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Multi-host pathogens and carnivore management in southern Africa

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Abstract

A retrospective serosurvey of multi-host feline and canine viruses among carnivore species in southern Africa ($n = 1018$) identified widespread pathogen exposure even in remote protected areas. In contrast to morality experienced in East African predators, canine distemper virus (CDV) infection among African wild dogs (*Lycaon pictus*) in Botswana was not associated with identifiable change in pup survivorship or disease related mortality of adults. A disease outbreak of unknown aetiology occurred in the same population over 4 weeks in 1996. Outbreak boundaries coincided with ecotones, not the spatial distribution of contiguous packs, highlighting the potential importance of landscape heterogeneities in these processes. Direct management of pathogens in domestic animal reservoirs is complicated by the apparent complexity of pathogen maintenance and transmission in these large systems. Conservation effort should be focused at securing large metapopulations able to compensate for expected episodic generalist pathogen

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invasion and attention directed to addressing underlying causes of population depression such as habitat loss and wildlife conflict.

Keywords: Vaccination; African wild dog; Lion; Predator; Distemper; Multi-host; Pathogens; Endangered; Landscape heterogeneity; Ecotones

Résumé

Au travers d'une étude sérologique rétrospective de virus affectant plusieurs espèces de carnivores d'Afrique du sud (n = 1073), nous montrons une exposition étendue aux pathogènes dans cette région jusque dans des parties reculées de zones protégées. Au contraire de la mortalité observée chez les prédateurs Est africains, les infections au virus de la maladie de Carre chez les chiens sauvage du Botswana n'était pas associée à un changement significatif de la survie des chiots. L'éruption d'une pathologie d'étiologie inconnue s'est déclenchée chez les chiens sauvages dans le delta de l'Okavango, au Botswana (1996). Les frontières de l'épidémie coïncidaient plus avec les écotones qu'avec la distribution géographique des meutes, ce qui souligne l'importance de l'hétérogénéité des paysages dans ces dynamiques. La gestion directe des pathogènes dans les réservoirs d'animaux domestiques se trouve compliquée par l'apparente complexité du maintient et de la transmission de pathogènes dans ces vastes systèmes. Les efforts de conservation devraient être portés sur la sécurisation de grandes métapopulations capable de compenser des invasions épisodiques prédictibles de pathogènes généralistes, ainsi que sur les causes de déclin de populations sauvages telles que des pertes d'habitat ou des conflits avec des activités humaines.

Mots clés : Chien sauvage africain ; *Lion* ; Prédateur ; Maladie de Carré ; Multi-hôte ; Pathogène ; Espèce menacée ; Hétérogénéité de paysage

1. Introduction

With human population expansion, escalating land transformation and changes in natural resource use, greater contact and overlap is identified among humans, their domestic animals and wildlife communities. These changes in both host ecology and the environment influence pathogen transmission potential (R_0 = basic reproductive rate) and the persistence of the pathogen in the environment [1]. Ecological change provides the window of opportunity for pathogen, host and the environment to interact in novel ways allowing emergence of disease.

Whereas historically our interest in wildlife disease ecology was directed at controlling disease transmission from wildlife to humans and domestic animals, emerging diseases are increasingly identified as a threat to wildlife populations themselves with disease transmission to wildlife emanating from both human (*Mycobacterium tuberculosis*) and domestic animal (*Mycobacterium bovis*, rabies, distemper) reservoirs [2–6]. Emerging pathogens are most likely to be those which utilize multi-hosts and have a wide host range [7], describing over 90% of canine pathogens [8], many identified as a key threat to survival of free-ranging wild carnivores [9,10].

At present, however, there is insufficient knowledge on the biology of pathogen transmission and the density at which hosts must occur so as to provide a significant force

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of infection for invasion and onward transmission in susceptible host populations and the influence of habitat heterogeneities on these processes [11]. Our understanding of the short- and long-term impacts of most canine pathogens on free-ranging predators is extremely limited and complicated further by variation in virulence of the pathogen, influence of environmental factors and consequence of co-infection with other parasites [12].

Despite limited understanding of pathogen biology and infection outcomes, it often remains necessary to undertake rational management strategies in an effort to prevent or reduce transmission of multi-host pathogens of concern to rare and endangered species, such as the African wild dog (*Lycaon pictus*) and the Ethiopian wolf (*Canis semensis*) [13]. A number of authors propose approaches to disease control [10,14–16]. However, application of interventions in free-ranging predators has not resulted in long-term successes and disease threats continue to challenge management of endangered and rare species [10]. Some researchers have identified concerns that interventions such as large-scale vaccination may not be effective and might have unintended effects on both reservoir host and target populations, ultimately increasing the risk of pathogen transmission [10,17,18].

