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BLACK-BACKED JACKAL EXPOSURE TO RABIES VIRUS, CANINE DISTEMPER VIRUS, AND *BACILLUS ANTHRACIS* IN ETOSHA NATIONAL PARK, NAMIBIA

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ABSTRACT: Canine distemper virus (CDV) and rabies virus (RABV) occur worldwide in wild carnivore and domestic dog populations and pose threats to wildlife conservation and public health. In Etosha National Park (ENP), Namibia, anthrax is endemic and generates carcasses frequently fed on by an unusually dense population of black-backed jackals (*Canis mesomelas*). Using serology, phylogenetic analyses (on samples obtained from February 2009–July 2010), and historical mortality records (1975–2011), we assessed jackal exposure to *Bacillus anthracis* (BA; the causal bacterial agent of anthrax), CDV, and RABV. Prevalence of antibodies against BA (95%, $n=86$) and CDV (71%, $n=80$) was relatively high, while that of antibodies against RABV was low (9%, $n=81$). Exposure to BA increased significantly with age, and all animals >6 mo old were antibody-positive. As with BA, prevalence of antibodies against CDV increased significantly with age, with similar age-specific trends during both years of the study. No significant effect of age was found on the prevalence of antibodies against RABV. Three of the seven animals with antibodies against RABV were monitored for more than 1 yr after sampling and showed no signs of active infection. Mortality records revealed that rabid animals are destroyed nearly every year inside the ENP tourist camps. Phylogenetic analyses demonstrated that jackal RABV in ENP is part of the same transmission cycle as other dog-jackal RABV cycles in Namibia.

Key words: Anthrax, *Bacillus anthracis*, black-backed jackal, canine distemper virus, *Canis mesomelas*, infectious disease, rabies virus.

INTRODUCTION

Canine distemper virus (CDV) and rabies virus (RABV) infect wild carnivore and domestic dog populations globally (Harder and Osterhaus, 1997; Rupprecht et al., 2002). As multihost pathogens, their dynamics are particularly complicated by the need to understand both intraspecific and interspecific transmission (Dobson, 2004). Moreover, because they are multihost pathogens, both CDV and RABV threaten endangered species conservation (Cleaveland et al., 2007), with the latter being a disease of major public health concern (Knobel et al., 2005). We conducted a serosurvey of CDV, RABV, and *Bacillus anthracis* (BA; the causal bacterial agent of anthrax) in one potentially epidemiologically important species, the black-backed jackal (*Canis mesomelas*), in Etosha National Park (ENP), Namibia.

The black-backed jackal (hereafter jackal) is a common canid species found across southern and eastern Africa (MacDonald et al., 2004). As opportunistic generalists, jackals are found in a variety of habitat types but prefer open grassland (Loveridge and MacDonald, 2003). Relatively high density, widespread geographic range, and long dispersal distances make jackals an epidemiologically important species for a variety of diseases of public health, domestic animal, or conservation

concern (Loveridge and MacDonald, 2001). Yet the role of jackals in the transmission of multispecies carnivore pathogens remains unclear, particularly with respect to whether they independently facilitate persistence of particular pathogens as well as the degree to which they are responsible for transmission of disease to wildlife, livestock, and humans.

Using mathematical models, Rhodes et al. (1998) argued that jackals (*C. mesomelas* and *C. adustus*) occur at densities too low to maintain (facilitate indefinite local transmission) RABV without repeated introduction of the pathogen from domestic dogs. Bingham (2005) responded that jackals are as capable as domestic dogs of facilitating RABV persistence (facilitating indefinite transmission in a larger metapopulation) and that the above conclusion resulted from ignoring how spatial scale and metapopulation structure affect pathogen dynamics. In addition, recent molecular analyses demonstrated that RABV cannot only persist over short time periods, but that it can persist in jackal populations in northern South Africa independent of spillover from domestic dogs (Zulu et al., 2009). Given such evidence and the proposed elimination of canine rabies in Africa via vaccination of domestic dogs (Hampson et al., 2009), it is especially important to further understand the role jackals play in RABV dynamics.

