Demography, Hunting Ecology, and Pathogen Exposure of Domestic Dogs in the Isoso of Bolivia

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Abstract: Disease is increasingly recognized as a threat to the conservation of wildlife, and in many cases the source of disease outbreaks in wild carnivores is the domestic dog. For disease to spill over from a domestic to a wild population, three conditions must be satisfied: susceptibility of the wild species, presence of the disease agent in the domestic population, and contact between the two populations of interest. We investigated the potential for disease spillover from the domestic dog population to the wild carnivore population in the Isoso of Bolivia, an area of tropical dry forest contiguous with a national park. Using questionnaires and discussions with residents, we gathered data on the demography of dogs in the Isoso, including adult and neonatal mortality, litter size, and hunting frequency. We analyzed a large data set containing self-recorded information on hunting in various communities of the Isoso to determine the extent of dog participation in hunting and the duration of hunting trips. Finally, we took blood samples from dogs in the Isoso for a serosurvey of common canine pathogens. More than 95% of dogs had positive titers to canine distemper virus and canine parvovirus. There was also a high seroprevalence in dogs for other pathogens, a high population turnover of dogs (which may allow diseases to be maintained endemically), and frequent opportunities for contact between domestic and wild carnivores. Based on our results and the susceptibility of wild species previously reported in the literature, domestic dogs represent a disease risk for wildlife in the Bolivian Isoso.

Keywords: buffer zones, carnivore conservation, disease ecology, disease spillover, domestic dogs, serosurvey

Demografía, Ecología Cinagética y Exposición a Patógenos de Perros Domésticos en el Isoso de Bolivia

Resumen: Cada vez más, las enfermedades son reconocidas como una amenaza a la conservación de vida silvestre, y en muchos casos el perro doméstico es la fuente del desencadenamiento de enfermedades de carnívoros silvestres. Para que una enfermedad pase de una población doméstica a una silvestre, se deben satisfacer tres condiciones: susceptibilidad de la especie silvestre, presencia del agente patógeno en la población doméstica y contacto entre las dos poblaciones de interés. Investigamos la potencial transmisión de enfermedades de la población de perros domésticos a la población de carnívoros silvestres en el Isoso de Bolivia, un área de bosque tropical seco contigua a un parque nacional. Mediante cuestionarios y discusiones con residentes, reunimos datos de la demografía de perros en el Isoso, incluyendo mortalidad de adultos y neonatos, tamaño de camada y frecuencia de cacería. Analizamos un extenso conjunto de datos conteniendo información sobre cacería en varias comunidades del Isoso para determinar la extensión de la participación de perros en la cacería y la duración de los viajes de cacería. Finalmente, tomamos muestras de sangre de perros en el Isoso para un muestreo de suero para buscar los patógenos caninos más comunes. Más de 95% de los perros fueron positivos a moquillo y parvovirus caninos. También hubo seroprevalencia alta para otros patógenos, una alta productividad en la población de perros (lo que puede mantener a las enfermedades endémicamente) y frecuentes

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oportunidades de contacto entre carnívoros domésticos y silvestres. Con base en nuestros resultados y en la susceptibilidad de especies silvestres previamente reportada en la literatura, los perros domésticos representan un riesgo de enfermedad para la vida silvestre en el Isoso Boliviano.

Palabras Clave: conservación de carnívoros, ecología de enfermedades, muestreo de suero, perros domésticos, secuela de enfermedades, zonas de amortiguamiento

Introduction

Disease in wildlife is increasingly recognized as a conservation concern (e.g., McCallum & Dobson 1995; Woodroffe 1999; Funk et al. 2001). Domestic animals often act as reservoir species that can maintain infectious diseases in their populations and periodically transmit these diseases to naïve wildlife populations (Cleaveland & Dye 1995; Rhodes et al. 1998; Lafferty & Gerber 2002). More attention is now being paid to the diseases of domestic dogs that live in areas surrounding protected areas and other regions with significant wildlife populations (e.g., Alexander et al. 1993; Laurenson et al. 1998; Cleaveland et al. 2000). Knowing which diseases are present and their prevalences are not the only important pieces of information; it is also necessary to understand the ecology of the dogs to determine their potential impact on the neighboring wildlife.