Through retrospective sampling, we investigated the extent of exposure of free-ranging predators to multi-host carnivore pathogens across various land uses in southern African. We addressed the following research questions: How common and widespread is exposure to multi-host domestic carnivore pathogens in the study region? Do large protected areas remote from domestic animal reservoirs provide large carnivore species protection from exposure to important pathogens? Is infection always linked to high levels of mortality as has been seen in predators in the Serengeti [19] and Mara ecosystem [3,20] in East Africa? In light of our exploration of these questions, we then provide recommendations for disease control in free-ranging wildlife with specific attention to their application to predator conservation in southern Africa.

2. Materials and methods

2.1. Serum sample collection and testing

Samples were collected from predator species under cooperative projects between co-authors working with predators and domestic dogs in Botswana, Namibia, South Africa and Zimbabwe (Table 1, Fig. 1).

Serum samples used in this study were stored at −20 °C until time of testing. Due to limits in available sera, not all tests were conducted on each sample. Serologic screening for samples from Botswana Zimbabwe and South Africa was conducted at the Department of Veterinary Tropical Diseases, Faculty of Veterinary Science, University of Pretoria. The Namibian samples were tested at Washington Animal Diagnostic Disease Laboratory, Washington State University, Pullman, WA, USA.

Canine distemper virus (CDV) antibodies were detected using a indirect fluorescent antibody test with the Ondersterport strain of CDV as the target antigen (University of Pretoria) [21]. Namibian serum samples were screened for CDV antibodies through a serum neutralization (SN) test (Washington State University) using the Rockborn CDV

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Table 1
Species tested, origin and year of sampling.

Species	Location	Year	No. sampled
Domestic dog	Okavango Delta, Botswana	1996	142
African wild dog	Okavango Delta, Botswana	1992–1999	106
Black-back Jackal	Etosha National Park, Namibia	1992–1996	10
Spotted hyena	Etosha National Park, Namibia	1993–1997	25
Lion	Okavango Delta, Botswana	1992–2000	63
	Chobe, Botswana	1996–2000	31
	Makagdikgadi National Park (MNP), Botswana	1999	17
	Kalhari Transfrontier Park (KTP), Botswana	1997–2001	35
	Zambezi Valley, Zimbabwe	1990–1998	41
	Caprivi, Namibia	1993–2001	78
	Etosha National Park, Namibia	1991–1996	145
	Tsumkwe, Namibia	1993–1997	13
	Hluhluwe-Imfolozi Game Reserve	1992–1997	48
	Kruger National Park, South Africa	1993–2000	264
Total			1018

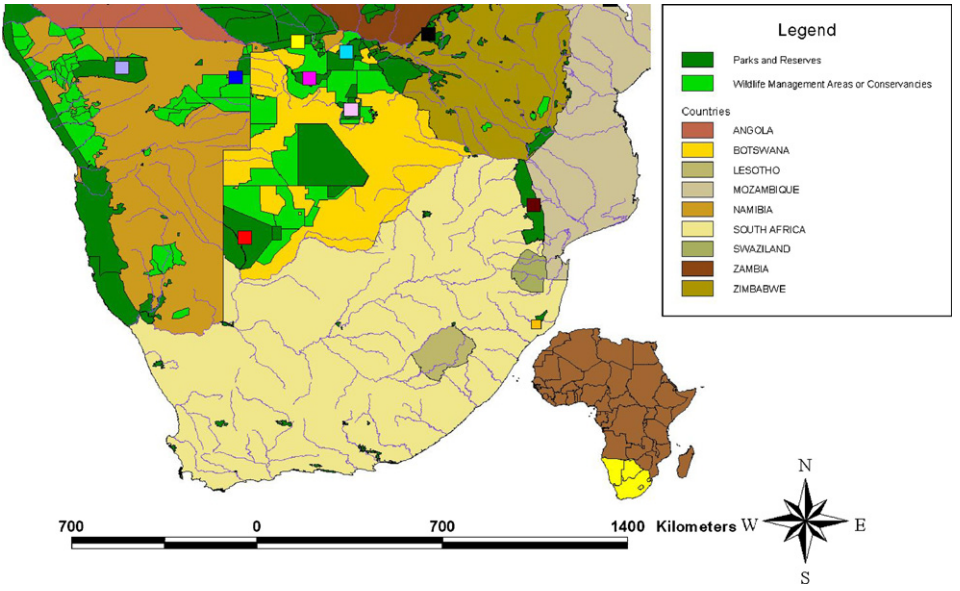

Fig. 1. Predator sampling locations in southern Africa (locations are marked with colour rectangles): Etosha National Park (lavender), Tsumkwe (blue), Caprivi (yellow): Namibia; Zambezi Valley (black), Zimbabwe; Chobe District (light blue), Okavango Delta (dark pink), Makgadikgadi National Park (light pink), Kalahari Transfrontier Park (red): Botswana; Kruger National Park (maroon), Hluhluwe-Imfolozi Game Reserve (orange): South Africa.

strain as the challenge virus. Vero cells were used as the indicator cell line with positive and negative control sera collected from ferrets that were inoculated with the prototype strain of CDV [22,23]. The Rockborn strain of CDV shares 99.23% homology with the Onderstepoort strain [24].

