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Infectious disease and the conservation of free-ranging large carnivores

Dennis L. Murray[1], Cynthia A. Kapke[1], James F. Evermann[2] and Todd K. Fuller[3]

[1] Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844, USA
[2] Department of Veterinary Clinical Sciences, College of Veterinary Medicine, Washington State University, Pullman, WA 99164, USA
[3] Department of Forestry and Wildlife Management, University of Massachusetts, Amherst, MA 01003, USA

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Abstract

Large carnivores are of vital importance to the stability and integrity of most ecosystems, but recent declines in free-ranging populations have highlighted the potentially devastating effect of infectious diseases on their conservation. We reviewed the literature on infectious diseases of 34 large (maximum body mass of adults >20 kg) terrestrial carnivore species, 18 of which are considered to be threatened in the wild, and examined reports of antibody prevalence (seroprevalence) and cases of infection, mortality and population decline. Of 52 diseases examined, 44% were viral, 31% bacterial and the remainder were protozoal or fungal. Many infections were endemic in carnivores and/or infected multiple taxonomic families, with the majority probably occurring *via* inhalation or ingestion. Most disease studies consisted of serological surveys for disease antibodies, and antibody detection tended to be widespread implying that exposure to micro-organisms was common. Seroprevalence was higher in tropical than temperate areas, and marginally higher for infections known to occur in multiple carnivore groups. Confirmation of active infection *via* micro-organism recovery was less common for ursids than other taxonomic groups. Published descriptions of disease-induced population decline or extinction were rare, and most outbreaks were allegedly the result of direct transmission of rabies or canine distemper virus (CDV) from abundant carnivore species to less-common large carnivores. We conclude that the threat of disease epidemics in large carnivores may be serious if otherwise lethal infections are endemic in reservoir hosts and transmitted horizontally among taxa. To prevent or mitigate future population declines, research efforts should be aimed at identifying both the diseases of potential importance to large carnivores and the ecological conditions associated with their spread and severity.

INTRODUCTION

Infectious diseases may affect the distribution and abundance of animals, but the potential role of disease in wildlife conservation has only recently drawn considerable attention (e.g. Dobson & May, 1986; May, 1988; Scott, 1988; Thorne & Williams, 1988; Macdonald, 1993, 1996). In general, it is understood that not all micro-organisms cause disease, nor are the effects of a given disease consistent among all outbreaks. Rather, disease impacts appear to be largely contingent on the particular ecological or epidemiological conditions associated with the outbreak. For example, it is unlikely that single-host infectious diseases will cause extinctions unless host populations are small and disease transmission is rapid and with a delayed impact. On the other hand, in cases where reservoir hosts also carry the infection and can sustain reinfection of the population, demographic effects of disease may occur regardless of host population size or disease transmission rate (Begon & Bowers, 1995, McCallum & Dobson, 1995). Many other ecological and epidemiological factors can influence the distribution of infections in a susceptible animal population; the challenge for conservation biologists is to identify conditions that are conducive to the spread of infections and severity of disease in advance of epidemics, and to implement control measures that will prevent or mitigate such epidemics.

Infectious disease may be particularly relevant to large carnivore conservation because many species or populations are already seriously threatened by factors such

All correspondence to: Dennis L. Murray. Tel: 208-885-7323; Fax: 208-885-9080; E-mail: dmurray@novell.uidaho.edu.

as restricted range, habitat destruction and over-exploitation of the predators themselves or their prey. Thus, otherwise minor diseases potentially can be devastating if occurring in populations of carnivores that are already small or in decline. In addition, carnivores are susceptible to a wide array of highly lethal or debilitating microparasites (Appel, 1987), many of which are either native to, or easily transmitted by, domestic species. Indeed, recent disease outbreaks in African wild dogs (*Lycaon pictus*) (Kat *et al*., 1995), Ethopian wolves (*Canis simensis*) (Sillero-Zubiri, King & Macdonald, 1996), and lions (*Panthera leo*) (Roelke-Parker *et al*., 1996), highlight the impact of diseases of domestic origin upon wild carnivore populations. Also, it is suspected that the effect of disease may be aggravated if it interacts with factors common to endangered populations, such as malnutrition, stress or inbreeding (O'Brien, Roelke *et al*., 1985; Ullrey, 1993; Lloyd, 1995). Such interactions have been suggested as being important in causing declines in cheetah (*Acinonyx jubatus*) and black-footed ferret (*Mustela nigripes*) populations (O'Brien & Evermann, 1988), although data supporting this idea are absent for free-ranging animals.