Jackals may also play an important role in CDV dynamics. Jackals appear to have spread CDV between domestic dog populations during an outbreak along the Namibian coast (Gowtage-Sequeira et al., 2009). Craft et al. (2009) suggested that during the 1994 CDV epidemic in the Serengeti lions, the virus must have been repeatedly introduced into the lion population from sympatric carnivores such as jackals and hyenas that may have been infected by domestic dogs. As jackals generally occur at greater densities than threatened carnivore species and are also found in human altered habitat, they may frequently provide an epidemiologic link between threatened wildlife and domestic dogs.

Transmission dynamics vary with density, movement, social contact networks, and demography. For directly transmitted pathogens, such as RABV and CDV, infectious contact rates between hosts are often considered to be density dependent, leading to the theoretical notion of a critical density threshold below which a pathogen goes extinct (Bartlett, 1957). However, infectious contact rates are rarely determined by density alone. Behavioral or ecologic processes can also play important roles in determining infectious contact network structure and subsequently transmission dynamics (Keeling, 2005). As jackals easily adapt to different environments and resource types (MacDonald et al., 2004), their transmission dynamics undoubtedly vary with density, movement, and social contact networks. We assessed jackal exposure to RABV and CDV in an unusually dense and mobile population of jackals that frequently scavenges on carrion produced by anthrax outbreaks in herbivores.

Anthrax, an environmentally transmitted and highly fatal disease of mammals, is seasonally endemic in the plains ungulates and elephants of ENP (Lindeque and Turnbull, 1994). Avian and mammalian scavenger species feed upon disease-generated carcasses. Jackals are the most frequently observed mammalian scavenger at anthrax-confirmed carcasses (Bellan, unpubl.). Carnivores are generally less susceptible than herbivores and frequently scavenge on BA-contaminated carrion without apparent morbidity or mortality (Hugh-Jones and de Vos, 2002). Yet the timescale on which animals develop and lose immunity to BA is unknown. Depending on the duration of immunity, scavengers may be useful biosentinels for anthrax surveillance, particularly in wildlife systems where carcasses are rarely detected. Serologic indicators of scavenger exposure to *B. anthracis* can be used to assess trends in anthrax incidence (Lembo

et al., 2011). Although anthrax does not appear to have any direct impacts on jackal health, there may be indirect impacts. In the Okaukuejo plains of ENP, the jackal population appears unusually dense with 85% isopleth home ranges of family groups (containing a mated pair, 2–5 pups, and sometimes subadult helpers) averaging 3.3 km^2 (SD=2.7) and aggregations at carcasses frequently number >20 and sometimes as many as >60 (Bellan, unpubl. data). The apparently high density of jackals in ENP may be due to the seasonal pulse in carrion available because of anthrax outbreaks (Getz, 2011). Large aggregations of jackals at carcasses may also facilitate transmission and spread of RABV or CDV, especially when jackals travel long distances to carcasses.

Estimating incidence of infection, disease, and mortality is difficult in wildlife because they are elusive and difficult to sample. When sampling blood from animals is feasible, the presence of antibodies to a pathogen can yield insight about its epidemiologic dynamics. For instance, consistent detection of antibodies in all age groups, especially in individuals <1 yr, over several years suggests that a pathogen may persist in a population or that frequent reintroductions occur from adjacent populations (Haydon et al., 2002). By contrast, in populations experiencing a recent epidemic, all animals born after the epidemic when transmission has ceased should be antibody-negative (unless they are young enough [<12 wk] to still have maternal antibodies). Duration of antibody responses must be considered when interpreting serologic data. While data on duration of naturally acquired immunity in wildlife are rare, data on duration of naturally acquired or vaccine-induced immunity in domestic dogs suggest that serologic responses to RABV and CDV frequently last multiple years (Coyne et al., 2001). We used antibody assays to assess jackal exposure to RABV, CDV, and BA in ENP. We compared assay results with concurrent mortality data and conducted a phylogenetic analysis of RABV isolates.