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Serum were tested for antibodies to feline coronavirus (FCoV), feline herpesvirus (FHV-1), feline calicivirus (FCV), feline panleukopenia virus (FPLV) and rotavirus (RV) by means of indirect fluorescent antibody techniques as previously described [25]. A serum neutralization test was used to detect antibodies to feline herpesvirus (FHV-1), feline calicivirus (FCV) among Namibian samples (Washington State University) using Crandell feline kidney cells [25].

Exposure to canine parvovirus (CPV-2), canine adenovirus (CAV-2), canine parainfluenzavirus (CPIV), canine coronavirus (CCV) was assessed through the use of a indirect fluorescent antibody test at University of Pretoria as previously described [26]. Because of the close antigenic relationship between feline and canine coronaviruses, FCoV was used as the capture antigen for detection of antibody reactive to corona virus in domestic dogs. Likewise, canine rotavirus belongs to the group A rotavirus and canine antibody against RV will react to group specific antigens of bovine group A rotaviruses in an IFA test and thus the type A strain of rotavirus of goat origin isolated in South Africa (V Da Costa Mendes, Medial University of Southern Africa) was used as the target antigen for this test. CPV-2 test antigens were obtained from field strains isolated from clinically ill domestic dogs and cats in South Africa (M. van Vuuran, University of Pretoria). The identity of all field strains was confirmed by means of specific fluorescein-conjugated antisera (VMRD Inc., Pullman, WA 99163, USA).

Feline lentivirus/lion lentivirus were detected by means of antibody reactive to puma lentivirus (PLV) with an indirect enzyme linked immunosorbent assay (ELISA) [27,28]. Antibodies to FIV in Namibian samples were detected using a commercial ELISA test (IDEXX, Maine, USA) as previously described [29]. Feline leukaemia virus (FeLV) group specific p27 antigens were identified through a commercial ELISA (ViaCHEK, Synbiotics, USA).

No site-specific cross comparisons of seroprevalence levels were conducted in this study but data were rather used to identify presence or absence of exposure in various study sites in southern Africa.

2.2. Longitudinal disease surveillance

Serologic data from longitudinal studies conducted in Botswana, Okavango Delta (1992–1999) and Kgalagadi Transfrontier Park (1997–2001) are assessed (both by University of Pretoria) in relation survivorship (African wild dog only) and mortality data for the respective populations.

2.3. African wild dogs – Okavango Delta, Botswana

2.3.1. Study area description

African wild dog research was conducted the Okavango Delta in Ngamiland District in Northern Botswana in an estimated 2600 km^2 study area situated in the eastern terminus of the Okavango Delta (19°31′S 23°37′E). The study area comprised part of the Moremi Game Reserve and several adjacent Wildlife Management Areas. The human population is concentrated in the northeast portion of the study area. More detailed descriptions of the study site have been previously published [30].

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The wild dog population in northern Botswana was estimated to be between 702 and 865 adults in 88–108 packs [31]. The focal study population reported here consisted of 7–13 packs per year (average = 8 packs/year; 1991–1999) considered representative of the regional population.

2.3.2. Pup survivorship

Survivorship of juvenile wild dogs was calculated from demographic, age-structured data and expressed as the percentage of pups at emergence from the den 4–6 weeks of age that subsequently survived to 1 year of age [32]. Individuals were recognized on the basis of unique coat pattern recorded from first sighting. Survival is presented as a minimum estimate. Packs that may have had surviving pups but were not relocated and counted 1 year later are assigned zero survivorship ($n = 4$ litters). In addition litters not recorded until pups were >10 weeks were assigned an average litter size (10) ($n = 3$ litters). Trends in pup survivorship data are analysed using a simple linear regression.

2.3.3. Prey density

Changes in density of wildlife and habitat are evaluated in relation to the perimeter of a disease outbreak. For this we used data on abundance of impala (*Aepyceros melampus*). Impala are a key prey species of a number of large predators including the African wild dog (86% of observed kills) [30] and are found throughout the study area with little habitat restrictions [33]. We compared the density of this species in the two coarse habitat types: floodplain (including associated woodlands) and woodland (mopane and acacia sandveldt). Densities were determined from ground surveys (1992–2000) where strip transects (18–36 km in length) [34] were identified along sections of existing roads.

2.4. Lions in the Kgalagadi Transfrontier Park (Botswana and Republic of South Africa)

2.4.1. Study area description

The study was conducted in the Kgalagadi Transfrontier Park (KTP) which is 36 000 km^2 in extent surrounded mostly by Wildlife Management Areas (a further 36 400 km^2) in Botswana, and livestock agricultural areas in Namibia and South Africa. The KTP lies within the south-western part of the Kalahari basin and is largely a semi-desert region entirely covered by Kalahari sand at varying depths, presenting a relatively flat and homogeneous landscape [35,36].

2.4.2. Age estimates

Cubs and sub-adults were aged according to published guidelines [37] where the shoulder height in relation to an adult lioness is used as an index of age. Adult lions were put into age categories at first immobilization based on the wear and discoloration of teeth, progression of mane development in males, general facial scaring and discoloration of the skin above the nose and below the eyes, relative body muscle mass and heart-chest girth [37].

