*) preyed on dogs in GCL, removing $\geqslant$6% of the dog population in 1993. Such predation provides ideal circumstances for disease transmission. Canid disease was prevalent in the study area; including rabies and probably distemper. The risk of infection is greatest during the dry season (May–October), when peaks in rates of disease, carnivore incursions into GCL, and predation on dogs coincided. The role of jackals (*Canis adustus* and *Canis mesomelas*) and spotted hyaena predation of dogs is discussed in relation to disease epidemics within wildlife reserves. With a dog population growth rate of 6.5% per annum, and the prevalence of canid diseases, the conservation threat posed by dogs is escalating on communal land–wildlife reserve boundaries in Zimbabwe. Measures to control dog numbers and improve vaccination coverage of dogs are discussed.

Keywords: Canid disease; Dogs; Predation; Wild carnivores; Zimbabwe

1. Introduction

Domestic dogs (*Canis familiaris*) are probably the most numerous carnivores in the world today (Daniels and Bekoff, 1989). Dogs have been introduced wherever man has settled, and consequently all continents and most islands have been colonised by this canid (WHO/WSPA, 1990; Wandeler et al., 1993). In many situations colonising dogs have acted as an invasive alien species, disrupting and modifying indigenous ecosystems (Clout, 1995).

Dogs are potentially effective predators of native fauna, for example in the Galapagos (MacFarland et al. 1974; Kruuk, 1979; Kruuk and Snell, 1981) and the West Indies (Iverson, 1978), and can therefore have competitive interactions with endemic wild carnivores. Dogs preying on blackbuck (*Antelope cervicapra*) fawns in India compete with the threatened Indian wolf (*Canis lupus pallipes*) (Jhala and Giles, 1991; Jhala, 1993), and in Africa they compete with the highly endangered Ethiopian wolf (*Canis simensis*) for rodents (Gottelli and Sillero-Zubiri, 1992; Sillero-Zubiri and Gottelli, 1994; Sillero-Zubiri and Gottelli, 1995). Competitive exclusion by dingoes (*Canis familiaris dingo*) introduced from Asia may have caused the extinctions of the marsupial

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wolf (*Thylacinus cynocephalus*) and Tasmanian devil (*Sarcophilus harrisii*) in mainland Australia (Corbett, 1995).

Dogs also pose a threat to wild carnivores by transmitting canid diseases. As reservoirs for rabies, canine distemper and parvovirus they were partly responsible for the extinction of the African wild dog (*Lycaon pictus*) in areas of the Serengeti ecosystem, Tanzania (reviewed by Woodroffe, 1999). Similarly, disease transmitted from sympatric dogs has been cited as one of the major threats to the existence of the Ethiopian wolf (reviewed by Woodroffe, 1999). Dogs were also implicated as the source of the 1994 canine distemper epidemic among Serengeti lions (*Panthera leo*) (Roelke-Parker et al., 1996). However, the nature of contact between dogs and large wild carnivores has never been accurately determined (e.g. Mebatsion et al., 1992; Alexander et al., 1993; Gascoyne et al., 1993; Alexander et al., 1994; Roelke-Parker et al., 1996).

Dogs were introduced to Zimbabwe ca. 1000 years ago by the Bantu immigration (Clutton-Brock et al., 1976; Clutton-Brock, 1993; Butler, 1998). Today >70% of the national dog population exists in communal lands (rural areas of traditional agro-pastoralism), which cover 42% of Zimbabwe's land area (Brooks, 1990). All dogs are owned but free-ranging, and breed freely whilst also depending on people for their basic needs (Butler and Bingham, 2000). Hence the exponential growth of the human population in the past century has led to an equally rapid increase in dog numbers. In 1954 there were 250,000 dogs nationally (Adamson, 1954). By 1994 the population in communal lands alone had reached 1.36 million, with an annual growth rate of 6.5% (Butler and Bingham, 2000).

Dog rabies was present in Zimbabwe during the 19th century, but had disappeared before European settlement in 1890. After a brief outbreak in 1902–1913 rabies was reintroduced via imported dogs in 1950, spreading to most areas of the country (Cumming, 1982; Foggin, 1988; Kennedy, 1988). Today dogs are the primary vector for rabies in Zimbabwe, contributing 46% of all confirmed cases in 1950–1996 (Bingham et al., 1999a). Because most dogs exist in communal lands they are the principal reservoir for the disease, and are targeted with annual vaccination campaigns by the Department of Veterinary Services (DVS) (Bingham et al., 1999a). Due to limited resources and logistical constraints adequate coverage was achieved in only two of seven communal lands surveyed in 1994 (Butler, 1995), and since then vaccination coverage has declined further in most communal lands (Bingham et al., 1999a).

