Infectious disease and the conservation of free-ranging large carnivores

Dennis L. Murray¹, Cynthia A. Kapke¹, James F. Evermann² and Todd K. Fuller³

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

(Received 8 June 1998; accepted 27 January 1999)

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
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), Ethiopian 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 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 actiology (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) 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 ($\chi^2 = 5.376$, 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 | Pneumonia; encephalitis; death / high | Inhalation; ingestion / intermediate | C, F, U, H  |
| Canine parvovirus | Fever; diarrhoea; dehydration / moderate (juveniles) | Ingestion; transplacently / intermediate | C, U          |
| Canine herpesvirus | Respiratory or generalized disease; death / moderate | Mucus membranes; transplacently / 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 | C, U          |
| Canine oral papilloma | Oral warts / low              | Wounded oral mucosa / indirect | C             |
| Feline panleukopenia | Fever; diarrhoea; vomition; death / moderate | Ingestion; transplacently / intermediate | F             |
| Feline leukaemia | Neoplasia; immunosuppression; death / moderate | Body fluids; faeces, bite wounds / direct | F             |
| Feline coronavirus (FIP) | Diarrhoea, peritonitis; granulomas; death / moderate | Ingestion; inhalation / intermediate | F             |
| Feline immunodeficiency |                             |                                        |                |
| Feline viral rhinotracheitis | Upper respiratory disease; rarely death / low | Mucus membranes, transplacently / 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 | C             |
| Pseudorabies | Pneumonia; cardiac or CNS disease; death / high | Ingestion; skin abrasion / intermediate | F, 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       |
| Vesicular stomatitis | Fever; oral ulcers; depression; anorexia / low | Direct contact; insect bite / indirect | F, U          |
| Encephalitis viruses | Encephalitis; fever / low | Insect bite / indirect | F, C, F, U    |
| **Bacteria** |                               |                                          |                |
| Babonic plague | Fever; vomition; large lymph nodes; death / high | Flea bite; ingestion of meat / indirect | C, F, U       |
| Pseudotuberculosis | 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 | Ingestion; ingestion / indirect | F             |
| Pasteurella | Pneumonia; haemorrhagic septicaemia / low | Normal oral inhabitant; ingestion / indirect | F             |
| Salmonella | Diarrhoea; vomition; occasionally death / low | Ingestion / indirect | F             |
| Ehrlichia | Haemorrhagia; occasionally death / moderate | Tick bite / indirect | C (not detected) |
| Coxiella | Fever; pneumonia; abortion / low | Tick bite; ingestion / indirect | C, U          |
| Other rickettsials | Fever / low | Tick bite / indirect | C, U          |
| Acholeplasma | Pneumonia / low | Ingestion / indirect | F             |
| Mycobacterium | Pneumonia; muscle wasting; death / moderate | Ingestion; wounds / intermediate | 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       |
| Trypanosoma | Lethargy; ascites; cardiac disorder / low | Insect bite / indirect | C, F          |
| Cystozoon | 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          |
| Thelidia | Dyspnoea; emaciation; weakness; sometimes death / low | Tick bite / indirect | F             |
| **Fungi** |                               |                                          |                |
| Blastomycosis | Multiple forms; pneumonia; death / moderate | Ingestion of infected soil / indirect | C             |
| Coccidioides | Pneumonia; infection; death / moderate | Ingestion 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).
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           | TS            | SF         |
| Canine parvovirus           | TSOF       | TS            | SF            |            |
| Canine parainfluenza        | S          | S             | S             |            |
| Canine coronavirus          | S          | 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              | S          | SO            |               |            |
| Leptospirosis               | TSO        | TSOMF         |               |            |
| Botulism                    | S          |               |               |            |
| Anthrax                     | TSO        |               |               |            |
| Lyme disease                | TS         |               |               |            |
| Tularemia                   | TS         |               |               |            |
| Brucellosis                 | TS         |               | TSO           |            |
| *Ehrlichia*                 | S          | T             |               |            |
| *Coxiella*                  | S          | S             | O             |            |
| Other rickettsials          | S          | S             | O             |            |
| *Mycobacter*                | OF         |               |               |            |
| **Protozoa**                |            |               |               |            |
| *Toxoplasma*                | S          | S             | S             |            |
| Sarcozystis                 | O          | O             | S             |            |
| *Hepatozoon*                | S          |               | O             |            |
| Trypanosoma                 | S          | S             |               |            |
| Babesia                     | S          |               |               |            |
| *Eimeria*                   | O          |               |               |            |
| Isospora                    | O          |               |               |            |
| *Hammondia*                 | O          |               |               |            |
| **Fungi**                   |            |               |               |            |
| Blastomycesis               | 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...
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...
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. However, although the most available data 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 blue-tongue 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 microorganisms infecting multiple taxonomic families, as well as those exhibiting high rates of direct or indirectly-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
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.
Acknowledgements