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2.5. Home range estimates African wild dogs and lions

Home range estimates were assessed on the basis of minimum convex polygons deriving from the cumulative location datasets (African wild dog (Okavango Delta): 1991–1999 and Lions (KTP): 1997–2001) using Program Home Range [38].

3. Results

African wild dogs and domestic dogs sampled in the Okavango Delta in Botswana showed evidence of exposure to all canine pathogens tested (Fig. 2). In Etosha National Park, Black-back jackals were serologically positive for CDV (1992–1993, 53%, $n = 15$) as were spotted hyena (1992–1993, 1996, 24%, $n = 25$). There was no evidence of exposure to CCV or Felv ($n = 12$) among spotted hyena although the sample size was small.

Lions were seropositive for CDV in all locations sampled with the exception of Hluhluwe-Imfolozi Game Reserve, South Africa and Tsumkwe, Namibia (Fig. 3). Only study sites in South Africa and Botswana were tested for antibodies to FPV and evidence of exposure was identified in both countries with the exception of lions from the Okavango Delta and Makgadikgadi National Park (MNP). High levels of exposure to FHV-1 were found in all sites tested. FCOV and FCV were common among lions with the exception of MNP. Evidence of infection with Feline lentiviruses or antigenically related lentiviruses was widespread in all tested feline populations with the exception of Hluhluwe-Imfolozi Game Reserve, South Africa and Etosha National Park in Namibia. FeLV infection was not detected among any tested animals in the four countries. In this study, animals were

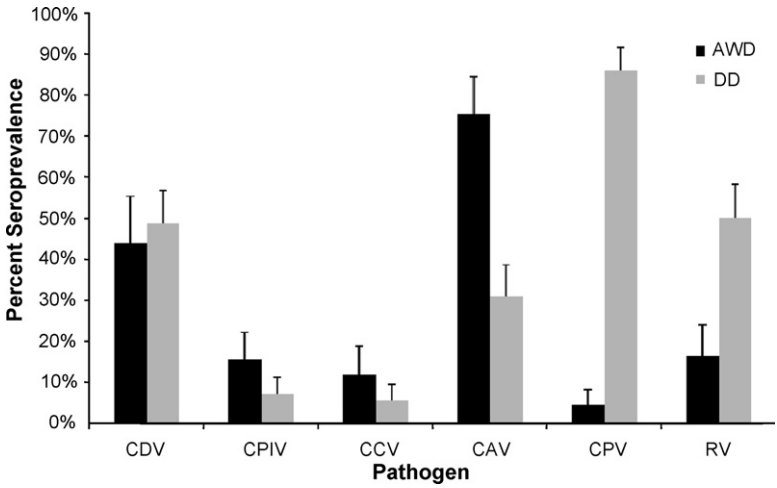

Fig. 2. Seroprevalence of canine distemper virus (CDV), canine parainfluenzavirus (CPIV), canine parvovirus (CPV), canine coronavirus (CCV), canine adenovirus (CAV), and rotavirus (RV) among retrospectively sampled African wild dogs (*Lycaon pictus*, AWD, 1993–1999) and domestic dogs (DD, 1996) in Okavango Delta, Botswana.

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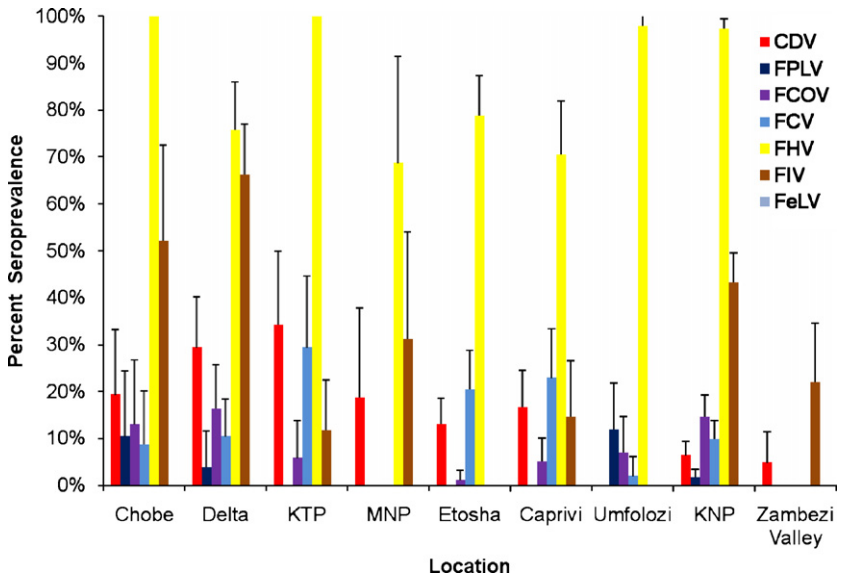