MATERIALS AND METHODS

Study area

This study was undertaken in ENP, a 22,915-km^2 fenced national park in northern Namibia between 18°30′S–19°30′S and 14°15′E–17°10′E. The vegetation is classified as arid savanna (Huntley, 1982) and exhibits a single wet and dry season each year with rain falling mainly between November and April (Engert, 1997). The park contains a 4,760 km^2 salt pan, a dominant landscape feature remnant of a palaeolake (Hipondoka et al., 2006). Mopane (*Colophospermum mopane*) shrubveld or treeveld cover much of ENP, but extensive sweet grassveld (the Okaukuejo plains) lie around the Etosha pan (Le Roux et al., 1988). Boreholes and artesian or contact springs supply the only perennial water (Auer, 1997).

This study was conducted on the Okaukuejo plains (Fig. 1) that feed migratory herds of plains ungulates. Jackals are opportunistic, monogamous, territorial carnivores whose young of both sexes often aid in rearing the next cohort of pups (their siblings) prior to dispersing the following year (Moehlman, 1979). On the Okaukuejo plains, jackals are abundant and feed on insects, fruit, and human food waste (near tourist camps). They also hunt small mammals and ungulates, and scavenge on lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*) kills as well as on disease-generated carcasses, many of which are generated by anthrax infection (Lindeque and Turnbull, 1994). Anthrax carcasses are generally found during the end of the wet season, in the preferred wet-season habitat of plains ungulates (northwest of the Okaukuejo tourist camp: Leeubron study area); during the dry seasons, the ungulate herds spend more time southeast of Okaukuejo (Gemsbokvlakte study area), and anthrax carcasses are found less frequently in this location and at this time (Fig. 1).

Jackal capture and sampling

Serum samples were obtained between January 2009 and July 2010 from 80 live-trapped jackals, five destroyed rabid jackals, and one jackal that was euthanized after a motor vehicle collision. All trapped jackals were captured within the two study areas defined in Figure 1 except for two animals:

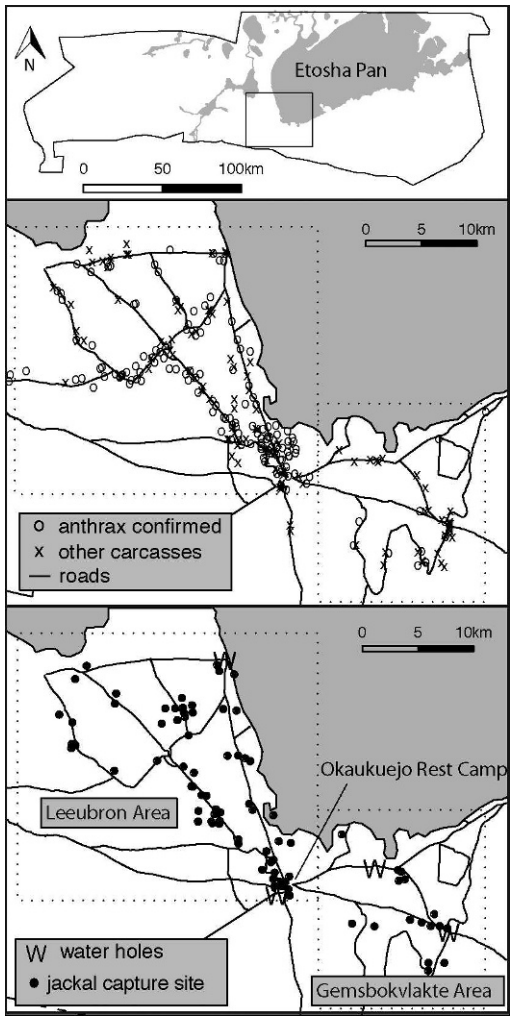

FIGURE 1. Top panel displays map of Etosha National Park, Namibia, boundaries with rectangle displaying the Okaukuejo plains where the research was conducted. Middle panel shows distribution of plains ungulate carcasses observed during opportunistic road-based surveillance over the duration of the study (January 2009–July 2010). Bottom panel shows distribution of captured black-backed jackals (*Canis mesomelas*). Dotted boxes show the division of the region into the Leeubron and Gemsbokvlatke study areas based on anthrax carcass distribution.