Many protected areas are surrounded by buffer zones and transition areas, which are used for hunting and other forms of resource extraction (Neumann 1997). Theoretically, buffer zones are considered areas where only low-

impact activities, compatible with protection of the central core of the reserve, occur (Shafer 1999; Smith 2003). In practice, however, buffer zones tend to be used for multiple purposes and are often the site of both sustainable and unsustainable resource exploitation (Sánchez-Azofeifa et al. 2003). In Bolivia protected areas include national parks and integrated management areas (IMA). The IMAs generally surround parks and may include or be contiguous with indigenous territories (Tierra Comunitaria de Origen, or TCO). Each TCO establishes its own zonation and management plan, defining regulations on resource extraction and land use that respect relevant national legislation.

Bolivia's Kaa-Iya del Gran Chaco National Park and IMA are contiguous, but nonoverlapping, with the Isoleño TCO, which is considered part of the "zona de influencia," or zone of influence, of the park (Kaa-Iya Project 2001) (Fig. 1). Although it does not have legal status that defines it as part of the park buffer zone, for practical purposes it functions as such. About 8000 Isoleños inhabit 23 communities clustered along the Rio Parapetí in the TCO and use this 3000–4000 km² region west of the park boundary

Figure 1. Location of Isoleño communities in relation to Kaa-Iya del Gran Chaco National Park, the Parapetí River, and the Isoso indigenous territory. Inset shows position of detailed area in Bolivia.

for subsistence and commercial hunting (Kaa-Iya Project 2001). Dogs are abundant in the communities, and may come into contact with wildlife in or near the communities. In addition, because nearly all hunting activities include dogs (Noss & Cuéllar 2001; Kaa-Iya Project, unpublished data) and hunters from the communities utilize much of the TCO, the transmission of infectious diseases from the domestic dogs to wildlife is a potential risk. Previous research in Bolivia indicates that many domestic dogs have been exposed to pathogens of conservation concern (Widdowson et al. 2002; Fiorello et al. 2004).

Many wild carnivores inhabit this area, including protected species, such as jaguars (*Panthera onca*), ocelots (*Leopardus pardalis*), Geoffroy's cats (*Oncifelis geoffroyi*), and other felids and canids, such as jaguarundis (*Herpailurus yagaurondi*), pumas (*Puma concolor*), crab-eating foxes (*Cerdocyon thous*), and pampas foxes (*Pseudalopex gymnocercus*) (Taber et al. 1997; Cuéllar 2000; Maffei et al. 2003, 2004). The disease susceptibility of captive South American carnivore species to domestic dog diseases is known from the literature. For example, heartworm disease has been reported in jaguars and jaguarundis (Otto 1974); canine parvovirus (CPV) has been reported in crab-eating foxes (Mann et al. 1980; Barker & Parrish 2001); and canine distemper has been reported in a jaguar (Appel et al. 1994) and a crab-eating fox (Rego et al. 1997). There is no reason to suppose that these species would not be susceptible in the wild; in fact, sarcoptic mange has been reported in free-ranging pampas foxes in the Isoso (Deem et al. 2002).

Our goal was to further our understanding of disease and population ecology of hunting dogs in a national park buffer zone in South America. We used a combination of blood sampling, informal discussions with local residents, a questionnaire survey, and a large data set on hunting to study domestic dogs in indigenous communities of southeastern Bolivia. Our specific aims were to determine whether domestic dogs serve as potential reservoirs of disease agents pathogenic to wild carnivores and have regular opportunities to come into contact with wild carnivores or their environment.

Methods

Demography

We developed a questionnaire to obtain basic information on the number, age, and mortality rates of domestic dogs. Informal discussions were also conducted on an ad hoc basis, and the age, vaccination status, and hunting status of sampled dogs were recorded (when known). The questionnaire was administered orally in Guaraní and Spanish by researchers (including local assistants) during sampling (see below) or by a hunting monitor from Iyobi.

We focused on the community of Iyobi, but also collected data opportunistically at hunting camps or on occasional trips to other communities. Copies of the questionnaire are available from C.V.F.