The present paper summarizes the current literature on infectious diseases in free-ranging large terrestrial carnivores by (i) comparing the diagnosis of disease in various species and (ii) examining patterns related to disease exposure in relation to ecological and epidemiological factors that may affect disease severity and spread. These include potential disease lethality to carnivores, apparent predominant mode of disease transmission, and documentation of the micro-organism's ability to infect multiple taxonomic families (i.e. horizontal transmission). Understanding such patterns is important because it may enable researchers to develop effective measures for prevention and control of future disease outbreaks.

METHODS

We reviewed the recent literature on infectious diseases in large (i.e. maximum body mass of adults > 20 kg: Fuller, 1995) terrestrial carnivores (n = 34 species), of which 18 species are considered to be either vulnerable or endangered in the wild (Groombridge, 1994) and therefore are of significant conservation interest. The following journals were surveyed completely: *Journal of the American Veterinary Medical Association* (1980–1996), *Journal of Wildlife Diseases* (1965–1996), *The Journal of Zoo and Wildlife Medicine* (1980–1996), *Onderstepoort Journal of Veterinary Research* (1980–1996) and *The Veterinary Record* (1980–1996); other journals and articles related to disease in free-ranging carnivores were reviewed as necessary. The literature review was restricted to large carnivores because (i) recent disease-induced declines in several populations have prompted concern over their conservation (e.g. Macdonald, 1996), (ii) carnivores are considered by many ecologists as 'umbrella' or 'keystone' species (Mills, Soulé & Doak, 1993; Estes, 1996; Noss *et al*., 1996), and (iii) inclusion of smaller carnivores would make the data set unwieldy (i.e. >200 species of carnivores).

Results from serological tests for the detection of antibodies to specific infectious disease micro-organisms were considered to be indicative of past or present infection with a particular disease agent rather than confirmation of clinical disease (Smith, 1995; Evermann, 1998; Evermann & Eriks, 1999). The review was restricted to microparasitic organisms (i.e. viruses, bacteria, protozoans and fungi); such species theoretically can have large demographic impacts on host populations (Anderson & May, 1978; May & Anderson, 1978; Heesterbeek & Roberts, 1995) and are responsible for the majority of recent disease outbreaks in free-ranging animals (Macdonald, 1996). Also, our analysis did not include infectious diseases reported exclusively in captive large carnivores because such diseases may not be present in free-ranging populations. Our survey generally considered congeneric pathogens (e.g. *Brucella abortus*, *Brucella canis* and *Brucella suis*), and serotypes sharing recent and similar origin and/or aetiology (e.g. canine parvovirus (CPV) types 2, 2a and 2b), as the same infection. Our list of infectious diseases of large carnivores is by no means exhaustive, but rather includes only those reported in international journals of relatively wide distribution. However, we consider our results to be generally representative of published information regarding infection and disease in large carnivore populations worldwide.

Prevalence of infection and disease in the sampled population was analyzed according to the following independent variables: (i) type of infection (virus, bacteria, protozoa, or fungus); (ii) number of taxonomic groups of carnivores known to be infected (1 *versus* >1); (iii) known or suspected mode of transmission (direct = directly between carnivores *via* saliva, transplacentally, etc; intermediate = possibly directly or less directly *via* food, aerosol, etc; indirectly = less directly *via* tick bites, wounds, etc); (iv) perceived lethality to carnivores based on previously published reports (high = usually results in death; moderate = may result in death depending on ecological or host condition; low = rarely/never results in death). In addition, the analysis considered: (v) location of study (temperate *versus* tropical) and (vi) and taxonomic carnivore family (canidae, felidae, ursidae or hyaenidae) infected with the micro-organism, as ecological factors potentially affecting disease spread and severity.

RESULTS

We identified 52 infectious diseases that were previously studied in free-ranging large carnivores (Table 1). Forty-four percent of infections were viral, with the remainder being bacterial (31%), protozoal (21%) and fungal (4%). Overall, viral, bacterial and protozoal infections did not differ in terms of their perceived lethality to carnivore hosts (χ^2 = 5.376, d.f. = 4, P = 0.25), based on previously-published reports on mortality in both

Table 1. Infectious agents with the potential to produce morbidity and mortality in free-ranging large (i.e. maximum body mass of adults >20kg) carnivore families