one captured 12 km west of the Leeubron study area and one captured 115 km east on the eastern edge of the park. All captured animals were unique except for CM02 (three captures) and CM26 (two captures). Twenty-two jackals were fitted with collars recording locations via GPS (global positioning system; African Wildlife Tracking, Pretoria, Republic of South Africa) hourly for 1–2 yr. All animals were captured and released safely under animal handling protocol ACUC R217-0509B (University of California, Berkeley).

Captured jackals were assigned to one of five age groups (<1, 1–2, 2–3, 3–4, >4 yr old) based on incisor wear (Lombaard, 1971). Ages of animals with missing teeth were considered unknown due to less predictable tooth wear. Jackals breed synchronously, with pups first emerging from dens 8 wk after parturition (Bingham and Purchase, 2002). In ENP pups are first sighted during late November and early December. Thus, we estimated approximate age in months by assuming all jackals were born in October. Animals categorized in the >4 yr age class were assumed to be 4–5 yr old when estimating age in months. Sample year was divided into jackal reproductive seasons with sample years hereafter referred to as 2008 and 2009, corresponding to October 2008–September 2009 and October 2009–September 2010, respectively. Not all serum samples were tested for all agents because of poor quality or insufficient quantity.

Serologic assays

Assessment of exposure to *B. anthracis* was performed using an enzyme-linked immunosorbent assay (ELISA) to measure antiprotective antigen (PA) antibody titers and was adapted from previous studies (Turnbull et al., 2004). Wild-type PA was provided by Bryan Krantz (University of California, Berkeley, California, USA) at a concentration of 8.5 mg PA/ml and used at a volume of 0.375 µl per ELISA plate well. Serial twofold dilutions, from 1:32 to 1:32,769, were made in duplicate for all samples. Goat-anti-dog IgG-heavy and light chain horseradish peroxidase conjugate (Bethyl Laboratories, Montgomery, Texas, USA) was used as the secondary antibody. Well optical density was read at 450 nm on a SpectraMax M2 Microplate Reader using SoftMax Pro software v5.3 (Molecular Devices, Sunnyvale, California, USA).

We obtained 20 serum samples to use as negative controls from jackals inhabiting the Laikipia region of Kenya (Prager, 2011). The Laikipia jackal samples were established as negative controls by first analyzing them individually using the above ELISA procedure. After determining that none of the samples had significant anti-PA titers, they were categorized as negative controls and were pooled equally into a single mixed negative control. Endpoint titers were defined as the last titer before a sample's mean optical

density (of duplicate serial dilutions) fell below that of the pooled negative control's mean optical density (of duplicate serial dilutions).

To assess exposure to CDV, we performed a serum-virus neutralization test (SN; Appel and Robson, 1973). Results were analyzed with cutoff titers of both ≥1:10 and ≥1:20. Two samples from ENP spotted hyenas were made available by collaborators and also tested.

Levels of neutralization activity to RABV in the serum samples were assessed by the standard fluorescent antibody virus neutralization test (FAVN; Cliquet et al., 1998).

Rabies virus phylogenetic analysis

Total viral RNA was extracted from approximately 100 μg of original brain tissues from destroyed rabid animals, and the partial N region of each viral isolate was amplified as described by Sabeta et al. (2007).

Mortality data

Since 1975 the Etosha Ecological Institute and visiting researchers have routinely recorded opportunistically observed mortalities. Brain samples from suspected rabid animals and fresh carnivore carcasses were routinely submitted to the Central Veterinary Laboratory for rabies analyses using the direct fluorescent antibody test or histopathology (Dean and Abelseth, 1973; Tierkel, 1973).