As the primary reservoir for rabies, communal-land dogs are responsible for triggering epidemics in the second most common vectors, side-striped jackals (*Canis adustus*) and black-backed jackals (*Canis mesomelas*) (Cumming, 1982; Bingham et al., 1999b). Jackals are the primary carnivore in commercial farming areas, where they reach densities high enough to sustain disease outbreaks (Cumming, 1982; Foggin, 1988). Consequently in 1950–1996, 89% of side-striped and 79% of black-backed jackal cases occurred in commercial farmland (Bingham et al., 1999b). In wildlife reserves and communal lands jackal rabies is very rare, possibly due to their naturally low density in these areas (Cumming, 1982; Bingham et al., 1999b).

The role of communal land dogs in the maintenance of other infectious diseases is not known. However, they are likely to be prevalent because, besides rabies vaccinations, dogs receive little other veterinary treatment, and 36% of fatalities are due to unidentified disease (Butler and Bingham, 2000). As in other rural areas of Africa, canine distemper virus is probably endemic. For example, in South Africa, 25% of diseased dog cases are attributed to this virus (Leisewitz et al., 2001), and distemper seroprevalence in north-western Tanzania reaches up to 90% among pastoralist dogs (Cleaveland et al., 2000). Since rabies is transmitted between communal land dogs and jackals, the presence of distemper and parvovirus in Zimbabwean jackals (Spencer et al., 1999) suggests that these diseases also occur among dogs.

With the growth of the communal land dog population and the prevalence of rabies, in particular, the potential impacts of dogs on large wild carnivores in Zimbabwe are greater now than ever before. Although dog-jackal interactions are important in the maintenance of canid disease in commercial farmland, the interface between dogs and lions, leopards (*Panthera pardus*), spotted hyaenas (*Crocuta crocuta*) and African wild dogs on communal land-wildlife reserve boundaries is of greater relevance for conservation. The potential for such interaction is great since 62% of Zimbabwe's reserve boundaries adjoin communal lands (Butler, 1998). This paper assesses the threats posed by free-ranging dogs as competing predators and vectors of infectious disease on communal land-wildlife reserve boundaries. In particular, consideration is given to predation of diseased dogs as a route of infection to large carnivores.

2. Methods

2.1. Study area

The study was carried out between January 1995 and June 1996. The study area was a 33 km^2 section of Gokwe Communal Land (GCL) bordering the Sengwa Wildlife Research Area (SWRA; 18° 10′S, 28° 15′E), which adjoins the Department of National Parks and Wildlife Management's (DNPWM) Chirisa Safari Area in north-western Zimbabwe (Fig. 1). The climate is

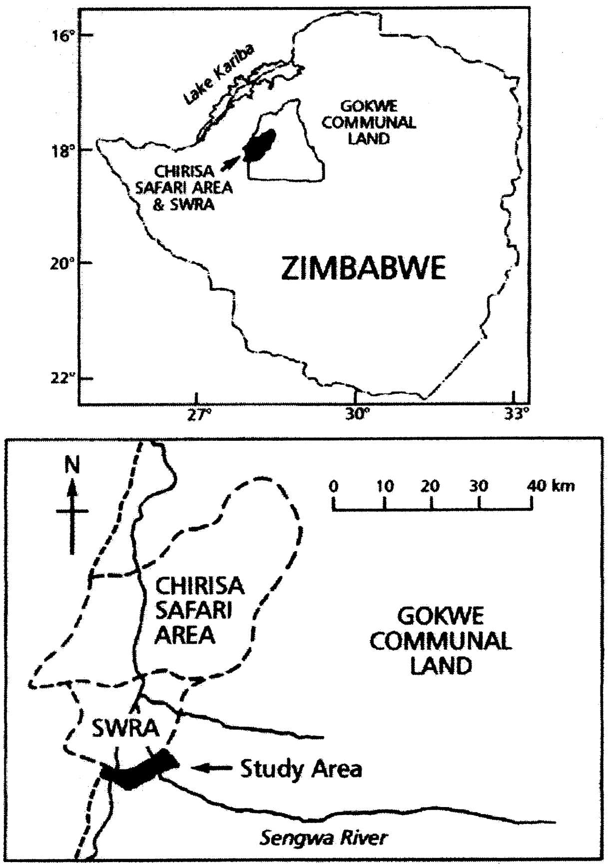

Fig. 1. The location of the Gokwe Communal Land study area and the Sengwa Wildlife Research Area (SWRA) in north-western Zimbabwe.

characterised by a wet season (November–April) and dry season (May–October). Mean annual rainfall and temperature is 662 mm and 22.2 °C, respectively. Vegetation is dominated by *Brachystegia-Julbernardia* and *Colophospermum mopane* savannah woodland (Guy et al., 1979).