Disease	Symptoms / perceived lethality	Mode of transmission / density dependence	Taxa infected†
Virus			
Rabies	CNS disease; death / high	Saliva; bite wounds / direct	C, F, U, H, M
Canine distemper	Pnuemonia; encephalitis; death / high	Inhalation; ingestion / intermediate	C, F, U, H
Canine parvovirus	Fever; diarrhoea; dehydration / moderate (juveniles)	Ingestion; transplacentally / intermediate	C, U
Canine herpesvirus	Respiratory or generalized disease; death / moderate	Mucus membranes; transplacentally / direct	U (not detected)
Canine parainfluenza	Respiratory disease; fever; encephalitis / moderate	Inhalation / intermediate	C, U
Canine coronavirus	Diarrhoea; vomition; occasionally death / low	Ingestion / intermediate	C, U
Canine hepatitis	Fever, diarrhoea; vomition; jaundice; death / high	Inhalation; ingestion / intermediate	C, U
Canine adenovirus	Respiratory disease / high	Inhalation; ingestion / intermediate	U
Canine oral papilloma	Oral warts / low	Wounded oral mucosa / indirect	C
Feline panleukopenia	Fever; diarrhoea; vomition; death / moderate	Ingestion; transplacentally / intermediate	F
Feline leukaemia	Neoplasia; immunosuppresion; death / moderate	Body fluids; faeces, bite wounds / direct	F
Feline coronavirus (FIP)	Diarrhoea, peritonitis; granulomas; death / moderate	Ingestion; inhalation / intermediate	F
Feline immunodeficiency	Gingivitis; pneumonia; diarrhoea; death / high	Saliva, especially bite wounds / direct	F
Feline viral rhinotracheitis	Upper respiratory disease; rarely death / low	Mucus membranes, transplacentally / direct	F (not detected)
Feline calicivirus	Upper respiratory disease; ulcers; lameness / low	Inhalation / intermediate	F
Feline oral papilloma	Oral warts / low	Wounded oral mucosa / indirect	F
Psuedorabies	Pneumonia; cardiac or CNS disease; death / high	Ingestion; skin abrasion / intermediate	F
Reovirus	Conjunctivitis / low	Ingestion; inhalation / intermediate	C, F
Rotavirus	Mild diarrhoea / low	Ingestion; inhalation / intermediate	C
Bluetongue	Oral ulcers; facial oedema; abortion; death / low	Mosquito bite; Ingestion of meat / indirect	C, F, H
African horse sickness	Respiratory; fever; lung oedema; death / low	Mosquito bite; ingestion of meat / indirect	C, F, H
Vesicual stomatitis	Fever; oral ulcers; depression; anorexia / low	Direct contact; insect bite / indirect	F, U
Encephalitis viruses	Encephalitis; fever / low	Insect bite / indirect	C, F, U
Bacteria			
Bubonic plague	Fever; vomition; large lymph nodes; death / high	Flea bite; inhalation; ingestion of meat / indirect	C, F, U
Psuedotuberculosis	Intestinal infection; mesenteric nodules / moderate	Ingestion / intermediate	F
Leptospirosis	Fever; jaundice; meningitis; renal failure / low	Mucus membranes, water or urine/ intermediate	C, F, H
Botulism	Muscle paralysis; CNS disease; death / high	Ingestion of soil or decaying meat / indirect	C, U
Anthrax	Pneumonia; skin lesions; sudden death / moderate	Inhalation; ingestion; skin abrasion/ indirect	C, F, H
Lyme disease	Polyarthritis / moderate	Tick bite / indirect	C, U
Tularemia	Pneumonia; large lymph nodes / low	Tick bite; ingestion of meat / indirect	C, F, U
Brucellosis	Abortion; epididymitis / low	Mucus membranes, ingestion of meat / indirect	C, F, U
Chlamydia	Abortion; enteritis; pneumonia; arthritis / low	Inhalation; ingestion / indirect	F
Pasteurella	Pneumonia; haemorrhagic septicaemia / low	Normal oral inhabitant; inhalation / indirect	F
Salmonella	Diarrhoea; vomition; occasionally death / low	Ingestion / indirect	F
Ehrlichia	Haehemhorrage; occasionally death / moderate	Tick bite / indirect	C (not detected)
Coxiella	Fever; pnuemonia; abortion / low	Tick bite; inhalation / indirect	C, U
Other rickettsials	Fever / low	Tick bite / indirect	C, U
Achoplasma	Pneumonia / low	Inhalation / indirect	F
Mycobacter	Pneumonia; muscle wasting; death / moderate	Inhalation; ingestion; wounds / indirect	C, M
Protozoa			
Toxoplasma	Fever; abortion; pneumonia; CNS disease / low	Ingestion / indirect	C, F, U
Sarcocystis	Diarrhoea; muscle disease; occasional death / low	Ingestion of meat / indirect	C, F
Hepatozoon	Fever; anaemia; weight loss / low	Tick bite / indirect	C, F, H
Trypanasoma	Lethargy; ascites; cardiac disorder / low	Insect bite / indirect	C, F
Cytauxzoon	Fever; anaemia; jaundice; death / moderate	Probably tick bite / indirect	F
Babesia	Fever; anaemia; jaundice / low	Tick bite / indirect	C
Giardia	Enteritis / low	Ingestion, especially in water / indirect	F
Eimeria	Diarrhoea and dysentery; rarely death / low	Ingestion / indirect	C
Isospora	Diarrhoea and dysentery; rarely death / low	Ingestion, especially meat / indirect	C, F
Hammondia	Usually no symptoms; abortion / low	Ingestion of meat / indirect	C, F
Theileria	Dyspnoea; emaciation; weakness; sometimes death / low	Tick bite / indirect	F
Fungi			
Blastomycosis	Multiple forms; pneumonia; death / moderate	Inhalation of infected soil / indirect	C
Coccidiosis	Pneumonia; infection; death / moderate	Inhalation of infected soil / indirect	F