Hunting Data Set

The Kaa-Iya Project is a collaborative effort of the Wildlife Conservation Society (WCS) and the Capitanía del Alto y Bajo Isoso (CABI), an indigenous organization in Bolivia that administers the Kaa-Iya del Gran Chaco National Park, IMA, and the Ioseño TCO. The Kaa-Iya Project employs members of the communities to serve as hunting monitors as part of their mission to manage the natural resources of the area. Data on hunting are collected to monitor harvests of game species, upon which the local people rely for protein. Hunters who volunteer to participate provide their community hunting monitor with information on location, date, time, and duration of each hunt and on weapons used, number of dogs present, the weather, and number and characteristics (age, sex, condition) of each animal harvested. Not all hunters in a given community participate, and those who do participate do not necessarily record complete data from every hunt. Individual communities differ in their level of hunter participation; in some, all hunters participate, whereas in others very few participate (Noss et al. 2003). However, despite these drawbacks, the data set does contain useful information. Based on hunts ($n = 140$) when researchers from the Kaa-Iya Project accompanied local hunters, we estimated that between 25 and 30% of hunts were successful (Kaa-Iya Project, unpublished data). Therefore, the data collected on successful hunts likely represent about 25% of the total hunting effort by participating hunters in the area.

Seroprevalence of Disease Agents

Extensive blood sampling of dogs was done in Iyobi, Rancho Viejo, and Yapiroa (Fig. 1), three communities that vary somewhat in size, location, and economic base (Table 1) (Noss & Cuéllar 2001). Iyobi and Yapiroa, two of the largest communities (Kaa-Iya Project, unpublished data),

Table 1. Village size, location, and number of domestic dogs sampled for serologic testing in the Bolivian Isoso.*

Village	Population in 1998	River bank	Number of dogs
Tamachindi	586	west	6
Yapiroa	620	west	15
Rancho Viejo	346	east	35
Iyobi	616	east	36
Cattle ranch	NA	east	4
Not specified	NA	NA	2
Total			98

*Population statistics from the Official census, Capitanía del Alto y Bajo Isoso (CABI), 1998; NA, not applicable.

have a more diverse economy and their inhabitants are less likely than those in small communities to rely on seasonal migratory work and hunting. Residents of Rancho Viejo, an intermediate-sized community, rely heavily on hunting during the months when seasonal agricultural work is unavailable. Situated in the northern part of the Isoso on the east bank of the river, Rancho Viejo and Iyobi are more isolated than Yapiroa. Yapiroa is located farther south, on the west bank of the river, closer to the nearest town and railroad station. Dogs living in Yapiroa might be expected to have more contact with dogs from outside the Isoso because this area is closer to main roads and it is not necessary to cross the river to reach them.

Accompanied by a community member, we walked from house to house, asking owners for permission to take blood samples from their dogs. To ensure that the antibodies detected were endogenous and not of maternal origin (Greene 1998a), only dogs 5 months of age and older were sampled. We drew blood from the jugular vein. On the few occasions when dogs were too fractious to handle, they were sedated with standard intramuscular doses of acepromazine (Boehringer-Ingelheim, Ingelheim, Germany).

In addition to sampling in the villages, we opportunistically sampled hunting dogs at research stations in the buffer zone. These stations sometimes double as hunting camps, where hunters and their animals spend the night during longer hunting trips. If hunters came through when we were present, we spent the evening talking with them and sampling their dogs.

Blood was placed into serum separator tubes and centrifuged for 10 minutes. Sera were drawn off, stored in cryotubes, and placed in liquid nitrogen. The samples were transported to the United States on ice and stored in a freezer at -80°C until analysis. Analyses were performed by commercial laboratories in the United States and Switzerland (Table 2). With the exception of the *Sarcoptes scabiei* test, assays for antibodies document infection at some point in the past. Antibodies to *S. scabiei* wane within 2 months of the infection clearing, so when they are found they indicate current or very recent infection (Lower et al. 2001). The assay for *Dirofilaria immitis*, the causative agent of heartworm disease, detects antigen and therefore indicates active infection or a recently (3–5 months) cleared infection (Goodwin 1998).