The study area bordered 16 km of the SWRA boundary, which was demarcated by a fence designed to control foot and mouth disease by restricting contact between buffalo (*Syncerus caffer*) and cattle (*Bos indicus*). Smaller wild and domestic ungulates were able to cross through the fence, as were all mammalian carnivores. Lions, leopards and spotted hyaenas made regular incursions into GCL to prey on livestock (Butler, 2000) and wild ungulates (Butler, 1998). Side-striped jackals were also present (Butler and du Toit, 2002). African wild dogs were last sighted in the area in 1982 (Childes, 1988).

In October 1995 a questionnaire survey of the 130 households within the study area recorded populations of 236 dogs and 937 people, with densities of 7.2 and 28.4/km^2, respectively (Butler, 1998). Homesteads were typical of communal lands, consisting of thatched huts within an unfenced yard.

2.2. Presence of dogs and wild carnivores on the GCL-SWRA boundary

In 1988–1995 DNPWM patrols recorded all sightings of dogs in the SWRA. To establish the relative abundance of dogs and wild carnivores along the GCL–SWRA boundary, the 16 km length of fence bordering the study area was considered a transect and walked at least six times every month during January 1995–June 1996. The track following the fence runs over sand, which enabled the identification of any crossing carnivore's spoor. Because wind disturbance of sand can obscure spoor (Stander, 1998) transects were started and completed in the morning before breeze developed. Transects were not undertaken if it had rained the previous night, since rain can also obscure spoor (Stander, 1998). To reduce completion time each transect was divided into two sections of 8 km and walked simultaneously by two people.

2.3. Dogs as predators

The predatory behaviour of dogs was assessed while carrying out direct feeding observations on 16 adult dogs (eight males and eight females) radio-collared at houses in the study area. These 'focal animals' were selected from households where dogs' owners were willing to participate in the study. Once habituated, focal animals were followed on foot for 3-, 6- or 12-h sessions pre-planned to cover the 24-h period. Local inhabitants and DNPWM staff were asked to report kills made by other dogs hunting independently of people in the study area. In each case the prey species was recorded and its body mass was derived from Estes (1991) for wild species, and from field estimates for domestic species. The group size of dogs responsible for each kill was also recorded.

2.4. Dogs as prey

A questionnaire survey was undertaken twice amongst all households in the study area, in October 1995 and June 1996. The 1995 survey asked people to recollect predation of dogs by wild carnivores since January 1993, while the 1996 survey collated losses subsequent to the first survey.

2.5. Incidence of disease

Disease-related dog fatalities were recorded during the course of focal animal observations, chance encounters and reports by households or DNPWM staff. Reports were followed up quickly, and a detailed case history was formed by interviewing witnesses, including clinical signs and contact with other animals. The time over which signs were observed ('morbidity period') was also noted. Where possible, samples of brain tissue were taken from dead animals for rabies diagnosis. Samples were stored in a solution of 50% glycerol and 50% phosphate-buffered saline and analysed by the Central Veterinary Laboratory, Harare, utilising the Fluorescent Antibody Test and Mouse Inoculation Test.

During the October 1995 questionnaire survey households were asked about the rabies vaccination status of their dogs. The occurrence of all DVS vaccination campaigns in the study area was also noted.

3. Results

3.1. Presence of dogs and wild carnivores on the GCL–SWRA boundary

In 1988–1995 the annual rate of dogs sighted within the SWRA by DNPWM patrols increased (Fig. 2). The marked escalation of sightings in 1995 followed a drought during the November 1994–April 1995 wet season. In 1995 dogs were found up to 6 km within the reserve when accompanied by people, and up to 3 km alone. The majority of locations were on the eastern periphery of the SWRA bordering GCL (Fig. 3).

The fence transects indicated that dogs were the most numerous carnivore on the GCL–SWRA boundary (Table 1), crossing almost eight times as frequently as the most common large wild carnivore, the leopard. Lions were the second most common large species, followed by spotted hyaenas. Tracking of spoor indicated that most wild carnivore crossings were nocturnal, with animals travelling up to 2 km into GCL. Dog crossing rates were similar in dry and wet season months, but rates for all wild species were at least twice as frequent during the dry season (Table 1).