Statistical analyses

Generalized linear models (McCulloch and Searle, 2001) were used to examine the effects of age, study area, and sample year on the three assay outcomes. All statistical analyses were conducted using R (R Development Core Team, 2010). For the RABV and CDV test results, we fit binary outcomes (positive or negative) with logistic regression. All CDV SN models were performed with positive titer cutoffs of both ≥1:10 and ≥1:20. Because nearly all jackals had detectable antibodies using the anti-PA ELISA, we modeled endpoint titer as an ordered multinomial response variable using a proportional odds logistic regression model (Faraway, 2006) using the R function *polr* in the MASS package. All independent variables were first fitted in a univariate model followed by a multivariate model including all three independent variables. Odds ratios and confidence intervals for univariate analyses between binary outcomes and binary explanatory variables were performed using Fisher's exact test. All other confidence intervals are profile likelihood confidence intervals (using the R function *confint*).

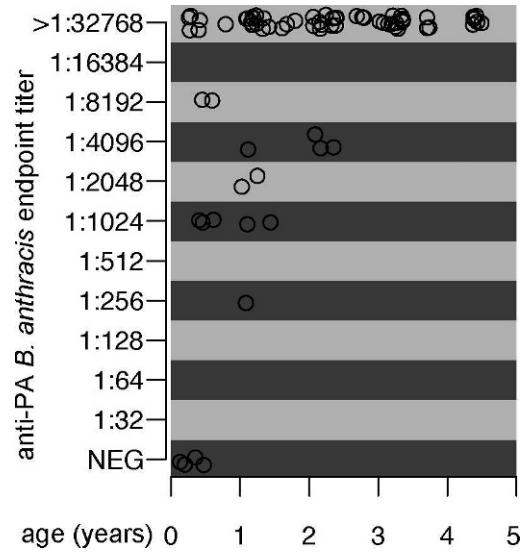

FIGURE 2. Endpoint titers in black-backed jackals (*Canis mesomelas*) sampled in Etosha National Park, Namibia, to the anti-protective antigen (anti-PA) enzyme-linked immunosorbent assay for exposure to *Bacillus anthracis* by age. Points have been jittered to facilitate display of number of samples when titers and ages are similar. Endpoint titers <1:32 were considered negative.

RESULTS

B. anthracis anti-protective antigen ELISA

The anti-PA ELISA curves for the 20 negative control samples were clustered at much lower optical densities at every titer for which they were evaluated than the ENP samples, suggesting that these animals were unlikely to have been exposed to BA (Fig. S1). The ELISA curves of 82/86 samples were above those of the negative controls for at least the lowest dilution (1:32). The four animals with titers <1:32 were considered to be negative and were <1 yr (Fig. 2). Age was the only significant explanatory variable in both univariate and multivariate analyses (Table 1), and titer increased with age in both seasons (Fig. 2). Two animals were tested from outside the study area, one

TABLE 1. Regression coefficients and their confidence intervals from univariate and multivariate models of how age, sample year, and study area affect *Bacillus anthracis* antiprotective antigen enzyme-linked immunosorbent assay (anti-PA ELISA) endpoint titers (proportional odds logistic regression), canine distemper virus serum neutralization test (CDV SN), and rabies fluorescent antibody virus neutralization test (RABV FAVN).

Assay	Parameter	Odds ratio (95% confidence interval)	
		Univariate model	Multivariate model
Bacillus anthracis anti-PA	Age	4.7* (2.2, 12)	4.7* (2.2, 12)
	Sample year[a]	0.34* (0.11, 0.96)	0.51 (0.13, 1.8)
	Study area[b]	0.54 (0.079, 2.2)	1.9 (0.20, 15)
CDV SN	Age	2.6* (1.5, 4.8)	2.8* (1.6, 5.4)
	Sample year	1.4 (0.46, 4.6)	1.8 (0.53, 6.6)
	Study area	2.2 (0.60, 7.6)	2.3 (0.45, 12)
RABV FAVN	Age	1.6 (0.77, 3.8)	1.4 (0.65, 3.4)[c]
	Sample year	0 (0, 1.1)	[c]
	Study area	1.6 (0.17, 77)	5.8×10^7 (0, Inf)[c]

* Odds ratio is significantly different from 1 ($P<0.05$).