Fig. 3. Percent seroprevalence of antiviral antibodies for canine distemper virus (CDV), feline panleukopenia virus (FPLV), feline herpesvirus type I (FHV-1), feline calcivirus (FCV), feline coronoavirus (FcoV), feline immunodeficiency virus (FIV), and feline leukaemia virus (FeLV), among retrospectively sampled lion (*Panthera leo)* in Botswana (Chobe District, Okavango Delta (Delta), Makgadikagdi National Park (MNP) and Kgalagadi Transfrontier Park (KTP)), Zimbabwe (Zambezi Valley), Namibia (Caprivi, Etosha National Park (Etosha)) and South Africa (Kruger National Park (KNP), Hluhluwe-Imfolozi Game Reserve (Imfolozi)).

antibody positive for domestic carnivore pathogens even in remote parts of protected areas extremely distant from populations of domestic animals (e.g. CDV, Fig. 4).

3.1. Pathogens, survivorship and mortality

3.1.1. African wild dogs, CDV seroconversion and survivorship

African wild dogs showed evidence of exposure to CDV across all study packs both in the mopane and flood plain habitats (Fig. 5). Previous assessments had identified only two animals seropositive for CDV prior to this study ($n = 24$, 1991–1992, Alexander unpublished data). Seven adults from six different packs showed evidence of active CDV seroconversion during the present study period, the larger proportion occurring between 1993 and 1994 (43%). There was no identifiable trend in pup survivorship ($\beta = -.01$, $R^2 = .09$, $F_{1,8} = 0.82$, $p = .39$) with the average (0.43 + 0.03, 1991–1999 ($N = 71$ litters) Fig. 6) being similar to the 15-year average for the study area [32]. There were no identified cases of disease related mortality among adults or pups during this period with the exception of the disease outbreak which occurred over a 4-week period in 1996.

3.1.2. Impala density

Average impala density was greater at the boundary and within the flood plain habitat (16.2/km^2), than the lower nutrient mopane woodlands (3.2 km^2).

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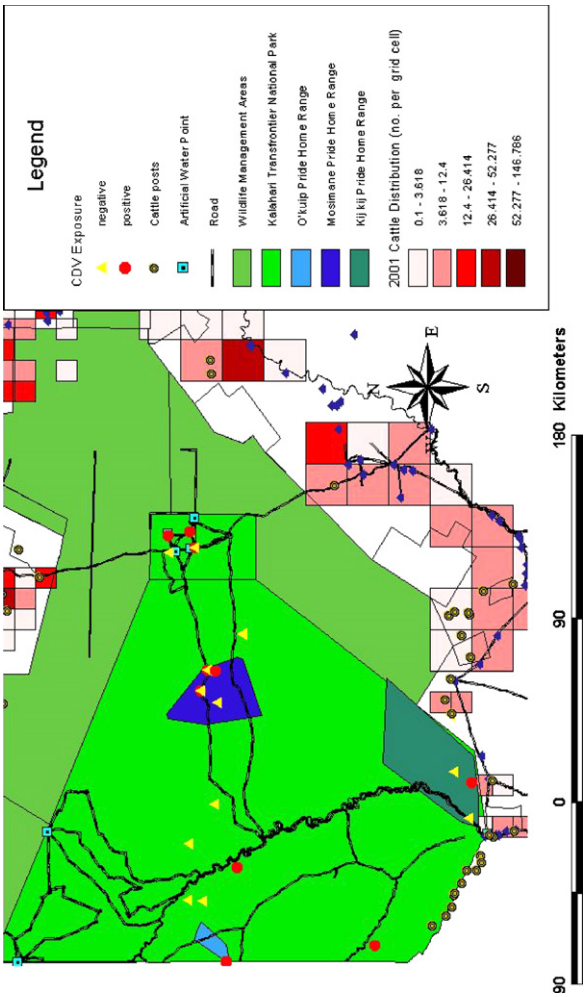

Fig. 4. The CDV antibody status of sampled lions and home range of three prides within the Kgalagadi Transfrontier Park (dark green), surrounding Wildlife Management Areas (light green) and cattle on tribal grazing areas (no colour). Cattle density is provided as an indicator of human and domestic animal density.

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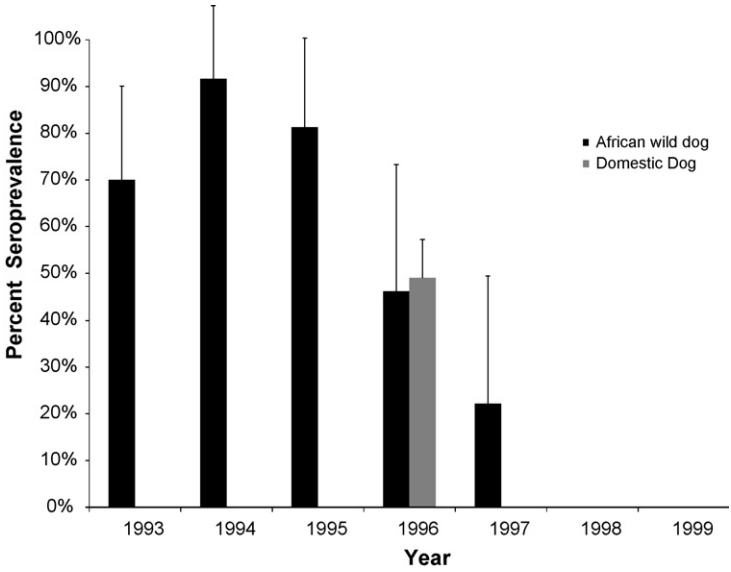

Fig. 5. CDV seroprevalence in African wild dogs (1993–1999) and domestic dogs (1996) in the Okavango Delta, Botswana.