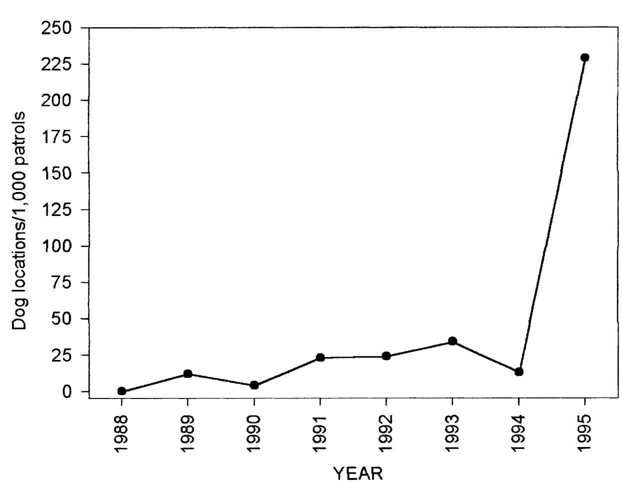

Fig. 2. The annual incidence of dog sightings within the SWRA, as reported by DNPWM patrols, 1988–1995.

Side-striped jackals were relatively uncommon on the GCL–SWRA boundary, occurring less frequently than leopards, but more regularly than lions or hyaenas (Table 1). By comparison, dogs occurred almost 10 times as frequently as jackals.

3.2. Dogs as predators

During a total of 486 h of observation focal animals were only seen to hunt mammalian prey opportunistically in GCL and the SWRA. While foraging they inadvertently disturbed scrub hares (*Lepus saxitilis*), bush squirrels (*Paraxerus cepapi*), duiker (*Sylvicapra grimmia*) and kudu (*Tragelaphus strepsiceros*) and gave chase unsuccessfully. There were 20 reported kills by other dogs, of which 11 (55%) were wild animals and nine (45%) were domestic (Table 2). Seventeen (85%) of the 20 animals taken were small, with a maximum body mass of $\leqslant$50 kg. The most common prey was domestic goat, comprising 30% of kills. One larger individual dog (mass 22.5 kg) was responsible for killing three wild ungulates, two impala (*Aepyceros melampus*) and one kudu, both within the SWRA. The mean ($\pm$S.E.) group size of dogs involved in the kills was 1.7 ($\pm$0.2, range 1–4).

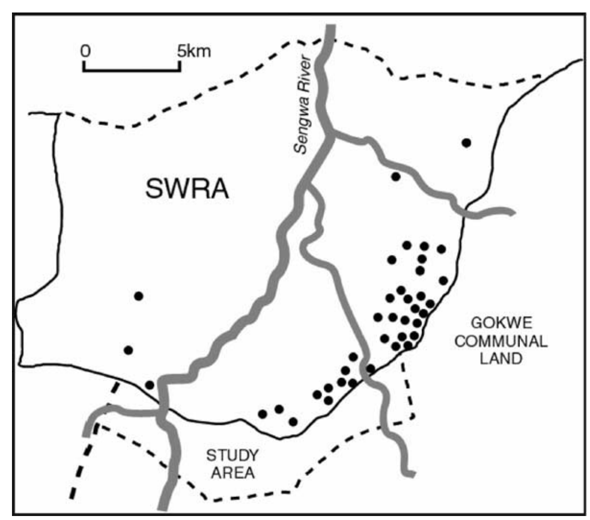

Fig. 3. Locations of 36 dog sightings (•) recorded by DNPWM patrols within the SWRA during 1995.

Table 1
A summary of carnivore crossing rates (crossings/transect) recorded from 143 spoor transects (79 wet season, 64 dry season) carried out along a 16 km section of game fence demarcating the GCL–SWRA boundary, January 1995–June 1996

	Dog	Leopard	Lion	Spotted hyaena	Side-striped jackal
Wet season	6.03	0.52	0.23	0.08	0.42
Dry season	5.52	1.02	0.72	0.20	0.81
Total	5.80	0.74	0.45	0.13	0.59

Table 2
A summary of 20 recorded kills made by dogs hunting independently of people in the study area during January 1995–June 1996

Prey species	Kills	%	Maximum body mass (kg)[a]
Goat (*Capra hircus*)	6	30	30.00
Impala (*Aepyceros melampus*)	2	10	60.00
Striped polecat (*Ictonyx striatus*)	2	10	0.97
Sheep (*Ovis aries*)	1	5	30.00
Kudu (*Tragelaphus strepsiceros*)	1	5	230.00
Domestic cat (*Felis domesticus*)	1	5	2.00
Baboon (*Papio usrinus*)	1	5	50.00
Vervet monkey (*Cercopithecus aethiops*)	1	5	9.00
Scrub hare (*Lepus saxitilis*)	1	5	1.50
Springhare (*Pedetes capensis*)	1	5	3.00
Hedgehog (*Erinaceus frontalis*)	1	5	0.40
Gerbil (*Gerbillurus paeba*)	1	5	0.10
Chicken (*Gallus domesticus*)	1	5	1.30

[a] Values for maximum body mass of wild prey species are from Estes (1991); those of domestic species are field estimates.