[a] Sample year odds ratios are OR_{2009}/OR_{2008}.

[b] Study area odds are $OR_{Leeubron}/OR_{Gemsbokvlakte}$.

[c] Multivariate models for RABV FAVN were only fitted to study area and age for 2008 sample year data because all samples were negative for this assay in 2009.

12 km west of the Okaukuejo area and one animal near the Namutoni tourist camp on the eastern edge of the park, approximately 115 km northeast; both had titers of >1:32,768.

Canine Distemper Virus serum neutralization test

All results were qualitatively similar using cutoff titers of either ≥1:10 or ≥1:20. Of 80 animals tested, 57 (71%) or 50 (63%) were antibody positive using cutoff titers of ≥1:10 or ≥1:20, respectively. Hereafter we consider titer cutoffs of ≥1:10 unless otherwise specified. Age was the only significant explanatory variable in both the univariate and multivariate analyses, with a steep climb in antibody prevalence during the first year (Tables 1 and 2). Of recaptured animals, CM02 was negative on the first two captures (January and July 2009) but had seroconverted by the third capture (January 2010), and CM26 increased in titer from 1:40 (March 2009) to >1:320 (June 2010) between captures. Of the two spotted hyenas tested, one had antibodies to CDV.

Rabies fluorescent antibody virus neutralization test

None of the explanatory variables exhibited a significant effect on prevalence of antibody to RABV. However, anti-RABV antibodies were detected in only 7/81 (9%) serum samples from live-captured animals, limiting statistical power. Three of the seven antibody-positive, live-captured jackals were fitted with GPS collars and remained healthy for at least 1 yr after testing. One of two serum

TABLE 2. Antibody prevalence (%) as determined by the canine distemper virus serum neutralization test for black-backed jackals (*Canis mesomelas*) by sample year and age class sampled in Etosha National Park, Namibia. Numbers in parentheses are sample sizes.

Age (yr)	2008	2009
0–1	11 (9)	33 (3)
1–2	57 (7)	75 (12)
2–3	100 (10)	71 (7)
3–4	82 (11)	100 (5)
4+	83 (6)	— (0)
Unknown	71 (7)	100 (2)
Total	68 (50)	77 (30)

TABLE 3. Number of laboratory-confirmed, rabid black-backed jackals (*Canis mesomelas*) and other animals destroyed yearly in the Okaukuejo tourist camp in Etosha National park, Namibia, 1975–2010.

Year	Jackal	Other
1975	0	0
1976	1	0
1977	0	1
1978	0	0
1979	0	0
1980	0	0
1981	0	0
1982	1	2
1983	1	1
1984	3	0
1985	6	1
1986	1	0
1987	5	4
1988	5	2
1989	0	0
1990	0	2
1991	5	4
1992	5	0
1993	0	0
1994	0	0
1995	0	0
1996	5	3
1997	1	1
1998	3	0
1999	1	0
2000	2	0
2001	0	0
2002	3	1
2003	4	2
2004	2	0
2005	0	2
2006	0	1
2007	1	0
2008	2	0
2009	6	2
2010	4	1

samples from laboratory-confirmed rabid animals was antibody-positive.

Rabies mortalities

During the 2008 sample year, six jackals and one honey badger (*Mellivora capensis*) were suspected rabid and destroyed, and one opportunistically found fresh lion carcass was also sampled; all eight samples were laboratory-confirmed positive for RABV. During the 2009 sample year, four jackals were destroyed and laboratory-confirmed positive for RABV. Historical records of laboratory-confirmed rabies demonstrate consistent circulation of RABV over the past several decades (Table 3).