We are indebted to R. Atkinson, W. Boyce, T. Caro, J. Gittleman, D. Macdonald, W. McComb and anonymous reviewers for insightful comments on an earlier draft. N. Sokoloski assisted with the preparation of the Appendix. D.L.M. wishes to acknowledge support from the University of Idaho.

References

Alexander, K. A. & Appel, M. J. G. (1994). African wild dogs (Lycaon pictus) endangered by a canine distemper epizootic among domestic dogs near the Masai Mara National Reserve, Kenya. J. Wildl. Dis. 30: 481–485.
Alexander, K. A., Conrad, P. A., Gardner, I. A., Parish, C., Appel, M., Levy, M. G., Lerche, N. & Kat, P. (1993). Serologic survey for selected microbial pathogens in African wild dogs (Lycaon pictus) and sympatric domestic dogs (Canis familiaris) in Masai Mara, Kenya. J. Zoo Wildl. Med. 24: 140–144.
Alexander, K. A., Kat, P. W., House, J., House, C., O’Brien, S. J., Laurenson, M. K., McNutt, J. W. & Osburn, B. I. (1995). African horse sickness and African carnivores. Vet. Microbiol. 47: 133–140.
Alexander, K. A., MacLachlan, N. J., Kat, P. W., House, C., O’Brien, S. J., Lerche, N. W., Sawyer, M., Frank, L. G., Holeckamp, K., Smale, L., McNutt, J. W., Laurenson, M. K., Mills, M. G. L. & Osburn, B. I. (1994). Evidence of natural bluetongue virus infection among African carnivores. Am. J. Trop. Med. Hyg. 51: 568–576.
Anderson, R. M. (1979). Parasite pathogenicity and the depression of host population equilibria. Nature, Lond. 282: 150–152.
Anderson, R. M. & May, R. M. (1978). Regulation and stability of host–parasite population interactions. Regulatory processes. J. Anim. Ecol. 47: 219–247.
Appel, M. J., (Ed.) (1987). Virus Infections of Carnivores. York: Elsevier Science, New York.
Ballard, W. B. & Kraussman, P. R. (1997). Occurrence of rabies in wolves of Alaska. J. Wildl. Dis. 33: 242–245.
Begon, M. & Bowers, R. G. (1995). Beyond host–paradigm dynamics. In Ecology of infectious diseases in natural populations: 478–509. Grenfell, B. T. & Dobson, A. P. (Eds). Cambridge: Cambridge University Press.
Bowman, D. D. (1995). Georgis’ parasitology for veterinarians. Philadelphia, PA: W. B. Saunders Co.
Burrows, R., Hofer, H. & East, M. L. (1994). Demography, extinction and intervention in a small population: the case of the Serengeti wild dogs. Proc. Roy. Soc. Lond. ser. B 256: 281–292.
Carbyn, L. N. (1982). Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. In Wolves of the world: perspectives of behavior, ecology, and conservation: 106–116. Harrington, F. H. & Paquet, P. C. (Eds). Park Ridge, NJ: Noves.
Chapman, R. C. (1978). Rabies: decimation of a wolf pack in Arctic Alaska. Science 201: 365–367.
Choquette, L. E. P. & Kuyt, E. (1974). Serological indication of canine distemper and of infectious canine hepatitis in wolves (Canis lupus L.) in northern Canada. J. Wildl. Dis. 10: 321–324.
Cree, S., Cree, N. M., Matovelo, J. A., Mumbo, M. M. A., Batamuizi, E. K. & Cooper, J. E. (1995). The effects of anthrax on endangered wild dogs (Lycaon pictus). J. Zool., Lond. 236: 199–209.
Davis, J. W., Karstad, L. H. & Trainer, D. O. (1970). Infectious diseases of wild mammals. Ames, IA: Iowa State University Press.
Dobson, A., & May, R. M. (1986). Disease and conservation. In Conservation biology: the science of scarcity and diversity: 345–365. Soulé, M. E. (Ed.). Sunderland, MA: Sinauer and Associates.
Estes, J. A. (1996). Predators and ecosystem management. Wildl. Soc. Bull. 24: 390–396.
Evermann, J. F. (1998). Laboratory diagnosis of viral and rickettsial infections. In Infectious diseases of the dog and cat: 1–6. Greene, C. (Ed.). Philadelphia, PA: W. B. Saunders Co.