Table 3
Wild carnivores responsible for 19 kills of dogs recorded in the GCL study area in January 1993–June 1996, and the seasonal rate of kills (22 wet season months, 20 dry season months)

	Total	%	Seasonal rate	
			Wet	Dry
Leopard	10	53	0.14	0.35
Lion	8	42	0.05	0.35
Spotted hyaena	1	5	0	0.05
Total	19		0.19	0.75

3.3. Dogs as prey

Nineteen kills of dogs by wild carnivores were reported between January 1993 and June 1996 (Table 3). A further four were reported to have disappeared at night and predation was suspected. Of confirmed kills, leopards were responsible for the most (53%), followed by lions (42%) and spotted hyaenas (5%). For all three predators the monthly rate of kills in the dry season was at least twice that for the wet season. In total, the rate of dry season kills (0.75/month) was almost four times greater than for the wet season (0.19/month). Five dogs were reported being taken from within the perimeter of homesteads. Dogs were killed up to 2.8 km from the SWRA boundary.

The greatest annual total of confirmed kills was 12 in 1993, plus two suspected kills. Assuming that the study area's dog population in 1993 was less than the 236 counted in 1995 (see 4.1), this equated to $\geqslant 6\%$ of the dog population being removed by large wild carnivores.

Between January 1993 and June 1996 a further 11 kills of dogs were made by adult male baboons (*Papio ursinus*). This was not regarded as predation, since the dogs were killed when used by their owners to chase baboons responsible for crop and livestock-raiding.

3.4. Incidence of disease

Fifty-eight disease-related dog fatalities were recorded between January 1995 and June 1996 (Fig. 4), at an overall rate of 3.2/month. The dry season rate (4.6/month) was more than twice that for the wet season (2.1/month). Fatalities were recorded in 15 (83%) of the 18 months monitored.

Of these fatalities, 24 (41%) were caused by rabies. The carcasses of seven were found prior to brain decomposition or removal by scavengers, and all were confirmed positive for rabies by laboratory tests. Sufficient clinical and circumstantial evidence was gathered about the remaining 17 to confidently diagnose them as rabid. The morbidity period ranged from 1 to 9 days. One adult goat was also confirmed positive by the laboratory tests having been bitten by a rabid dog. Three rabid dogs died within the SWRA having travelled 0.1, 1 and 2 km from the boundary fence. The dry season fatality rate (1.6/month) was twice that for the wet season (0.8/month). Vaccination coverage of all dogs surveyed in October 1995 was 24%. Despite three DVS vaccination campaigns during the study period, rabies cases occurred in 10 of the 18 months monitored (Fig. 4).

The remaining 34 fatalities were probably caused by other diseases, and occurred throughout the study (Fig. 4). Signs included choking, in-coordination, ataxia, twitching and convulsions, all of which are symptoms of distemper as described by Van Heerden et al. (1989) and Roelke-Parker et al. (1996). For these cases the dry season fatality rate (2.6/month) was twice that for the wet season (1.3/month). Many other cases of dogs showing similar signs were observed which did not result in death. No cases of diseased wild carnivores were recorded.

4. Discussion

4.1. Presence of dogs and wild carnivores on the GCL–SWRA boundary

Because dogs and large wild carnivores could move freely through the SWRA fence, they were effectively sympatric in the GCL–SWRA boundary area. Dogs travelled up to 6 km within the reserve with people and up to 3 km alone, while leopards, lions and spotted hyaenas were tracked up to 2 km within GCL, and killed dogs up to 2.8 km within the study area. Dogs were the most numerous carnivores along the boundary, and therefore potentially have the greatest ecological interaction with leopards, the most common large wild species,