Data are based on symptoms and known or suspected mode of transmission as reported in Davis, Karstad & Trainer, 1970; Fowler, 1986; Appel, 1987; Timoney *et al*. 1988 and Bowman, 1995. Groups infected are taxonomic families where the infection either tested positive *via* serological tests (seroprevalence was assumed to represent prior infection), or observed directly *via* organism recovery (see Tables 3–6). Three infections were not found to be seroprevalent in free-ranging carnivores. For statistical analysis, we classified each disease subjectively according to perceived lethality to carnivores (high, moderate and low) and density-dependence of the apparent predominant mode of transmission (direct between carnivores, intermediate (possibly directly or less direct) and indirect).

†C, Canidae; F, Felidae; U, Ursidae; H, Hyaenidae; M, Mustelidae.

wild and domestic carnivores (Table 1). However, there was a tendency for more viruses, than other infections, to be considered highly lethal to carnivores. The majority of other infections either occasionally caused death in carnivores, or were usually associated with sublethal symptoms such as weakness, pneumonia and abortion; these attributes could also be significant to carnivore population demography. We used known or suspected routes of transmission to classify each disease according to its probable mode of spread. Viruses appeared to be more commonly transmitted *via* direct contact between carnivores than were bacterial or protozoal infections ($\chi^2 = 24.147$, d.f. = 4, $P < 0.001$; Table 1). Therefore, transmission of many viruses is probably highly dependent on local carnivore densities. Bacteria and protozoa seemingly were transmitted between carnivores largely through inhalation or ingestion (i.e. intermediate density-dependence), or *via* insect or arthropod bites or consumption of infected food (i.e. largely indirectly; Table 1). The proportion of infections known to occur in multiple taxonomic families was similar among the three categories of disease ($\chi^2 = 0.820$, d.f. = 2, $P = 0.66$; Table 1), with an overall average of 52% of infections occurring in multiple groups. Such infections potentially could exhibit extensive horizontal transmission in the wild. However, it is important to note that there may exist a sampling bias in tests showing seroprevalence in multiple taxonomic families; infections that are more widely tested are more likely to be detected in several groups.

Antibody presence and disease manifestation

Among the Canidae, 32 infectious diseases were studied, 97% of which were found to have infected at least one species (Table 2). However, only 53% of infections were also shown to actually result in disease establishment, as determined by organism recovery, morbidity and/or fatality. Thirty-six infectious diseases were studied in large felids, 92% of which were seropositive in at least one species, but only 58% were also associated with organism recovery and/or clinical signs (Table 3). For ursids, seroprevalence was evaluated for 20, and confirmed for 16, infections, although only 14% of infections were associated with signs of active infection or disease (Table 4). For hyaenids, only six infections were surveyed in a single species; four were associated with micro-organisms or clinical signs (Table 4). Overall, significantly fewer instances of disease occurrence, morbidity, or fatality were reported for diseases surveyed in ursids than those studied in canids, felids, or hyaenids ($\chi^2 = 12.277$, d.f. = 3, $P < 0.001$). Rates of disease occurrence did not differ among levels of perceived disease lethality to carnivores ($\chi^2 = 3.844$, d.f. = 2, $P = 0.15$), probable modes of disease transmission ($\chi^2 = 3.551$, d.f. = 2, $P = 0.17$), or whether or not infections were known to affect multiple taxonomic families of carnivores ($\chi^2 = 0.014$, d.f. = 1, $P = 0.97$).

Table 2. Evidence of exposure to infectious agents in free-ranging large (i.e. maximum adult body mass >20kg) canids

Disease	*Canis lupus*	*Lycaon pictus*	*Canis latrans*	*Canis dingo*
Virus				
Rabies	SOMF	TSOMF		
Canine distemper	S	TSO	TSF	
Canine parvovirus	TSOF	TS	SF	
Canine parainfluenza			S	
Canine coronavirus		S	TS	
Canine hepatitis	S	S	S	
Canine oral papilloma	OM		OM	
Reovirus		S		
Rotavirus		S		
Bluetongue		S	T	
African horse sickness		S		
Encephalitis viruses		O	TS	
Bacteria				
Bubonic plague			SO	
Leptospirosis	S		TSM	
Botulism			S	
Anthrax		TSOMF		
Lyme disease	TS		S	
Tularemia	TS		S	
Brucellosis	TS		TSO	
Ehrlichia		T		
Coxiella	S	S	O	
Other rickettsials		S		
Mycobacter	OF			
Protozoa				
Toxoplasma		S	S	S
Sarcocystis	O		O	S
Hepatozoon		S	O	
Trypanasoma			S	
Babesia		S		
Eimeria			O	
Isospora			O	
Hammondia			O	
Fungi				
Blastomycosis	SMF			

No surveys of infection or disease were found for *Canis rufus*, *Cuon alpinus* or *Chrysocyon brachyurus*. References for articles reviewed for this table are found in the Appendix.