Statistics

We used Statview (SAS 1999) for all statistical analyses. Unpaired *t* tests and analyses of variance (ANOVA) were used for comparing ages for both sexes and across towns; chi-square tests were used to compare sex ratios across towns. We used ANOVA to compare length of hunts and number of dogs and chi-square tests to compare the percentage of dogs with positive titers to different pathogens among different towns, differences between the sides of

Table 2. Methodologies and positive cutoff values used by commercial laboratories to detect disease agents or disease exposure in serum.^a

<i>Pathogen</i>	<i>Methodology</i>	<i>Positive cutoff^b</i>
Canine adenovirus	antibody SN	1:4
Canine coronavirus	antibody SN	1:8
Canine distemper virus	antibody SN	1:8
Canine herpesvirus	antibody SN	1:8
Canine parvovirus	antibody HAI	1:10
<i>Dirofilaria immitis</i>	antigen ELISA	P/N
<i>Toxoplasma gondii</i>	antibody IHA	1:64
<i>Leptospira interrogans</i>	antibody MA	1:100
<i>Brucella canis</i>	slide agglutination/AGID	P/N
<i>Sarcoptes scabiei</i>	antibody ELISA	P/N

^aAll analyses were performed at the Cornell University Veterinary Diagnostic Lab, Section of Virology, Ithaca, New York, with the exception of the *S. scabiei* assay, performed at Labor Laupenack, Bern, Switzerland. Abbreviations: SN, serum neutralization; HAI, hemagglutination-inhibition; ELISA, enzyme-linked immunosorbent assay; IHA, indirect hemagglutination; MA, microagglutination; AGID, agar gel immunodiffusion; P/N, no cut-off value, test results scored as either positive or negative.

^bGreatest dilution at which antibodies or antigen were detected.

the Rio Parapetí, and to explore correlations among disease agents. Where sample sizes were too small for chi-square tests, *G* tests were used. We also used *G* tests to compare percentage of male and female dogs with positive titers. We used unpaired *t* tests to compare the ages of dogs with positive titers for various disease agents. Significance was accepted at $p < 0.05$.

Results

Demography

Thirty-nine households from Iyobi (slightly over 25%) completed the questionnaire, providing information on 155 dogs (Table 3). Partially completed questionnaires were obtained from nine households from other communities. Information on sex, age, vaccination status, and hunting status of dogs was obtained during sampling of 85 dogs (37 from Iyobi, 28 from Rancho Viejo, 9 from Yapiroa, and 11 from other communities; Table 1). Sex and age data on dogs obtained during sampling both including and excluding Iyobi were compared with data obtained from the survey. The results were nearly identical and thus are not reported here.

Based on the surveys and discussions with residents, we concluded that essentially all households had dogs. The rare household without a dog resulted from the temporary absence of adult men—who took their dogs with them when they left to do seasonal work—or the recent death of dogs that had not yet been replaced. Dogs in the Isoso are all owned, and are considered necessary for hunting all terrestrial species except brocket

Table 3. Demographic data (mean $\pm$ SD) of domestic dogs in the Bolivian Isoño obtained from questionnaires and during blood sampling.*

Parameter	Questionnaire responses (n = 48)	Data obtained during sampling (n = 99)
Number of adult dogs owned now	3.8 $\pm$ 2.1	NA
Number of female dogs	36	45
Number of male dogs	49	54
Number of female dogs/household	1.6 $\pm$ 1.2	NA
Number of male dogs/household	2.4 $\pm$ 1.5	NA
Sex ratio (male to female)	1.5:1	1.2:1
Age of female dogs (years)	3.5 $\pm$ 1.4	3.0 $\pm$ 2.1
Age of male dogs (years)	3.5 $\pm$ 1.8	2.9 $\pm$ 2.4
Litter size	4.1 $\pm$ 1.5	NA
Number of pups that die/litter	3.2 $\pm$ 1.9	NA
Annual pup mortality	0.73 $\pm$ 0.31	NA
Annual adult mortality	0.34 $\pm$ 0.50	NA
Dogs vaccinated against rabies	11%	3%
Dogs that hunt	86 $\pm$ 0.28%	90%