Rabies virus phylogenetic analysis

Amplicons of the expected size were obtained from four virus isolates. The isolates were closely related to previously characterized viruses from dogs, jackals, and greater kudu (*Tragelaphus strepsiceros*) from the same geographic region, demonstrating that these viruses belong to the same dog-jackal transmission cycle (Fig. S2).

DISCUSSION

Anthrax

Our results suggest that jackals within the study area are exposed early and repeatedly to *B. anthracis* and that pups are frequently exposed, but still survive, when immunologically naive. Without knowing the exposure history of Laikipia jackals, the ELISA patterns still suggest that both they and four juvenile jackals in ENP had not been exposed to BA (Fig. S1). The four antibody-negative juveniles and the youngest antibody-positive animal were estimated to be 2–6 mo old and 3 mo old, respectively. Maternal antibodies are assumed to be absent by 12 wk. All adult females were antibody-positive, indicating that if maternal antibodies are passed to pups, then they likely disappear before juveniles develop their own antibodies, indicating that naive juvenile jackals must survive an initial challenge. Jackal carcasses are small and difficult to detect. Thus, if juveniles occasionally died from anthrax before developing immunity we would be unlikely to observe them. Although herbivores are generally more susceptible to anthrax than carnivores, anthrax-confirmed carnivore deaths have historically been recorded in ENP (since 1975: one jackal, three lions, nine cheetahs) and

elsewhere (Hugh-Jones and de Vos, 2002; Clegg et al., 2007).

Generally high titers to BA in ENP jackals were not surprising given the frequency of anthrax carcasses in the region sampled (Fig. 1). Antibody prevalence to BA did not differ between study areas, which may be explained by ENP jackal mobility. Movement data from GPS-collared jackals indicated that territorial animals frequently traveled tens of kilometers to carcasses (Bellan, unpubl. data). Thus, the spatial scale of this study was too small to adequately compare jackals affected by anthrax-generated carrion with those who were not. Serologic analysis of BA antibodies from jackals may thus be useful as an indicator for anthrax presence at wider spatial scales, though data concerning the duration of immunity would help to clarify the timing of the exposure event.

Canine distemper virus

Serologic results indicate ongoing transmission of CDV in our study areas during the 2-yr study period as evidenced by the following: CDV antibody prevalence in Etosha jackals was high in both years and study areas; antibody-positive juveniles (<1 yr) were present in both sample years; of two recaptured animals seroconversion occurred in one, and the titer of the other increased between the two sample years. CDV antibody prevalence was significantly associated with increased age in both sample years and may be due to increased hazard of exposure with age, decreased case fatality rate with age, or simply the accumulation of hazard with age. A similar association between antibody prevalence and increased age was noted by Gowtage-Sequeria et al. (2009) during a recent CDV epidemic on the Namibian coast; however, important differences exist between the interannual patterns they found and those that we detected in the jackals of ENP. Gowtage-Sequeria et al. (2009) found that, prior to the 6-mo outbreak in 2002 in the coastal jackal population, no animals had antibodies to CDV. During the year of the outbreak, antibody-positive animals occurred in all age classes and prevalence increased with age; and in the year after the outbreak, the juvenile age class was entirely antibody-negative, and the proportion of antibody-positive jackals in the older classes was lower than that in the outbreak year. These data strongly suggest the occurrence of an epidemic in an immunologically naive population. Our results—relatively consistent age antibody prevalence trends along with antibody-positive juveniles and seroconversion of recaptured animals—suggest a different pattern of transmission and are consistent with ongoing transmission of CDV in the jackals in ENP over 18 mo. The potential for long-term persistence of CDV in jackals is unlikely without repeated reintroductions from other species (Cleaveland et al., 2007). Yet, the high density and mobility of the ENP population may permit cycles of transmission after recruitment of susceptible juveniles even when levels of population immunity are high (from recent outbreaks). Such epidemics may be of longer duration than those introduced into immunologically naive populations (Pulliam et al., 2007), potentially explaining the persistence of transmission over 18 mo. Alternatively, the diversity of carnivore species may facilitate longer transmission of cycles.