Evermann, J. F. & Eriks, I. S. (1999). Diagnostic medicine: the challenge of differentiating infection from disease and making sense for the veterinary clinician. Advan. Vet. Med. 41: 25–38.
Fowler, M. E. (Ed.) (1986). Zoo and wild animal medicine. Philadelphia, PA: W. B. Saunders Co.
Fuller, T. K. (1995). An international review of large carnivore conservation status. In Integrating people and wildlife for a sustainable future: 410–412. Bissonnette, J. A. & Krauseman, P. R. (Eds). Proceedings of the First International Wildlife Management Congress. Bethesda, MD: The Wildlife Society.
Gardner, I. A., Hietala, S. & Boyce, W. M. (1996). Validity of using serological tests for diagnosis of diseases in wild animals. Rev. Sci. Tech. Epic. 15: 323–335.
Gascogne, S. C., King, A. A., Laurenson, M. K., Borner, M., Schildger, B. & Barratt, J. (1993). Aspect of rabies infection and control in the conservation of the African wild dog (Lycaon pictus) in the Serengeti region, Tanzania. Onderst. J. Vet. Res. 60: 415–420.
Gese, E. M., Schultz, R. D., Johnson, M. R., Williams, E. S., Crabtree, R. L. & Ruff, R. L. (1997). Serological survey for diseases in free-ranging coyotes (Canis latrans) in Yellowstone National Park, Wyoming. J. Wildl. Dis. 33: 47–56.
Gese, E. M., Schultz, R. D., Rongstad, O. J. & Anderson, D. E. (1991). Prevalence of antibodies against canine parvovirus and canine distemper virus in wild coyotes in southeastern Colorado. J. Wildl. Dis. 27: 320–323.
Groombridge, B. (Ed.) (1994). IUCN red list of threatened animals. Gland, Switzerland and Cambridge, United Kingdom: IUCN.
Guo, W., Evermann, J. F., Foreyt, W. J., Knowlton, F. F. & Windberg, L. A. (1986). Canine distemper virus in coyotes: a serologic survey. J. Am. Vet. Med. Assoc. 189: 1099–1100.
Heesterbeek, J. A. P. & Roberts, M. G. (1995). Mathematical models for micro-parasites of wildlife. In Ecology of infectious diseases in natural populations: 90–122. Grenfell, B. T. & Dobson, A. P. (Eds). Cambridge: Cambridge University Press.
Holtzman, S., Conroy, M. J. & Davidson, W. R. (1992). Diseases, parasites and survival of coyotes in south-central Georgia. J. Wildl. Dis. 28: 572–580.
Johnson, M. R., Boyd, D. K. & Pletscher, D. H. (1994). Serologic investigations of canine parvovirus and canine distemper in relation to wolf (Canis lupus) pup mortalities. J. Wildl. Dis. 30: 270–273.
Kat, F. W., Alexander, K. A., Smith, J. S. & Munson, L. (1995). Rabies and African wild dogs in Kenya. Phil. Trans. Roy. Soc. Lond. ser. B 262: 229–233.
Lloyd, S. (1995). Environmental influences on host immunity. In Ecology of infectious diseases in natural populations: 327–361. Grenfell, B. T. & Dobson, A. P. (Eds). Cambridge: Cambridge University Press.
Lyles, A. M. & Dobson, A. P. (1993). Infectious disease and intensive management: population dynamics, threatened hosts, and their parasites. J. Zoo Wildl. Med. 24: 315–326.
Macdonald, D. W. (1993). Rabies and wildlife. A conservation problem? Onderst. J. Vet. Res. 60: 351–355.
Macdonald, D. W. (1996). Dangerous liaisons and disease. Nature, Lond. 379: 400–401.
May, R. M. (1988). Conservation and disease. Conserv. Biol. 2: 28–30.
May, R. M. & Anderson, R. M. (1978). Regulation and stability of host–parasite population interactions. II. Destabilizing processes. J. Anim. Ecol. 47: 249–267.
McCallum, H. & Dobson, A. (1995). Detecting disease and parasite threats to endangered species and ecosystems. *Trends Ecol. Evol.* **10**: 190–194.