T, test performed but no antibodies or antigen were detected; S, serological test for antibodies was positive; O, micro-organism recovered; M, morbidity observed; F, fatality observed.

Prevalence of antibodies in carnivore populations

We compared the percentage of animals from carnivore populations sampled by researchers, that were either seropositive or infected with various micro-organisms. Of 191 cases where antibodies/micro-organisms were determined for a cohort of large carnivores, 90% of studies detected antibody/micro-organism presence in at least one individual. Using only these latter cases ($n = 172$), we found that the percentage of a sampled population that was either seropositive or infected was higher (factorial ANOVA: $F_{1,160} = 9.035$, $P = 0.003$) in tropical than temperate areas, and marginally higher ($F_{1,160} = 3.028$, $P = 0.084$) for micro-organisms known to infect multiple taxonomic families than those apparently restricted to a single group (Table 5). We failed to find significant differences in antibody or micro-organism

Table 3. Evidence of exposure to infectious agents in free-ranging large (i.e. maximum adult body mass >20kg) felids

Disease	*Panthera leo*	*Panthera pardus*	*Panthera onca*	*Panthera tigris*	*Acinonyx jubatus*	*Puma concolor*	*Lynx rufus*	*Lynx canadensis*
Virus								
Rabies		SO			SO	SO		
Canine distemper	OMF							
Feline panleukopenia						S		
Feline leukemia	T	T			T	TSOM		
Feline coronavirus (FIP)						S		
Feline immunodeficiency		S	S			TS	TS	S
Feline viral rhinotracheitis							TS	
Feline calicivirus						S		
Feline oral papilloma	OM							
Psuedorabies						TO		
Reovirus						S		
Bluetongue	S				T			
African horse sickness	S				S			
Vesicular stomatitis							S	
Encephalitis viruses								TS
Bacteria								
Bubonic plague						S	O	
Psuedotuberculosis							O	
Leptospirosis							S	
Anthrax		F			OMF			
Tularemia							S	
Brucellosis	S					T		
Chlamydia						T		
Pasteurella								O
Salmonella							O	
Other rickettsials							T	
Achoplasma								O
Protozoa								
Toxoplasma	S	O	O	O		TS	SOMF	
Sarcocystis		O	T	O		TO	O	
Hepatozoon	O	O			O		OMF	
Trypanasoma	O				T			
Cytauxzoon							TSO	
Giardia		O		O				
Isospora		O	O	O		T	S	
Hammondia			O			O		
Theileria	O				O			
Fungi								
Coccidiosis						SOM		

No surveys of infection or disease were found for *Panthera uncia*, *Neofelis nebulosa*, *Lynx lynx* or *Lynx pardina*. References for articles reviewed for this table are found in the Appendix.

T, test performed but no antibodies or antigen were detected; S, serological test for antibodies was positive; O, micro-organism recovered M, morbidity observed; F, fatality observed

prevalence between carnivore families ($F_{3,160}$ = 2.111, P = 0.10), types of disease ($F_{2,160}$ = 2.282, P = 0.11), or perceived disease lethality ($F_{2,160}$ = 2.269, P = 0.11), although the relatively low statistical probabilities for each of these tests may be indicative of weak relationships (Table 5). Apparent mode of transmission also failed to be associated to antibody/micro-organism prevalence ($F_{2,160}$ = 0.431, P = 0.65, Table 5).