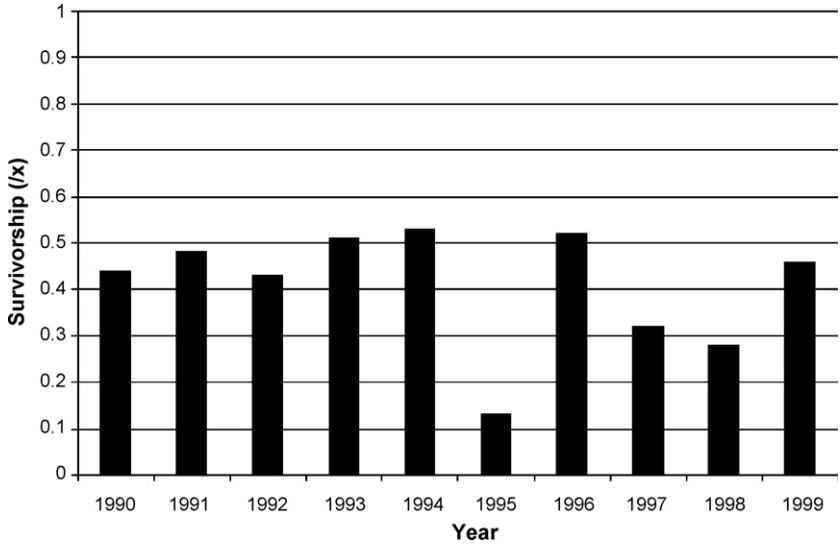

Fig. 6. Minimum survivorship (l_x) to 1 year for African wild dog pups born 1990–1999 ($N = 71$ litters).

3.1.3. Unknown disease outbreak

Early in 1996, five of six packs with pups born in June–July of 1995 died and/or disappeared in a period of approximately 4 weeks (Fig. 7). These packs had shown evidence of significant exposure and immunity to CDV (Fig. 5) and thus CDV was not considered a candidate pathogen for this outbreak. Rabies was documented in a

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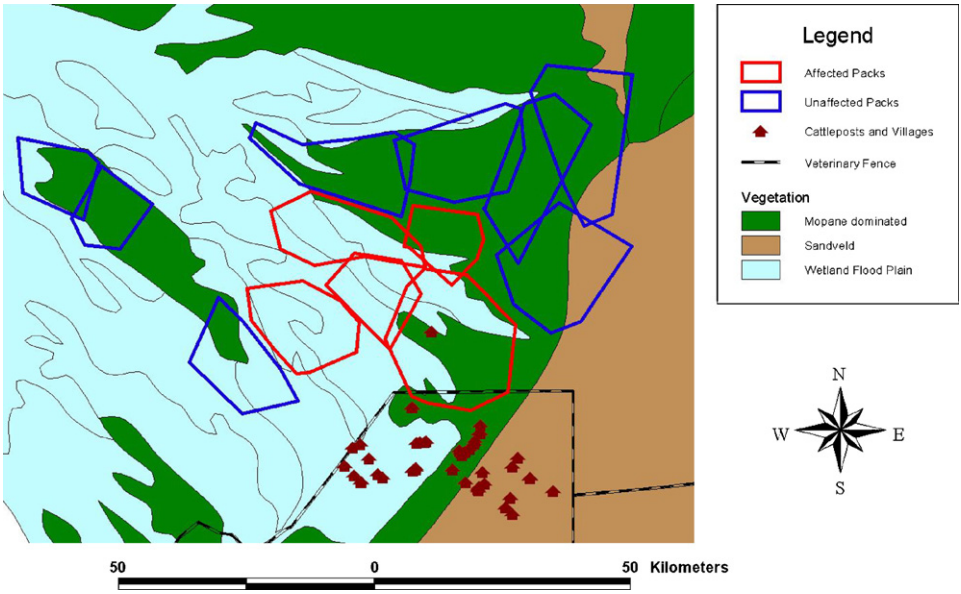

Fig. 7. African wild dog home range (n = 12 packs) is identified in relation to habitat, villages and cattle posts. Five packs died from an unknown infectious disease that spread rapidly in February 1996 (red) leaving seven packs surviving (blue). Of the five packs to the North that survived, two contributed to repopulating the vacated area along with the packs from the southwest. Mopane woodland (green) is a low-density prey area as opposed to the wetlands habitats, which is predominately flooded grassland. Deeper water on the southern boundary of the outbreak area and lower wildlife density to the north in the Mopane woodlands circumscribed the outbreak area.