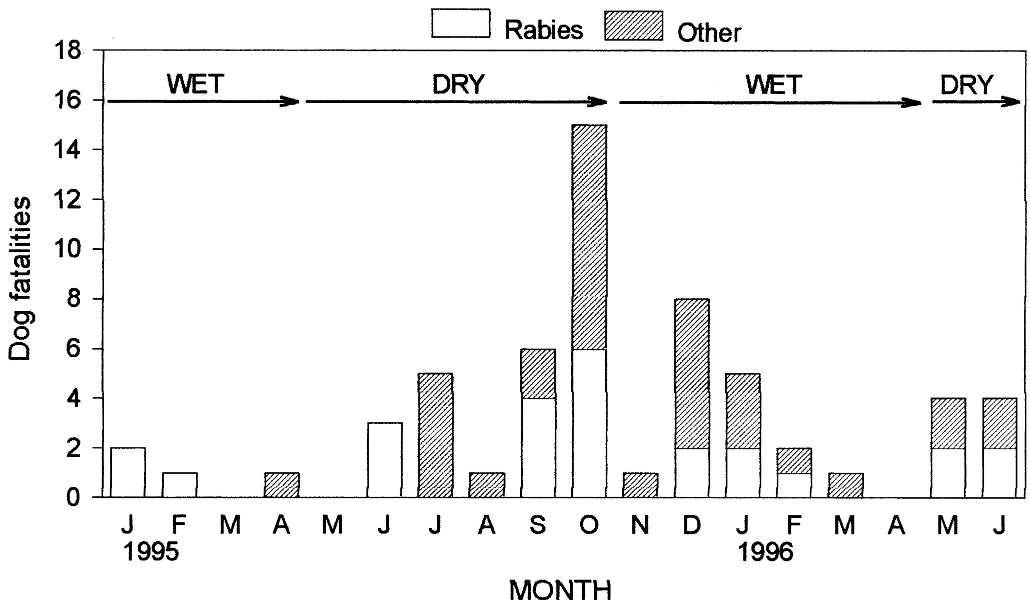

Fig. 4. The monthly occurrence of 58 disease-related dog fatalities (24 rabies, 34 other) in the GCL study area in January 1995–June 1996, relative to dry and wet seasons.

followed by lions and spotted hyaenas. Due to the absence of African wild dogs in the study area, it was impossible to consider interactions with this species.

Human settlement of GCL began in 1979, and since then the population has grown by up to 25% per annum (Cumming et al., 1988). After the eradication in 1984 of tsetse fly (*Glossina* spp.), the host for trypanosomiasis, numbers of domestic mammals such as dogs increased rapidly (Cumming et al., 1988). Dog and human densities are positively correlated in Zimbabwean communal lands (Butler, 1995; Butler and Bingham, 2000). Therefore the growth rate of the GCL dog population has probably paralleled that of the human population, and this may explain the increasing occurrence of dogs within the SWRA during 1988–1995.

The sudden escalation in dog sightings in 1995 followed the failed wet season of November 1994–April 1995, suggesting that drought conditions may exacerbate dog incursions into the SWRA. This could have been linked to illegal hunting within the reserve by GCL inhabitants and their accompanying dogs, which may have increased due to food shortages. Dogs may also have entered the SWRA independently in search of carrion due to a dwindling availability of waste human food in GCL. This is corroborated by a survey of seven communal lands in 1994 which recorded greater incidences of stray dogs during droughts when food became scarce (Butler, 1998).

4.2. Dogs as predators

Of the interactions that dogs have with large wild carnivores, our results suggest that their influence as competitive predators is the least significant. In southern African woodland savannah, leopards prey largely upon small and medium-sized wild ungulates (Pienaar, 1969; Smith, 1977; Mills and Biggs, 1993), while lions and spotted hyaenas are primarily predators of medium and large-sized ungulates (Pienaar, 1969; Bearder, 1977; Henschel and Skinner, 1990; Mills and Biggs, 1993). To compete with these species, dogs would have to remove significant numbers of potential prey from the GCL–SWRA boundary. This was not the case, however, since they rarely took live prey, and only a minority of these were wild ungulates. Dogs were also rarely recorded taking live prey by the survey of other communal lands in 1994 (Butler, 1998).

There are four possible reasons for their inefficiency as predators. First, dogs have little need to hunt, since they are mainly scavengers of abundant human waste and carrion (Butler and du Toit, 2002). Second, due to the inert and widely-dispersed nature of their food supply, dogs forage alone or in pairs and do not maintain cohesive packs (Butler, 1998), as demonstrated by the small group sizes involved in the kills (mean 1.7). Consequently, if an opportunity arises to hunt medium or large-sized wild prey (>50 kg body mass) they are unlikely to succeed, since among canids the efficient capture of such prey depends upon cooperative group behaviour (Griffiths, 1980; Packer and Ruttan, 1988). This is endorsed by the generally small size of recorded kills, and the occurrence of the goat, a small domestic species, as their most common prey. Third, their ability to take larger ungulates was compromised by their small body mass (mean 14.7 kg; Butler, 1998). This is corroborated by the fact that the only dog known to kill impala and kudu was unusually large (22.5 kg). Finally, 75% of the dog population in the study area were juveniles (<1 year old; Butler, 1998), and therefore the density of adult dogs most capable of taking large prey was very low, further limiting their potential impact on the prey base of wild ungulates.