Given the short time period of this study these results must be interpreted cautiously. However, historical serologic data available on CDV exposure in ENP also show relatively high levels of exposure: Prevalence of antibodies to CDV was 53% ($n=15$, 1992–93), 24% ($n=25$, 1992–93, 1996), and 13% ($n=145$, 1991–96) in jackals, hyenas, and lions, respectively (Alexander et al., 2010). While it is difficult to understand pathogen dynamics from short-term data, we find it interesting that prevalence of antibodies to CDV in ENP jackals is consistently high for all periods sampled (both this 2-yr study and the 2-yr study by Alexander et al. [2010]).

No evidence of clinical CDV has been observed in any ENP carnivores with the

exception of six jackals and four captive wild dogs (*Lycaon pictus*) suspected to have died of distemper in the 1980s, though no laboratory-confirmation was performed (Etosha Ecological Institute unpubl. data). This contrasts with the morbidity and mortality observed during the recent CDV epidemic in the jackals along the Namibian coast (Gowtage-Sequeira et al., 2009) suggesting differences in either CDV strain, immunologic status of the jackal populations, or perhaps differences in the rigor of surveillance systems. In general, however, CDV is not always associated with population declines in southern African carnivores (Alexander et al., 2010). Still, CDV may pose a risk to sympatric carnivores such as lions and spotted hyenas as evidenced by the Serengeti lion and wild dog outbreaks, particularly when animals are immunocompromised due to coinfections (Munson et al., 2008; Goller et al., 2010).

Rabies virus

Serologic results and laboratory-confirmed rabies infections in jackals indicate that transmission events leading to exposure occurred throughout our 2-yr study period. Historical data indicate that at least one rabid animal was destroyed in the Okaukuejo tourist camp in 26 of 36 years. Phylogenetic analyses suggest that the rabies strains infecting the jackals are closely related to those previously identified in dogs, jackals, bat-eared foxes (*Otocyon megalotis*), and greater kudu from Namibia (Mansfield et al., 2006). The relatively high level of rabies exposure and mortality in ENP jackals suggests that they may have the potential to play an important role in rabies transmission dynamics. Given recent proposals for the necessity and feasibility of eliminating canine rabies in Africa (Hampson et al., 2009), further research into the role of jackals and other wildlife in RABV transmission dynamics is critical to developing effective management plans.

Finally, RABV dynamics in ENP may have particular implications for the reintroduction of wild dogs into the park. Three attempts were made to reintroduce wild dogs to the park between 1978 and 1990. Each attempt failed, with the last one failing because several animals succumbed to rabies (Scheepers and Venzke, 1995). This, in addition to their susceptibility to anthrax (Clegg et al., 2007), suggests that future reintroductions must take infectious disease into account.

In summary, due to their widespread distribution and opportunistic scavenging, jackals may potentially be useful as biosentinels for anthrax. Without knowing the exposure history of jackals sampled in Laikipia, Kenya, the grouping of their results with juvenile jackals from ENP suggests that these animals had not been exposed to anthrax-generated carrion. In contrast, jackals sampled in the Okaukuejo area of ENP have all been exposed to anthrax carrion by their first year of age. Increasing titers with age suggests that consumption of carrion throughout life continually boosts their immunity to BA. Increasing prevalence of antibody to CDV with age in both years, and relatively high antibody prevalence in general suggest longer epidemic durations in ENP jackals than noted in other populations. Rabies cases are detected in the majority of years in the Okaukejo tourist camp and a relatively large proportion of live-captured jackals exhibited immunity to RABV. These results suggest that the ENP jackal population may play an epidemiologically important role in CDV and RABV transmission, though long-term data sets and mathematical modeling are necessary to clarify these transmission dynamics.

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