*There were no significant differences in age between males and females or between questionnaire responses and data obtained during sampling (unpaired *t* tests, *p* values $\geq$ 0.446); NA, not available.

deer (*Mazama gouazoubira*). We did not collect data on the source of dogs, but informal discussions indicated that most dogs were received or purchased from friends or relatives in the Isoño, with an occasional dog being purchased in nearby cities. There were on average 3.8 adult dogs/household (Table 3) and 4.9 people/household (Kaa-Iya Project, unpublished data). There was roughly one dog for every 1.5 persons. Based on these estimates and the population census, a community the size of Iyobi has approximately 522 dogs (Table 1). Data from the questionnaires indicated that 17 of 161 dogs (11%) were vaccinated against rabies. During sampling, however, rabies vaccination status was recorded for 60 dogs, and only 2 of these (3%) were vaccinated. Eighty-six percent (based on questionnaires) or 90% (based on sampling data) of dogs were reported to hunt, which in a village of Iyobi's size equals 448–470 dogs (Table 3).

The average age and annual mortality of the dog population indicated that turnover was quite high. The sex ratio of dogs indicated a male bias, although the average age of male and female adult dogs was similar (Table 3). When data from the questionnaire were compared with those collected during sampling, average age of dogs was nearly identical (mean $\pm$ SD: 3.1 $\pm$ 1.7 from questionnaire vs. 2.9 $\pm$ 2.3 from sampling, *p* = 0.945, unpaired *t* test). Average age of dogs did not differ among communities (*p* = 0.912, ANOVA; data not shown), or between the east and west banks of the river (*p* = 0.272, unpaired *t* test, data

not shown). The average annual mortality of adult dogs, based on the number of dogs that owners reported dying in the past year, was 34%. Average litter size was 4.2, and females were reported to have 1 litter/year. An average of 73% of puppies died as neonates. When questioned about the cause of death of puppies, dog owners mentioned diarrhea (48.1%), mange (44.4%), worms (25.9%), vomiting (22.2%), anorexia (3.7%), and infanticide (3.7%); 34.7% said they did not know.

Hunting Ecology

Dogs of both sexes and all ages (starting at approximately 8–10 months of age) hunted; in addition, younger dogs often accompanied their dams into the forest on hunts, although their owners claimed that these dogs do not actively hunt. Because these young dogs were not included when owners were asked how many hunting dogs they have, the estimate that 86–90% of dogs hunt is actually an underestimate of the number of dogs that go into the forest. Eighty-two percent of hunting dogs were reported to hunt weekly or more often (i.e., a minimum of 367 dogs from Iyobi entering the forest each week, or 52 dogs/day).

Data were available for 6466 hunts between August 1996 and November 2002. Slightly less than half, or 42.5% (2745 hunts), had information regarding dog participation. For just under 12% of hunts, the number of dogs was recorded simply as “one or more.” The vast majority (2633/2745, or 95.9%) of hunts included at least one dog, and the average number of dogs/hunt was 2.7 $\pm$ 1.6 (*n* = 2421). Of hunts with dogs, 14.3% involved one dog, 33.1% involved two dogs, 25.7% involved three dogs, and 26.9% involved four or more dogs. Successful hunts included significantly more dogs (2.8 $\pm$ 1.5, *n* = 2264) than unsuccessful hunts (2.2 $\pm$ 1.9, *n* = 157) (unpaired *t* test, *p* < 0.0001).

Information on duration of hunt was available for 3721 (57.5%) of hunts. Most (92.9%) hunts lasted for <24 hours, and the average duration was 10 hours (Fig. 2).

Figure 2. Percentage of hunts of differing lengths by Isoño men in the Integrated Management Area (IMA) of Kaa-Iya del Gran Chaco National Park. Total number of hunts was 3719.

Nearly half (47.7%) of all hunts were between 6 and 12 hours. The mean duration of hunts that included dogs (9.4 ± 9.4 hours) did not differ from the duration of hunts in which dogs did not participate (9.0 ± 8.7 hours) (unpaired t test, $p = 0.6311$). Similarly, mean duration was not different for successful (9.5 ± 9.3 hours) and unsuccessful (9.5 ± 12.1 hours) hunts (unpaired t test, $p = 0.9830$). In general, as hunts got longer, more dogs were present (ANOVA, $p < 0.0001$).