Disease impacts on large carnivore populations

Our review identified 16 published studies of population change in free-ranging large carnivore populations that may have been at least partly caused by disease; these were restricted to four carnivore species and five micro-organisms, three of which were viral (Table 6). The estimated magnitude of population decline ranged from 6% to 100%, but not all losses were attributable to disease and most estimates were obtained from disappearance of known animals rather than positive identification of disease-induced mortality. Thus, few studies were able to distinguish between effects of disease *versus* those of other deleterious factors. Most reports were published retrospectively, usually following an apparent population decline. Few studies measured disease effects in seemingly stable large carnivore populations. Most rabies and CDV outbreaks documented in North America were probably caused by contact with arctic fox (*Alopex lagopus*) or red fox (*Vulpes vulpes*), whereas those occurring in Africa were probably transmitted by domestic dogs (*Canis familiaris*). Two anthrax epidemics in wild dogs were probably attributable to

Table 4. Evidence of exposure to infectious agents in free-ranging large (i.e. maximum body mass >20kg) ursids, hyaenids and mustelids

Disease	*Ursus maritimus*	*Ursus arctos*	*Ursus americanus*	*Ailuropoda melanoleuca*	*Crocuta crocuta*	*Gulo gulo*
Virus						
Rabies	TOMF				TSO	
Canine distemper	S			S	SO	
Canine parvovirus		S		S		
Canine herpesvirus				T		
Canine parainfluenza		T				
Canine coronavirus			S			
Canine hepatitis			SO			
Canine adenovirus				S		
Pseudorabies			S	T		
Vesicular stomatitis			S			
Bluetongue					S	
African horse sickness					S	
Encephalitis viruses			S			
Bacteria						
Bubonic plague			S			
Leptospirosis		S	S	S		
Botulism			TS			
Anthrax			O		F	
Tularemia			TS			
Brucellosis		S	S			
Chlamydia		T				
Coxiella			S			
Other rickettsials			S			
Protozoa						
Toxoplasmosis		S	S			
Sarcocystis						T
Hepatozoon					O	

No surveys of infection or disease were found for *Selenarctos thibetanus*, *Helarctos malayanus*, *Melursus ursinus*, *Tremarctos ornatus, Hyaena hyaena*, *Hyaena brunnea*, *Proteles cristatus*, *Enhydra lutris* and *Pteronura brasiliensis*. References for articles reviewed for this table are found in the Appendix.

T, test performed but no antibodies or antigen were detected; S, serological test for antibodies was positive; O, micro-organism recovered; M, morbidity observed, F, fatality observed

consumption of infected prey. Sample sizes were not adequate to perform statistical tests of disease effects in free-ranging populations. However, we compared qualitatively the rates of population change between wolves and wild dogs and observed differences between the two species in terms of percentage population change (wolf, 25.2 (± 7.8)% (mean ± SE), $n = 6$; wild dog, 57.0 (± 16.0)%, $n = 6$) while rate of change was remarkably similar (wolf, 11.2 (± 9.8)% /month, $n = 6$; wild dog, 12.5 (±9.7)% /month, $n = 6$).

DISCUSSION

Serological studies and carnivore disease

Numerous infectious diseases have been tested by serological tests, and most surveys have found antibodies to be present in the sampled population. Although this may imply that exposure to pathogens is widespread, these results should be treated with caution when applied to wild animals. Many serological tests have not been validated for non-domestic species (Gardner, Hietala & Boyce, 1996), and high antibody titres also may represent prior infection with an avirulent strain or micro-organisms with cross-reacting antigens; these possibilities are indistinguishable based exclusively on serum antibodies. Furthermore, there is a tendency among some wildlife biologists to equate seroprevalence with past or current infection with disease (e.g. Choquette & Kuyt, 1974). However, micro-organisms need not be present for the detection of antibodies if immunity has eliminated the infection, and in order to confirm disease presence clinical signs and detection of the micro-organism are necessary (Evermann & Eriks, 1999). For instance, antibodies for viruses such as bluetongue and African horse sickness have been detected in several carnivore species (Alexander, MacLachlan *et al*., 1994; Alexander, Kat *et al*., 1995), even though at present there is little evidence suggesting that these infections actually cause disease symptoms in carnivores. Thus, although useful as a means of evaluating prior exposure to micro-organisms, serological tests are of limited utility in the absence of additional information (Gardner *et al*., 1996).

Impact of disease on large carnivore populations

Our analysis showed that the percentage of sampled populations of carnivores that tested positive for either antibodies or micro-organisms tended to be higher in

Table 5. Percentage ± SE of individual large carnivores from free-ranging populations having disease antibodies or from which micro-organisms were recovered

1. Location of study	
Temperate:	33.9 ± 2.5 (128)
Tropical:	49.3 ± 4.8 (44)†
2. Number of taxonomic families showing exposure to disease	
Multiple:	38.3 ± 2.6 (140)
Single:	31.8 ± 4.7 (32)‡
3. Taxonomic family	
Canidae:	37.9 ± 3.6 (73)
Felidae:	43.0 ± 3.9 (60)
Ursidae:	28.8 ± 4.9 (35)
Hyaenidae:	39.3 ± 7.0 (4)
4. Type of disease	
Virus:	43.8 ± 3.2 (81)
Bacteria:	25.5 ± 4.2 (40)
Protozoa:	37.6 ± 4.5 (51)
5. Perceived lethality of disease	
High:	31.1 ± 4.1 (39)
Moderate:	50.5 ± 5.5 (32)
Low:	36.5 ± 3.1 (101)
6. Predominant mode of disease transmission	
Direct:	33.4 ± 6.1 (18)
Moderate:	42.4 ± 4.0 (56)
Indirect:	35.9 ± 3.1 (98)

†$P < 0.05$.
‡$P < 0.10$.