Mech, L. D. & Goyal, S. M. (1993). Canine parvovirus effect on wolf population change and pup survival. *J. Wildl. Dis.* **29**: 330–333.

Mills, L. S., Soulé, M. E. & Doak, D. F. (1993). The keystone species concept in ecology and conservation. *BioScience* **43**: 219–224.

Minchella, D. J. & Scott, M. E. (1991). Parasitism: a cryptic determinant of animal community structure. *Trends Ecol. Evol.* **6**: 250–254.

Murray, D. L., Cary, J. R. & Keith, L. B. (1997). Interactive effects of sublethal parasitism and nutritional status on snowshoe hare vulnerability to predation. *J. Anim. Ecol.* **66**: 250–264.

Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T. & Paquet, P. C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. *Conserv. Biol.* **10**: 949–963.

O’Brien, S. J. & Evermann, J. F. (1988). Interactive influence of infectious disease and genetic diversity in natural populations. *Trends Ecol. Evol.* **3**: 254–259.

Paquet, P. C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. *Conserv. Biol.* **10**: 949–963.

Ulrey, D. E. (1993). Nutrition and predisposition to infectious disease. *J. Zoo Wildl. Med.* **24**: 304–314.

Van Heerden, J., Mills, M. G. L., Van Vuuren, M. J., Kelly, P. J. & Dreyer, M. J. (1995). An investigation into the health status and diseases of wild dogs (*Lycaon pictus*) in the Kruger National Park. *J. South Afr. Vet. Assoc.* **66**: 18–27.

Weiler, G. J., Garner, G. W. & Ritter, D. G. (1995). Occurrence of rabies in a wolf population in northeastern Alaska. *J. Wildl. Dis.* **31**: 79–82.

Zarnke, R. L. & Ballard, W. B. (1987). Serologic survey for selected microbial pathogens of wolves in Alaska, 1975–1982. *J. Wildl. Dis.* **23**: 77–85.

**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.

**CANIDAE**

Alexander, K. A. & Appel, M. J. G. (1994). African wild dogs (*Lycaon pictus*) endangered by a canine distemper epizootic among domestic dogs near the Masai Mara National Reserve, Kenya. *J. Wildl. Dis.* **30**: 481–485.

Alexander, K. A., Conrad, P. A., Gardner, I. A., Parish, C., Appel, M., Levy, M. G., Lerche, N. & Kat, P. (1993). Serologic survey for selected microbial pathogens in African wild dogs (*Lycaon pictus*) and sympatric domestic dogs (*Canis familiaris*) in Masai Mara, Kenya. *J. Zoo Wildl. Med.* **24**: 140–144.

Alexander, K. A., Kat, P. W., House, J., House, C., O’Brien, S. J., Laursen, M. K., McNutt, J. W. & Osburn, B. I. (1995). African horse sickness and African carnivores. *Vet. Microbiol.* **47**: 133–140.

Alexander, K. A., Kat, P. W., Munson, L. A., Kalake, A. & Appel, M. J. (1996). Canine distemper-related mortality among wild dogs (*Lycaon pictus*) in Chobe National Park, Botswana. *J. Zoo Wildl. Med.* **27**: 426–427.

Alexander, K. A., MacLachlan, N. J., Kat, P. W., House, C., O’Brien, S. J., Lerche, N. W., Sawyer, M., Frank, L. G., Holekamp, K., Smale, L., McNutt, J. W., Laursen, M. K., Mills, M. G. L. & Osburn, B. (1994). Evidence of natural bluetongue virus infection among African carnivores. *Am. J. Trop. Hyg.* **51**: 568–576.

Alexander, K. A., Smith, J. S., Macharia, M. J. & King, A. A. (1993). Rabies in the Masai Mara, Kenya: preliminary report. *Onderst. J. Vet. Res.* **60**: 411–414.

Arther, R. G. & Post, G. (1977). Coccidia of coyotes in eastern Colorado. *J. Wildl. Dis.* **13**: 97–100.

Ballard, W. B. & Krausman, P. R. (1997). Occurrence of rabies in wolves of Alaska. *J. Wildl. Dis.* **33**: 242–245.

Broughton, E., Graesser, F. E., Carbyn, L. N. & Choquette, L. P. (1992). World prevalence of lentivirus infection in wild feline species: epidemiologic and phylogenetic aspects. *Am. J. Trop. Med.* **66**: 400–407.