4.3. Dogs as prey

Instead, dogs probably pose a greater threat as reservoirs and vectors of rabies and possibly distemper. Disease was endemic amongst the study area's dog population, as demonstrated by the occurrence of disease-related fatalities in 83% of the months monitored, at a rate of 3.2/month. The prevalence of disease was certainly underestimated due to the limitations of the surveillance programme in GCL and the SWRA and the exclusion of non-fatal cases. Rabies was persistent despite three attempted DVS vaccination campaigns during the study period. This was to be expected, since the dog population's vaccination coverage of 24% in October 1995 was far below the minimum annual coverage of 70% required to prevent outbreaks (Bögel and Meslin, 1990; Coleman and Dye, 1996).

Leopards, lions and spotted hyaenas preyed on dogs in GCL during January 1993–June 1996, and took $\geqslant$6% of the study area's population in 1993. This type of physical contact provides ideal circumstances for the transmission of infectious diseases. Rabies virus is shed by the salivary glands, and is usually transmitted when the infective host bites or licks a susceptible victim, transferring the virus into a wound or onto mucus membranes (reviewed by Foggin, 1988; Wandeler et al., 1994). Alternatively, it is possible that infection is contracted when a susceptible animal consumes virus-infected tissue either via predation or scavenging (reviewed by Foggin, 1988; Wandeler et al., 1994). Canine distemper is excreted as an airborne aerosolised virus, and is usually contracted by inhalation (Alexander and Appel, 1994).

The potential for large carnivores to contract disease via predation of dogs appeared to be significant. The monthly rate of disease amongst dogs peaked during the dry season, coinciding with the highest carnivore crossing rates into GCL and the highest rates of dog predation. In addition, the range of morbidity period for rabies was 1–9 days, resulting in each case remaining infective for an extended time. Some rabid dogs wander large distances (Foggin, 1988; Kennedy, 1988; Butler, 1998), and in this study three died within the SWRA. Such incapacitated dogs would offer easy prey if found by predators, either in GCL or the SWRA. Diseased dogs within homesteads would also provide easy prey, as proven by the fact that five were taken from inside household perimeters. Furthermore, dogs, leopards, lions and spotted hyaenas scavenged carcasses at night on the periphery of the SWRA, providing further opportunities for predation of dogs (Butler and du Toit, 2002). Dead dogs were also the most common form of carrion along the GCL–SWRA boundary (Butler and du Toit, 2002), and scavengers could have been exposed to infection when consuming rabid dog carcasses. Finally, leopards, lions and hyaenas regularly preyed upon livestock in GCL (Butler, 2000), and could have contracted disease from animals such as the rabid goat which was infected by a dog.

Despite the risk of infection no cases of disease were found amongst wild carnivores during the study. For rabies this equates with the DVS' national surveillance programme, which recorded only nine spotted hyaena cases, three leopard cases, and no lion cases in 1950–1995 (Table 4). There are four possible explanations for the low number of recorded cases, both within the study area and nationally. First, wild carnivores in the study area were itinerant visitors to GCL, and if diseased would probably die within the SWRA. There was no detailed monitoring programme for wild carnivore populations in the SWRA akin to that which identified the distemper epidemic amongst Serengeti lions (see Roelke-Parker et al., 1996). Second, DVS disease surveillance in remote communal lands and wildlife reserves is poor due to resource constraints, underestimating the occurrence of cases (Foggin, 1988; Butler, 1998; Bingham et al., 1999a). Third, carcasses are scavenged quickly within the SWRA and GCL (Mundy, 1982; Butler and du Toit, 2002), and combined with rapid decomposition due to high ambient temperatures the opportunities for sampling tissue from fatalities were minimal. Similar problems have been encountered by other surveillance programmes in rural Africa (Alexander and Appel, 1994; Cleaveland and Dye, 1995; Kat et al., 1995). Finally, the rate of transmission in the small study area may have been too low for any cases to have occurred in the 18 months monitored.