Perceived disease lethality and predominant mode of transmission were based on known and suspected patterns of infection and disease symptoms (Table 1). Number of taxonomic families exposed or infected was determined from previously-published reports (see Tables 1–4). Only infections that were present in populations were included in the analysis. Prevalence was transformed to the arcsin of the square root prior to analysis and sample sizes are in parentheses. Statistical analysis of the six independent variables involved factorial ANOVA without interaction terms.

carnivore populations from tropical areas as well as for diseases known to infect multiple taxonomic groups. Because infections present in a high proportion of hosts are probably not of major demographic importance unless their effects are time-delayed (Anderson 1979), or interactive with other factors, high prevalence of antibodies or micro-organisms is most often indicative of a sublethal infection or of effective host immunity. However, it is also possible that higher rates of seroprevalence are attributable to differences in infection rates, longer time delays in the manifestation of lethal effects, or simply a bias in the infections tested by wildlife researchers. The diseases of greatest concern, rabies and CDV, have a world-wide distribution and are largely similar in their severity among carnivore species and areas of occurrence (Table 6). Both diseases are found in several carnivore taxa and therefore have the potential for extensive horizontal transmission between species. This phenomenon was recently illustrated by the probable transmission of CDV from domestic dogs to African wild dogs and Serengeti lions, which resulted in significant population declines (Kat *et al*., 1995; Roelke-Parker *et al*., 1996). In most populations outside epidemic situations, antibodies for rabies and CDV generally are rare (<20% seropositive rate), (e.g. Stephenson, Ritter & Nielsen, 1982; Zarnke & Ballard, 1987; Alexander & Appel, 1994; Alexander, Kat *et al*., 1995), indicating that these infections usually are not endemic in free-ranging carnivores. However, higher rates of seroprevalence (>50%) are not necessarily associated with population declines in some carnivores (e.g. Guo *et al*., 1986; Gese, Schultz, Rongstad *et al*., 1991; Gese, Schultz, Johnson *et al*., 1997), and rates of CDV seroprevalence were found to be as high as 76% for domestic dogs in Africa (Alexander & Appel, 1994). For those host species, otherwise lethal infections may fail to be of immediate demographic significance, and although this may be beneficial for the species in question, it may have negative implications for other carnivores if infections are transmitted horizontally. Thus, an important value of serological tests in wildlife conservation may be in the identification of potential reservoir host species through analyses of antibody prevalence.

Reports of disease-induced population decline in carnivores highlight the fact that most epidemics in large carnivores are viral, and are probably initiated by transmission from abundant carnivores either directly through saliva, or less directly *via* inhalation or ingestion. Wolf population declines usually are initiated by disease transmission from arctic or red fox, whereas domestic dogs are implicated in disease-induced declines in African wild dogs and lions. Consistent with this theme, theory predicts a higher likelihood of extinction in small populations living sympatrically with larger, reservoir, populations (Begon & Bowers, 1995). Thus, it often may be most effective to mitigate population declines by targeting reservoir hosts, as illustrated by the recent attempts to control epidemics in wild dogs and lions through vaccination of domestic dogs (e.g. Burrows, Hofer & East, 1994; Roelke-Parker *et al*., 1996).

It is likely that the role of reservoir hosts in the transmission of infectious diseases will become increasingly important as many free-ranging carnivores experience reduced numbers, range restrictions, higher densities and higher rates of contact with domestic or other free-ranging carnivores (Lyles & Dobson, 1993; Perry, 1993; McCallum & Dobson, 1995). This implies that micro-organisms infecting multiple taxonomic families, as well as those exhibiting high rates of direct or intermediately-direct transmission among hosts, will be of greatest conservation concern. Such infections should be the focus of intensive research in an effort to better understand the factors associated with their spread and severity. Vaccines against the most important diseases should be developed and tested in domestic and captive large carnivores, and deployed in the field when necessary.