Bush, M., Martenson, J. S. & O’Brien, S. J. (1992). Worldwide epidemiology: a problem oriented approach: *Infectious Diseases in Large Carnivores*. 2nd ed. CRC Press, Boca Raton, FL.

Burrows, R. (1992). Rabies in wild dogs. *Nature, Lond.* **359**: 277.

Burgess, E. C. & Windberg, L. A. (1989). *Borrelia* sp. infection in coyotes, black-tailed jack rabbits and desert cottontails in southern Texas. *J. Wildl. Dis.* **25**: 47–51.

Carbyn, L. N. (1982). Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. In *Wolves of the world: perspectives of behavior, ecology, and conservation*: 106–116.

Carbyn, L. N. (1982). Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. In *Wolves of the world: perspectives of behavior, ecology, and conservation*: 106–116.

Carpenter, M., O’Brien, S. J., Pospischil, A., Hofmann-Lehmann, R., Lutz, H., Mwamengele, G. L. M., Gmasa, M. N., Machange, G. A., Summers, B. A. & Appel, M. J. G. (1996). A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature, Lond.* **379**: 441–445.

Covich, A. P. (1989). Oral papillomatosis in the coyote in western Canada. *J. Wildl. Dis.* **25**: 57–63.

O’Brien, S. J. & Evermann, J. F. (1988). Interactive influence of infectious disease and genetic diversity in natural populations. *Trends Ecol. Evol.* **3**: 254–259.

Alexander, K. A., Smith, J. S., Macharia, M. J. & King, A. A. (1993). Rabies in the Masai Mara, Kenya: preliminary report. *Onderst. J. Vet. Res.* **60**: 411–414.

Arther, R. G. & Post, G. (1977). Coccidia of coyotes in eastern Colorado. *J. Wildl. Dis.* **13**: 97–100.

Ballard, W. B. & Krausman, P. R. (1997). Occurrence of rabies in wolves of Alaska. *J. Wildl. Dis.* **33**: 242–245.

Broughton, E., Graesser, F. E., Carbyn, L. N. & Choquette, L. P. (1992). Oral papillomatosis in the coyote in western Canada. *J. Wildl. Dis.* **25**: 47–51.

Burrows, R. (1992). Rabies in wild dogs. *Nature, Lond.* **359**: 277.

Carbyn, L. N. (1982). Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. In *Wolves of the world: perspectives of behavior, ecology, and conservation*: 106–116.

Harrington, F. H. & Paquet, P. C. (Eds). Park Ridge, NJ: Noyes.

Chapman, R. C. (1978). Rabies: decimation of a wolf pack in Arctic Alaska. *Science* **201**: 365–367.
Choquette, L. P. E. & Kuyt, E. (1974). Serological indication of canine distemper and infectious canine hepatitis in wolves (Canis lupus L.) in northern Canada. J. Wildl. Dis. 10: 321–324. Creel, S. (1992). Cause of wild dog deaths. Nature, Lond. 360: 633.

Creel, S., Creel, N. M., Matovelo, J. A., Mtambo, M. M. A., Batamuzi, E. K. & Cooper, J. E. (1995). The effects of anthrax on endangered African wild dogs (Lycaon pictus). J. Zool., Lond. 236: 199–209.

Davis, D. S., Boeer, W. J., Mims, J. P., Heck, F. C. & Adams, L. G. (1979). Brucella abortus in coyotes. I. A serologic and bacteriologic survey in eastern Texas. J. Wildl. Dis. 15: 367–372. Davis, D. S., Robinson, R. M. & Craig, T. M. (1978). Naturally occurring hepatocoonzosis in a coyote. J. Wildl. Dis. 14: 244–246. Drewek, J., Noon, T. H., Trautman, R. J. & Bicknell, E. J. (1981). Serologic evidence of leptospirosis in a southern Arizona coyote population. J. Wildl. Dis. 17: 33–37.

Dubey, J. P., Fayer, R. & Seesee, F. M. (1978). Sarcocystis in feces of coyotes from Montana: prevalence and experimental transmission to sheep and cattle. J. Anim. Vet. Med. Assoc. 173: 1167–1170.

Emnett, C. W. (1986). Prevalence of Sarcocystis in wolves and white-tailed deer in northeastern Minnesota. J. Wildl. Dis. 22: 193–195.