bat-eared fox 2 weeks after the disease outbreak in the wild dog population began (IFA, National Veterinary Laboratories, Gaborone Botswana). The affected packs held territories consisting mainly of flood plain habitat including two territories overlapping villages supporting domestic dog populations (ca. 200–300). The geographic extent of the outbreak area was delimited by changes in coarse habitat type with the outbreak spatially limited to the high prey and higher wild dog density flood plain habitat and the boundaries identified by either deep (permanent) water or continuous woodlands with lower densities of impala. The disease vacated area (ca. 1600 km^2) was re-colonized by four newly formed packs within the following 10 months by dispersing wild dogs from packs within and outside of the focal study area.

3.2. Lions in the Kgalagadi Transfrontier Park

3.2.1. CDV and mortality

Age-specific seroprevalence rates for CDV antibodies suggested population exposure in the first half of 1990s (Fig. 8) similar to the African Wild dogs with no recent exposure among study prides sampled. There were no reports of outbreaks of disease mortality in this population during that time from park staff monitoring the population.

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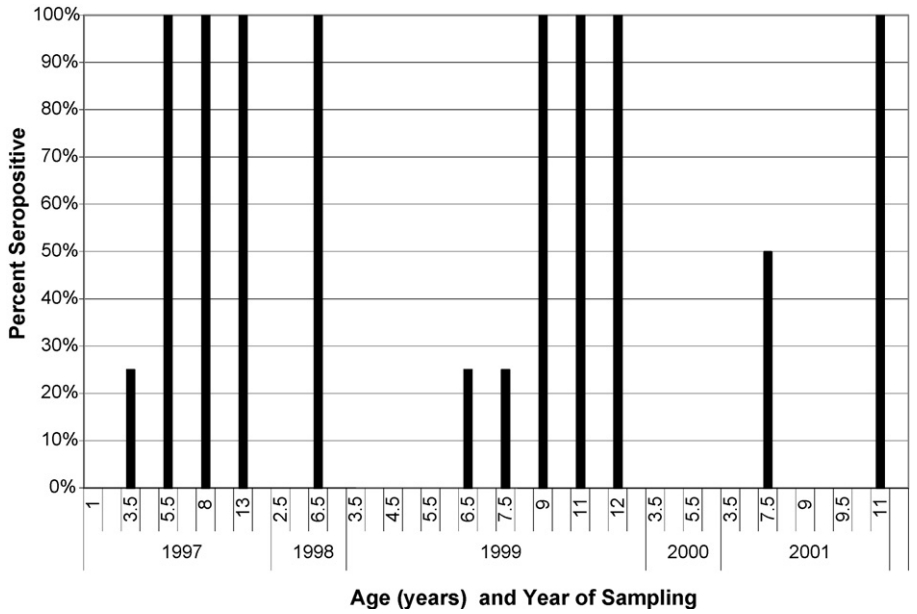

Fig. 8. Age-specific CDV seroprevalence among lions (year) in the Kgalagadi Transfrontier Park (KTP) in Botswana ($n = 32$).

4. Discussion

This study identified widespread exposure to a number of multi-host canine pathogens among domestic dogs and free-ranging predators in four countries across both protected and unprotected areas in southern Africa (Fig. 1). Many areas were remote from large domestic animal populations. In this study, CDV seropositive lions were found deep within the Kgalagadi Transfrontier Park more than 70 km from the park border (Fig. 4). Similarly, wild dogs living in Moremi Game Reserve (approximately 5000 km^2) tracked from birth to death, never left the boundaries of the reserve, yet tested antibody positive for canine pathogens. Given this, how do we manage disease risks to predator populations?

Persistence of a pathogen in the environment is an important prerequisite for pathogen exposure and requires the continued presence of a biological reservoir. With wide distribution, high densities, mobility and rapid population turnover (creation of susceptible population), domestic dog populations are identified as a key reservoir for a variety of canine pathogens [39–42]. However, pathogen exposure may not be a simple function of the presence or absence of a large domestic dog population at some identified interface. CDV and other multi-host canine pathogens can infect a wide variety of wild and domestic carnivore hosts increasing potential for pathogen maintenance in the system through interspecies transmission [43]. In general, individual wild carnivore species are unlikely to occur at sufficient densities to attain critical community size necessary to maintain most pathogens. Domestic dogs, dependent on population number and required critical community size for a pathogen could be considered non-maintenance or maintenance

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populations for a pathogen [14]. Coupling all susceptible species populations together could constitute a maintenance community irrespective of the size of a particular species component. Therefore even small and low density domestic dog populations could provide the ecosystem with the pathogen flow to allow invasion into a diverse community of susceptible hosts which together reach the critical community size required for pathogen invasion and onward transmission.