Deficiencies in existing data

A number of important points emerge from the present analysis regarding our general lack of understanding of disease in carnivores. Of 34 species of large terrestrial

Table 6. Published actual or suspected cases of population change in free-ranging large carnivores that were at least partly attributable to infectious disease, or where disease was being monitored concurrent to population decline

Carnivore species	Disease	Location	% population change	Duration (months)	Source species	Reference
Wolf (*Canis lupus*)	Rabies	Alaska	> –60% (10)	1	Arctic fox	Chapman (1978)
	Rabies	Alaska	–27% (26)	5	Arctic fox	Weiler, Garner & Ritter (1995)
	Rabies	Ontario	–11% (57)†	60	Red fox	Theberge *et al.* (1994)
	Rabies	Alaska	–30% (37)	24	Arctic or red fox	Ballard & Krausman (1997)
	CPV	Minnesota	–9% (54)†	132	Domestic dog or endemic	Mech & Goyal (1993)
	CDV & mycobacter	Manitoba	–14% (21)	36	Probably coyote	Carbyn (1982)
	CDV or CPV	Montana	?	60	?	Johnson, Boyd & Pletscher (1994)
Wild dog (*Lycaon pictus*)	Rabies	Kenya	–91% (23)†	1.5	Domestic dog	Kat *et al.* (1995)
	Rabies	South Africa	–10% (62)	36	Domestic dog	Van Heerden *et al.* (1995)
	Rabies	Tanzania	> –60% (20)†	12	Domestic dog	Gascoyne *et al.* (1993)
	CDV or Rabies?	Tanzania	–71% (77)†	252	Domestic dog	Burrows *et al.* (1994)
	CDV or Rabies?	Kenya	–100% (16)†	12	Domestic dog	Alexander & Appel (1994)
	Anthrax?	Zambia	?†	24	Hippopotamus	Turnbull *et al.* (1991)
	Anthrax	Tanzania	–10% (42)	0.75	Probably impala	Creel *et al.* (1995)
Coyote (*Canis latrans*)	CDV & CPV	Georgia	–6% (17)	17	Probably endemic	Holtzman, Conroy & Davidson (1992)
Lion (*Panthera leo*)	CDV	Tanzania	–33% (3000)†	8	Domestic dog	Roelke-Parker *et al.* (1996)

Percentage reduction was estimated as population size at the end relative to the beginning of the study. Numbers of animals at the beginning of the study are in parentheses and duration of decline is given in months and in many cases is an estimate. In many cases diagnosis of disease was determined qualitatively and thus population change may not have been entirely due to disease.

?, Instances where specific disease or magnitude of population change was uncertain or not reported
† Population change was inferred largely from disappearance of known animals rather than carcass recovery and disease identification.

carnivores, 18 of which are considered to be threatened in the wild (Groombridge, 1994), only 18 have published reports of serological surveys or disease recovery in free-ranging populations (Tables 2–4). There exist numerous surveys for several North American species as well as African wild dogs and lions. However, little attention has been afforded to other large carnivores even though in many instances these species are of significant conservation concern and subject to high disease risk. Also, little is known about the role of most pathogens on carnivore population dynamics, particularly when effects are either non-epidemic, apparently sublethal, or aggravated through interactions with other factors or diseases. However, it would be naive to assume that such diseases fail to affect carnivore demography simply because they do not cause outbreaks. For instance, even though there are no published reports of symptoms or deaths resulting from feline immunodeficiency virus in wild species, at least three carnivore species have shown antibodies for the virus (Olmstead *et al.*, 1992; Table 3), and captive lions have demonstrated morbidity and mortality caused by the disease (Poli *et al.*, 1996). However, because wild animals dying of disease rarely are found and recovered, and such problems are exacerbated for large carnivores owing to their low densities and secretive behaviour patterns, the role of many diseases in wild carnivore population dynamics remains poorly understood.

CONCLUSIONS

Although endangerment of large carnivores is usually caused by habitat loss or over-exploitation, infectious disease can further reduce small or isolated populations. Furthermore, in the future as large carnivores experience greater range restriction and increased encroachment by humans, transmission of infectious diseases from domestic to free-ranging carnivores will become increasingly common. In order to develop effective programmes aimed at infectious disease prevention and mitigation, it is necessary to develop a clearer understanding of the epidemiological and ecological factors associated with microbial infection, disease spread and severity. This requires that serological surveys and disease monitoring programmes be made more comprehensive by targeting geographical areas and species for which little information is currently available, including potential reservoir hosts. Attempts to recover micro-organisms should complement all serological surveys. Field-based research should assess the impacts of disease in stable and declining carnivore populations through intensive survival monitoring and carcass recovery and necropsy. Field experiments manipulating disease levels in abundant carnivores should also be undertaken to better model epidemiology in rarer species (Minchella & Scott, 1991; McCallum & Dobson 1995; also see Murray, Cary & Keith, 1997). Finally, effective vaccines for control of the most important diseases in large carnivores and reservoir hosts should be developed, tested and deployed when necessary.

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APPENDIX

Literature reviewed for infection and disease in free-ranging large (i.e. >20kg) carnivores and used to generate Tables 3–6. A database of publications on infectious diseases in large carnivores is maintained at: www.uidaho.edu/fishwild/fw.html.

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