Enright, J. B., Behymer, D. E., Franti, C. E., Dutzon, V. J., Longhurst, W. M., Wright, M. E. & Goggin, J. E. (1971). The behavior of Q fever rickettsiae isolated from wild animals in northern California. J. Wildl. Dis. 7: 83–90.

Forey, J. W. & Evermann, J. F. (1985). Serologic survey of canine coronavirus in wild coyotes in the western United States, 1972–1982. J. Wildl. Dis. 21: 428–430.

Gascoyne, S. C., King, A. A., Laurenson, M. K., Borner, M., Schildger, B. & Barrat, J. (1993). Aspects of rabies infection and control in the conservation of the African wild dog (Lycaon pictus) in the Serengeti region, Tanzania. Onderst. J. Vet. Res. 60: 415–420.

Gascoyne, S. C., Laurenson, M. K., Lelo, S. & Borner, M. (1993). Rabies in African wild dogs (Lycaon pictus) in the Serengeti region, Tanzania. J. Wildl. Dis. 29: 396–402.

Gese, E. M., Schultz, R. D., Johnson, M. R., Williams, E. S., Crabtree, R. L. & Ruff, R. L. (1997). Serological survey for diseases in free-ranging coyotes (Canis latrans) in Yellowstone National Park, Wyoming. J. Wildl. Dis. 33: 47–56.

Gese, E. M., Schultz, R. D., Rongstad, O. J. & Andersen, D. E. (1991). Prevalence of antibodies against canine parvovirus and canine distemper virus in wild coyotes in southeastern Colorado. J. Wildl. Dis. 27: 320–323.

Grögl, M., Kuhn, R. E., Davis, D. S. & Green, G. E. (1984). Antibodies to Trypanosoma cruzi in coyotes in Texas. J. Parasitol. 70: 189–191.

Guo, W., Evermann, J. F., Forey, W. J., Knowlton, F. F. & Winberg, L. A. (1986). Canine distemper virus in coyotes: A serologic survey. Am. J. Vet. Med. Assoc. 9: 1099–1100.

Hoff, G. L., Yuill, T. M., Iversen, J. O. & Hanson, R. P. (1970). Selected microbial agents in snowshoe hares and other vertebrates of Alberta. J. Wildl. Dis. 6: 472–478.

Holzman, S. J., Conroy, M. J. & Davidson, W. R. (1992). Diseases, parasites and survival of coyotes in south-central Georgia. J. Wildl. Dis. 28: 572–580.

Iwao, O., Sakaguchi, G., Riemann, H., Behymer, D. & Harvell, B. (1979). Antibodies to Clostridium botulinum toxins in free-living birds and mammals. J. Wildl. Dis. 15: 3–9.

Johnson, M. R., Boyd, D. K. & Pletscher, D. H. (1994). Serologic investigations of canine parvovirus and canine distemper in relation to wolf (Canis lupus) pup mortalities. J. Wildl. Dis. 30: 270–273.

Johnson, A. M., Phillips, P. & Jenkins, D. (1990). Prevalence of Toxoplasma gondii antibodies in dingoes. J. Wildl. Dis. 26: 383–386.
in wild coyotes from Texas, Utah, and Idaho (1972 to 1983). Am. J. Vet. Med. Assoc. 185: 1283–1287.

Trainer, D. O., Knowlton, F. F. & Karstad, L. (1968). Oral pili-

Blouin, E. F., Kocan, A. A., Glenn, B. L. & Kocan, K.M. (1984). FELIDAE

Brown, E. W., Yuhki, N., Packer, C. & O’Brien, S. J. (1987). Fatal neonatal toxoplasmosis in a bobcat (Lynx rufus). J. Wildl. Dis. 23: 324–327.

Dubey, J. P. & Swangamoi, O. (1994). Microbesnoitia leoni Swangamoi, 1989, from the African lion (Panthera leo) re-

Dubey, J. P. (1982). Sarcocystis and other coccidia in foxes and other wild carnivores from Montana. J. Am. Vet. Med. Assoc. 181: 1270–1271.

Evermann, J. F., Foreyt, W. J., Hall, B. & McKeirnan, A. J. (1997). Occurrence of puma lentivirus infection in cougars from Washington. J. Wildl. Dis. 33: 316–320.

Glass, C. M., McLean, R. G., Katz, J. B., Maehr, D. S., Crop, C. B., Kirk, L. J., McKeirnan, A. J. & Evermann, J. F. (1994). Isolation of pseudorabies (Aujeszky’s disease) virus from a Florida panther. J. Wildl. Dis. 30: 180–184.