Serosurvey

Sufficient quantities of serum for at least one analysis were collected from 98 dogs. The number of dogs sampled from each town is included in Table 1. Not all dogs were tested for all disease agents because of a lack of serum and financial limitations.

Exposure to canine distemper virus (CDV) and CPV was extremely common (Fig. 3). Positive titers to *S. scabiei*, canine herpesvirus, and canine coronavirus were present in 50% or more of dogs tested. All dogs tested positive for exposure to at least one pathogen. With the exceptions of *Toxoplasma gondii* and canine adenovirus, the percentage of dogs positive for a given pathogen did not differ among towns on the east and west sides of the river. Positive titers for *T. gondii* were more common on the east side of the river, but this was due to the fact that dogs positive for this agent were more commonly found in Rancho Viejo (48%) or a neighboring ranch (100%, compared to 26% in all other communities; $p = 0.007$). When these two locations were removed from the analysis, *T. gondii* titers did not differ between sides of the river ($p = 0.10$). Similarly, positive titers to adenovirus were very common in the village of Yapiroa (73% vs. 25% in all other

communities; $p = 0.002$). When Yapiroa was excluded from the analysis, there was no difference between villages on the east and west sides of the river ($p = 0.230$).

The seroprevalence of most diseases increased with age. Antibodies to *T. gondii*, CPV, adenovirus, coronavirus, and *Brucella canis* were found more commonly in older dogs. This effect was particularly strong for coronavirus (Fig. 4). All four of the dogs negative for CPV were under 1 year of age, and three out of four of the dogs negative for CDV were <1 year old. There were no significant differences in disease prevalence between male and female dogs.

Discussion

Three conditions must be satisfied for disease spillover from domestic to wild carnivores to occur: (1) the wild carnivores of interest must be susceptible to the disease agent, (2) the disease agent must be present—and preferably endemic—in the domestic carnivore population, and (3) there must be an ecological mechanism for contact between the two populations (or their infectious material) to occur. These conditions appear to be in place in the Isoso. Wild carnivore susceptibility to disease agents is known from the literature, and our results suggest that many diseases are maintained in the domestic dog population and that opportunities for contact between domestic and wild carnivores are plentiful.

The seroprevalence of common canine diseases was quite high in domestic dogs in the Isoso when compared with similar surveys performed in other regions. For example, in the Serengeti area of Tanzania, seropositivity to CDV ranged from 10 to 80%, with a higher proportion of positive dogs in the older age classes (Cleaveland et al. 2000). In the Brazilian Amazon, seropositivity to CDV and CPV was 9% and 13%, respectively, (Courtenay et al. 2001). A study in Ethiopia found 100% seropositivity to CPV in 18 dogs sampled, but seroprevalence of other viruses was lower. For CDV it was approximately 32%, whereas for canine adenovirus it ranged from 0 to 90%, depending on the region (Laurenson et al. 1998). Antibodies to *B. canis* were found in 7% of stray dogs in São Paulo, Brazil (Larsson et al. 1981), and antibodies to *Leptospira* spp. were found in 14% of dogs in southern Bolivia (Ciceroni et al. 1997). A survey of dogs in northwestern Bolivia found seroprevalences similar to those in the Isoso for many canine pathogens (Fiorello et al. 2004).

The presence of these disease agents—at least during the period of our study—appears certain. Seropositivity was highest for CDV and CPV, the most common canine pathogens worldwide, and major threats to endangered wildlife elsewhere (Mech & Goyal 1993; Laurenson et al. 1998; Cleaveland et al. 2001; Hedrick et al. 2003). Other viruses are also relatively common in this population. Although these pathogens may be of less conservation

Figure 3. Percentage of dogs with positive titers to selected disease agents ($n = 96$ unless otherwise indicated): CAV, canine adenovirus; CCV, canine coronavirus; CDV, canine distemper virus; CHV, canine herpesvirus; CPV, canine parvovirus; HWD, heartworm disease; Toxo, *Toxoplasma gondii*; Lepto, *Leptospira interrogans*; Bruc, *Brucella canis*; Sarc, *Sarcoptes scabiei*.