This conclusion suggests that land use alone is unlikely to provide complete protection for endangered or rare carnivores from exposure to canine pathogens. In other words, establishment of large protected areas for carnivore conservation (often identified as a key strategic component in many predator management plans e.g. Botswana Predator Management Plan) might simply be inadequate to protect free-ranging carnivores from disease threats. This may be particularly significant for smaller populations at greater risk of extinction due to effective population size [44].

Besides rabies, CDV is probably the most important pathogen affecting large predator populations in southern Africa. In this study, we did not detect significant population impacts related to CDV exposure. Among lions in the KTP, CDV appears to have entered in the early 1990s (Fig. 8). Although data are limited, the lion population appears to have remained remarkably stable over a 25-year period. Based on a survey conducted in 1976 on the South African side of the park, the maximum estimate for the lion was 140 individuals [45], whereas the same estimate in 1996 was 125 individuals [46] and 131 individuals in 2001 [47]. No observations of unusual mortality were made by Park staff during that period. Thus, at the population level, CDV occurrence in this ecosystem cannot be linked to any significant long-term changes in lion population size.

While active exposure to CDV occurred in African wild dogs in the Okavango Delta also in the early 1990s with a peak in 1993–1995, there were no identified changes in pup survivorship trends over that period or disease related mortality in pups and adults during that time. However a CDV outbreak in 1994 among African wild dogs in northern Chobe National Park, northeast of the Okavango Delta resulted in localized extinction of an extremely small population of resident African wild dogs [4].

Boots et al. [48] provide theoretical evidence for bistability in the evolution of pathogen virulence with the existence of both avirulent and highly virulent strains developing in association with divergent host population structures. Low density population structures would favour a pathogen with a high level of virulence as killing the host would prevent immune individuals from impeding the spread of the pathogen. In high density populations, evolution would favour avirulence. Further research is needed to better understand the potential role of host population structure on divergent patterns of mortality seen with CDV outbreaks in predator populations in Africa.

While population impact could not be ascribed to CDV in African wild dogs, five packs disappeared over a 4-week period in 1996, after the apparent epidemic peak of CDV. Rabies was evident in the study area at the time, as indicated by the identification of a positive case in a bat-eared fox (*Otocyon megalotis*) in the area 2 weeks after the outbreak began. The epidemic profile was also consistent with the profile of previous outbreaks of rabies in wild dogs reported elsewhere [3]. However no suitable carcasses could be obtained for a confirmatory diagnosis. Within the following 12 months, the disease-vacated area was re-colonized through dispersal and range expansion of adjacent wild dog packs.

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While the agent is unknown, the outbreak perimeter was defined by ecotones (Fig. 7) or transition zones between vegetation communities. In directly transmitted multi-host pathogens, areas of transition between habitats can influence community structure, distribution and density of susceptible hosts, contact rates and pathogen transmission dynamics, the extent of which will be influenced by R_0. In this instance, the outbreak of disease was limited to African wild dog packs in the high wildlife density flood plain but failed to continue to contiguous packs in the low wildlife density mopane woodlands habitat or those resident beyond expansive water courses.

Large-scale infectious disease mortality in African predator populations has only been reported in East Africa in the more homogenous landscape of the Serengeti and Mara grasslands. In these cases, pathogen spread was extensive through the ecosystem resulting in local extinction events [3,49], something, that has not been observed in similarly monitored southern African predator populations. This is an intriguing contrast. The explanation may relate in part to varying levels of ecological heterogeneity in these systems and the presence or absence of ecotones which are known to be associated with infectious diseases processes [50]. In contrast to the East African grasslands, the Okavango Delta is characterized by substantial number of ecotones or areas of habitat change. These transition areas may present a barrier or damp to pathogen invasion to contiguous susceptible hosts due to habitat mediated host density changes and reduction in critical community size [14] or extinction of the pathogen related to changes in host spatial structure across patches [51]. Strategic use of ecotones in conservation land use planning might offer a way of establishing ‘‘quasi-metapopulations’’ in the same land management area and increasing the potential that some proportion of a contiguous rare and vulnerable population may survive a major disease outbreak.

4.1. Predator disease control in southern Africa

At present, there are no clear mechanisms to protect large predator populations from disease threats. With wide spread exposure to canine pathogens over vast areas in southern Africa, mass vaccination of domestic dog reservoirs at the human wildlife interface has no clear application, particularly in light of the apparent complexity of pathogen maintenance in these ecosystems and lack of clarity on where this ‘‘interface’’ occurs. Minimizing contact with domestic animal disease reservoirs through the establishment of large protected areas still remains an important conservation strategy, but will not prevent exposure of free-ranging carnivores to important multi-host pathogens. Strategic use of ecotones in conservation land use planning, however, may prevent local extinction events. Further research is required to identify the utility and application of this approach.

We conclude that conservation effort should be directed at securing large metapopulations able to compensate for expected episodic generalist pathogen invasions and intervention, where required, limited to strategic vaccination of threatened populations [52]. Integrated management approaches must be developed which identify and mitigate other sources of underlying population depression such as habitat loss and wildlife conflict. This will be essential to the successful conservation of large predators in southern Africa.

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