Glen, B. L., Kocan, A. A. & Blouin, E. F. (1983). Cytauxzoonosis in bobcats. Am. J. Vet. Med. Assoc. 183: 1155–1158.

Greiner, E. C., Roelke, M. E., Atkinson, C. T., Dubey, J. P. & Wright, S. D. (1989). Sarcocystis sp. in muscles of free-ranging Florida panthers and cougars (Felis concolor). J. Wildl. Dis. 25: 623–628.

Heeney, J. L., Evermann, J. F., McKeirnan, A. J., Marker-Kraus, L., Roelke, M. E., Bush, M., Wildt, D. E., Meltzer, D. G., Colly, L., Lukas, J., Manton, V. J., Caro, T. & O’Brien, S. J. (1990). Prevalence and implications of feline coronavirus infections of captive and free-ranging cheetahs (Acinonyx jubatus). J. Virol. 64: 1964–1972.

Heidt, A. A., Rucker, R. A., Kennedy, M. L. & Baeyens, M. E. (1988). Hematology, intestinal parasites, and selected disease 

Anderson, A. J., Greiner, E. C., Atkinson, C. T. & Roelke, M. E. (1992). Sarcocysts in the Florida bobcat (Felis rufus floridanus). J. Wildl. Dis. 28: 116–120.

Averbick, G. A., Bjork, K. E., Packer, C. & Herbst, L. (1990). Prevalence of hematozoans in lions (Panthera leo) and cheetahs (Acinonyx jubatus) in Serengeti National Park and Ngorongoro Crater, Tanzania. J. Wildl. Dis. 26: 392–394.

Barnard, B. J. H. (1979). The role played by wildlife in the epi-

Zarnke, R. L. & Yull, T. M. (1981). Serologic survey for selected microbial agents in mammals from Alberta, 1976. J. Wildl. Dis. 17: 453–461.

FELIDAE

Aguire, A. A., McLean, R. G., Cook, R. S. & Quan, T. J. (1992). Serologic survey for selected arboviruses and other potential pathogens in wildlife from Mexico. J. Wildl. Dis. 28: 435–442.

Alexander, K. A., Kat, P. W., House, J., House, C., O’Brien, S. J., Laurenson, M. K., McNett, J. W. & Osburn, B. I. (1995). African horse sickness and African carnivores. Vet. Microbiol. 47: 133–140.

Alexander, K. A., MacLachlan, N. J., Kat, P. W., House, C., O’Brien, S. J., Lerche, N. W., Sawyer, M., Frank, L. G., Holekamp, K., Smale, L., McNett, J. W., Laurenson, M. K., Mills, M. G. L. & Osburn, B. (1994). Evidence of natural blue-

tongue virus infection among African carnivores. Am. J. Trop. Hyg. 51: 568–576.

Aguire, A. A., McLean, R. G., Cook, R. S. & Quan, T. J. (1992). Serologic survey for selected arboviruses and other potential pathogens in wildlife from Mexico. J. Wildl. Dis. 28: 435–442.

Alexander, K. A., Kat, P. W., House, J., House, C., O’Brien, S. J., Laurenson, M. K., McNett, J. W. & Osburn, B. I. (1995). African horse sickness and African carnivores. Vet. Microbiol. 47: 133–140.

Alexander, K. A., MacLachlan, N. J., Kat, P. W., House, C., O’Brien, S. J., Lerche, N. W., Sawyer, M., Frank, L. G., Holekamp, K., Smale, L., McNett, J. W., Laurenson, M. K., Mills, M. G. L. & Osburn, B. (1994). Evidence of natural blue-

tongue virus infection among African carnivores. Am. J. Trop. Hyg. 51: 568–576.

Anderson, A. J., Greiner, E. C., Atkinson, C. T. & Roelke, M. E. (1992). Sarcocysts in the Florida bobcat (Felis rufus floridanus). J. Wildl. Dis. 28: 116–120.

Averbick, G. A., Bjork, K. E., Packer, C. & Herbst, L. (1990). Prevalence of hematozoans in lions (Panthera leo) and cheetahs (Acinonyx jubatus) in Serengeti National Park and Ngorongoro Crater, Tanzania. J. Wildl. Dis. 26: 392–394.