Figure 4. Seroprevalence of 10 pathogens by age class in domestic dogs in the Bolivian Isoso. The number in parentheses below each bar indicates the total number of dogs in that age class that were tested for that pathogen. Age classes were defined as follows: juvenile, up to 1 year of age; young adult, 1 year up to 3 years; adult, 3 years up to 5 years; senior, over 5 years.

concern than CDV or CPV, they may still represent a risk for wild carnivores (Evermann et al. 2005). First, because exposure to these less prevalent pathogens is not uniform, some dogs are becoming infected during their adulthood, and it is adult dogs that are most likely to encounter wildlife. Second, coinfection with some viruses, including canine coronavirus and canine adenovirus, can cause much more severe disease than single infection (Pratelli et al. 1999, 2001), and it may increase the amount and duration of viral shedding of one or both pathogens (Pratelli et al. 2001). Most dogs had antibodies to more than one disease agent. Although we have no data to demonstrate whether these are sequential or simultaneous infections, it is reasonable to assume that at least some of these dogs had simultaneous infections.

In general, seropositive animals were found in all communities and on both sides of the river, although there were some interesting differences that may have a biolog-

ical basis. The finding that antibodies to *T. gondii* were more common in dogs living near a cattle ranch may reflect their proximity to cats. Domestic cats are rare in the Isoso; however, several cats lived on or around this ranch. Felids are the definitive host for *T. gondii*, and so the dogs living near the ranch may be more likely to be exposed to infectious cysts shed in cats' feces. Although dogs may become infected from eating wild prey, they are rarely given meat by their owners and do not seem to hunt much on their own. It is also possible that they are being infected by cysts in the feces of wild felids, although this would not explain the higher seroprevalence in dogs near the ranch. Regardless of how they are being exposed, these dogs share an environment with their human caretakers, who are also susceptible to this zoonotic pathogen.

In contrast, there is no obvious reason why canine adenovirus exposure was more common in the village of Yapiroa. This virus may persist in the environment and

can be shed for prolonged periods of time in the urine of recovered dogs (Greene 1998b). It is possible that the environment in Yapiroa is more contaminated with this virus than other areas. Because the data we collected for this study were cross-sectional, it is possible that an outbreak was beginning in Yapiroa and will continue to spread to other communities. If additional sampling is done in the future, we may be able to determine whether the pattern of higher exposure in Yapiroa is persisting or whether it represented an epidemic wave that spread through the Isoso. Based on the data from other pathogens, it does not appear that the river is serving as a geographic barrier to disease transmission among domestic dogs.

The finding that, for several pathogens, seroprevalence increased with age is typical for many disease agents (Giesecke 2002). The longer an individual organism is alive, the more opportunities it has to be exposed to pathogens. In the Isoso, nearly all dogs that reach the age of 1 year will have been exposed to CDV and CPV (Fig. 4). This is reassuring because those that survive the infection are likely to be immune for several years, and given the short lifespan of most Isosño dogs, they are probably immune for life. Thus, only a small proportion of hunting dogs would be exposed to pathogens as adults, and would be actively shedding virus during their working years.

Showing that antibodies to disease agents were common in the dog population at the time of sampling is not equivalent to demonstrating that these diseases are endemic in the population. However, we do have compelling evidence that Isosño dogs are ideal disease reservoirs (i.e., able to maintain virulent pathogens in their population). First, Isosño communities have an abundance of dogs. These dogs are infrequently vaccinated and receive no other preventive health care, an unsurprising finding in a place where people are often unable to obtain adequate health care for themselves and their families. Second, the high mortality of dogs, and especially of puppies, suggests that mortality from disease is playing a large role in regulating the canine population. Owners' descriptions of the clinical signs exhibited by puppies support the conclusion that many of the pups are suffering from infectious diseases. Third, the apparent high turnover of the population—over 1000 puppies born just in Iyobi each year—provides for many new susceptible hosts to contract and shed pathogens, thus preventing disease agents from dying out.