In other areas of Africa jackals are regarded as the primary vectors of canid diseases to large wild carnivores within wildlife reserves (e.g. Alexander et al., 1994; Hofmeyr et al., 2000). In Zimbabwe jackals occur at high densities in commercial farmland and contact with rabid dogs on boundaries with communal lands

Table 4
Comparison of laboratory-confirmed rabies cases among spotted hyaenas, leopards and lions in surveillance programmes undertaken in five African countries

Country	Spotted hyaena	Leopard	Lion	Source
Zimbabwe (1950–1995)	9	3	0	DVS records
Botswana (1992–1994)	2	0	0	Sehularo (1995)
Tanzania (1966–1970)	5	0	0	Rweyemamu et al. (1973)
Malawi (1992–1994)	6	0	0	Mwiyeriwa (1995)
Kenya (1992–1993)	1	0	0	Alexander et al. (1993)

drives most rabies epidemics among jackals (Bingham et al., 1999b). However, jackal densities in wildlife reserves and communal lands are thought to be too low to sustain outbreaks (Cumming, 1982; Foggin, 1988; Bingham et al., 1999b). If spoor counts provide an index of relative density (Stander, 1998), then our results suggest that the density of side-striped jackals was indeed low on the GCL–SWRA boundary. By comparison dogs were almost 10 times more abundant. If this scenario is common throughout Zimbabwe, then dogs rather than jackals are the most likely agent for canid disease transmission to large wild carnivores on communal land-wildlife reserve boundaries.

Spotted hyaenas may play an intermediate role in the transmission of canid disease from dogs to other large wild carnivore species, as suggested by Roelke-Parker et al. (1996) for the Serengeti distemper epidemic among lions. Although in this study hyaenas were at least risk of contracting disease, rarely entering GCL and accounting for only 5% of dog kills, they may be influential in other locations. They are resident in some Zimbabwean communal lands, where they are a major cause of livestock losses (Bowler, 1991; Hawkes, 1991; Madzudzo, 1994). They also scavenge around humans elsewhere in Africa, for example in Harar town, Ethiopia (Kruuk, 1968), South Africa's Kruger National Park (Pienaar, 1969), the Serengeti (Kruuk, 1972), and Uganda (Pomeroy, 1975). In these situations predation of dogs and contact with canid diseases would be more common. If infected, the hyaenas' social ecology would ensure rapid transmission to conspecifics (Mills, 1993). In turn, their kleptoparasitic behaviour could lead to physical contact with other large carnivores at kills, such as lions (e.g. Kruuk, 1972; Schaller, 1972, Mills and Biggs, 1993) and African wild dogs (e.g. Fuller et al., 1995; Creel and Creel, 1996), and hence inter-specific transmission. This hypothesis is supported by the consistently greater prevalence of spotted hyaena rabies cases in five African countries relative to cases amongst leopards and lions (Table 4).

5. Conclusions

Dog ecology varies little amongst Zimbabwean communal lands, and the fundamental characteristics are typical of dog populations throughout rural sub-Saharan Africa (Butler and Bingham, 2000). Therefore the predatory behaviour of free-ranging dogs and their potential competitive relationships with large wild carnivores are likely to be similar on most communal land-wildlife reserve boundaries, both in Zimbabwe and elsewhere. The results of this study suggest that although colonising dogs may be successful predators in other parts of the world, their competitive impact on large African carnivores is minimal.

This is not the case for canid diseases, however. Detailed investigations in the Serengeti have identified free-ranging dogs as the probable reservoir for several pathogens which have decimated local populations of wild dogs and lions (reviewed by Woodroffe, 1999). Such epidemics have not been detected within Zimbabwean wildlife reserves since 1960–1961, when an unidentified disease caused the mortality of wild dogs in Hwange National Park (Childes, 1988). Our study suggests that disease transmission probably can occur, but due to inadequate surveillance in remote areas, cases are not readily detected. The most likely scenario for transmission to large wild carnivores is via predation of diseased dogs, and spotted hyaenas may be key intermediate hosts on some communal land-wildlife reserve boundaries.

Given the dog population's growth rate of 6.5% per annum in Zimbabwean communal lands, and the prevalence of canid diseases, the threat of ecological disruption can only escalate. To counter this, improved coverage of rabies vaccination campaigns on wildlife reserve boundaries is a priority, and vaccination should be extended to cover other pathogens including distemper and parvovirus. Similar exercises have been recommended and undertaken around the Serengeti National Park, Tanzania (Roelke-Parker et al, 1996; Woodroffe, 1999), and the Bale Mountains National Park, Ethiopia (Sillero-Zubiri and Macdonald, 1997). Restricting dog numbers through contraception or removal could also limit contact rates between dogs and wild carnivores, and hence disease prevalence (Butler, 1998). However, reducing dog numbers is not compatible with communal land farmers' demand for dogs as deterrents of crop and livestock-raiding wildlife in areas bordering reserves (Butler and Bingham, 2000). Instead, improved waste disposal could provide a more indirect method of moderating population growth (Butler, 1998), because dogs rely on human waste for their food requirements (Butler and du Toit, 2002). Formulating a programme of disease control from these measures is a priority for the future conservation of large carnivores in Zimbabwe.

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