Barnard, B. J. H. (1979). The role played by wildlife in the epi-

Zarnke, R. L. & Yull, T. M. (1981). Serologic survey for selected microbial agents in mammals from Alberta, 1976. J. Wildl. Dis. 17: 453–461.

FELIDAE

Aguire, A. A., McLean, R. G., Cook, R. S. & Quan, T. J. (1992). Serologic survey for selected arboviruses and other potential pathogens in wildlife from Mexico. J. Wildl. Dis. 28: 435–442.

Alexander, K. A., Kat, P. W., House, J., House, C., O’Brien, S. J., Laurenson, M. K., McNett, J. W. & Osburn, B. I. (1995). African horse sickness and African carnivores. Vet. Microbiol. 47: 133–140.

Alexander, K. A., MacLachlan, N. J., Kat, P. W., House, C., O’Brien, S. J., Lerche, N. W., Sawyer, M., Frank, L. G., Holekamp, K., Smale, L., McNett, J. W., Laurenson, M. K., Mills, M. G. L. & Osburn, B. (1994). Evidence of natural blue-

tongue virus infection among African carnivores. Am. J. Trop. Hyg. 51: 568–576.

Anderson, A. J., Greiner, E. C., Atkinson, C. T. & Roelke, M. E. (1992). Sarcocysts in the Florida bobcat (Felis rufus floridanus). J. Wildl. Dis. 28: 116–120.

Averbick, G. A., Bjork, K. E., Packer, C. & Herbst, L. (1990). Prevalence of hematozoans in lions (Panthera leo) and cheetahs (Acinonyx jubatus) in Serengeti National Park and Ngorongoro Crater, Tanzania. J. Wildl. Dis. 26: 392–394.

Barnard, B. J. H. (1979). The role played by wildlife in the epi-

Zarnke, R. L. & Yull, T. M. (1981). Serologic survey for selected microbial agents in mammals from Alberta, 1976. J. Wildl. Dis. 17: 453–461.
Neiland, K. A. (1975). Further observations on rangiferine brucellosis in Alaskan carnivores. *J. Wildl. Dis.* 11: 45–53.

Pirtle, E. C., Roelke, M. E. & Brady, J. (1986). Antibodies against pseudorabies virus in the serum of a Florida black bear cub. *Am. J. Vet. Med. Assoc.* 189: 1164.

Prestrud, P., Krogsrud, J. & Gjertz, I. (1992). The occurrence of rabies in the Svalbard Islands of Norway. *J. Wildl. Dis.* 28: 57–63.

Pursell, A. R., Stuart, B. P. & Styer, E. (1983). Isolation of an adenovirus from black bear cubs. *J. Wildl. Dis.* 19: 269–271.

Quinn, P. J., Ramsden, R. O. & Johnston, D. H. (1976). Toxoplasmosis: a serological survey in Ontario wildlife. *J. Wildl. Dis.* 12: 504–510.

Röttcher, D. & Sawchuk, A. M. (1978). Wildlife rabies in Zambia. *J. Wildl. Dis.* 14: 513–517.

Ruppanner, R., Jessup, D. A., Ohishi, I., Behymer, D. E. & Franti, C. E. (1982). Serologic survey for certain zoonotic diseases in black bears in California. *Am. J. Vet. Med. Assoc.* 181: 1288–1291.

Taylor, M., Elkin, B. & Bradley, M. (1991). Observation of a polar bear with rabies. *J. Wildl. Dis.* 27: 337–339.

Zarnke, R. L. (1983). Serologic survey for selected microbial pathogens in Alaskan wildlife. *J. Wildl. Dis.* 19: 324–329.

Zarnke, R. L., Calisher, C. H. & Kerschner, J. (1983). Serologic evidence of arbovirus infections in humans and wild animals in Alaska. *J. Wildl. Dis.* 19: 175–179.

Zarnke, R. L., Dubey, J. P., Kwok, O. C. H. & Ver Hoef, J. M. (1997). Serologic survey for *Toxoplasma gondii* in grizzly bears from Alaska. *J. Wildl. Dis.* 33: 267–270.

Zarnke, R. L. & Evans, M. B. (1989). Serologic survey for infectious canine hepatitis virus in grizzly bears (*Ursus arctos*) from Alaska, 1973 to 1987. *J. Wildl. Dis.* 25: 568–573.

Zarnke, R. L. & Yuill, T. M. (1981). Serologic survey for selected microbial agents in mammals from Alberta, 1976. *J. Wildl. Dis.* 17: 453–461.