Contact between wild and domestic carnivores occurs regularly in this habitat. Hunters with dogs capture and kill wild cats when encountered inside and outside communities, and presumably some cats escape after physical contact with dogs (Noss 1998; Cuéllar 2000; Noss et al. 2003). Although hunters do not target foxes, they report frequent encounters with foxes on hunting trips, and foxes are observed near communities on a daily basis (Kaa Iya Project, unpublished data; C.V.E., unpublished

data). Both local residents and researchers have observed foxes and wild cats enter communities to take chickens and goats (C.V.E., unpublished data).

This anecdotal evidence, however, does not provide a quantitative measure of contact. Using our questionnaire results and the hunting data set, we estimated the amount of time dogs were spending in the forest. If there are 8000 people in the Isoso and 1 dog for every 1.5 persons, if 86% of dogs hunt, and if 82% of these dogs hunt at least weekly, the result is over 3000 dogs entering the forest each week in an area smaller than 4000 km². If each of these dogs is in the forest for an average of 11 hours, the total is 33,000 dog-hours in the forest. Even if only a small fraction of dogs were infectious at any given time, it nonetheless represents a large number of infectious hosts that have the potential to encounter susceptible wild carnivores. Fifteen percent of all dogs sampled (only dogs > 5 months old were sampled) were < 1 year old. If only 5% of these young dogs were shedding virus, it amounts to over 20 dogs/week, or 220 infectious dog-hours.

These numbers may overestimate the amount of time infectious dogs are likely to spend in the forest because very sick dogs are unlikely to go hunting. However, dogs seem to greatly enjoy hunting and so are highly motivated to follow their owners if they are able. Dogs also shed virus before they are symptomatic and/or after clinical recovery. And, puppies that are not yet hunting often accompany their dams into the forest. These puppies are the most likely to be actively infected with pathogens, especially CDV and CPV.

The hunting range of the Isoso is between 3000 and 4000 km². Assuming that 3000 hunting dogs "occupy" this range each week, the dog density is between 0.75 and 1.0 dog/km². However, the effective density is much higher, because dogs and wild carnivores are not evenly distributed across the landscape. Isosños and their dogs hunt by walking roads and trails, and camera-trap data confirm that wild felids (jaguars, pumas, ocelots) spend a disproportionate amount of their time on roads and trails (Maffei et al. 2003, 2004). Other carnivores, especially foxes, are commonly seen using roads, and carnivore scats are deposited along trails, presumably to mark territories. The potential for contact—especially indirect contact—is greatly magnified because of the preference of both domestic and wild carnivores for roads and trails. Roads represent an area of concentrated use, whereas wildlife is likely to encounter dogs and the infectious materials that dogs may leave behind.

Disease spillover can only occur if infected domestic dogs are encountering susceptible wild carnivores. Our results demonstrate that domestic dogs are commonly infected with pathogens and that they regularly contact wild carnivores. Although some serology data are available from wildlife (Fiorello 2004), as yet no data are available regarding the pathogenicity of the local viral strains for wild carnivores in this habitat or on whether the

strains circulating in the dog population are in fact the same as those circulating in the wild carnivore populations, as has been shown in other systems (Battilani et al. 2001). Research on those questions is urgently needed to inform conservation management planning. However, if a cautionary stance is adopted and the evidence from the literature that these carnivores are susceptible to canine pathogens is accepted, it must be acknowledged that the possibility for disease spillover in the Isoso exists.

The Isoleños rely heavily on their dogs during hunting, which is a major contributor to their economy. It is therefore likely that domestic dogs will continue to live in the Isoso and enter the forest and the habitat of wild carnivores, and that domestic and wild carnivores will continue to overlap in and around communities. Although hunters apparently do not regularly move between the TCO and the park, wild carnivores (especially jaguar and puma) presumably do—and when they do, they almost certainly use the same roads and trails that hunting dogs are frequenting. These dogs represent a risk to wildlife in the buffer zone of Kaa-Iya del Gran Chaco National Park, and in the park itself. Additional work is needed to investigate methods of reducing the disease risk to the wild carnivores of the area. Such methods may include vaccination of domestic dogs, prohibition on ill dogs participating in hunting activities, and sterilization campaigns to limit the number of dogs in the community.

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