5-2018

Defending Wild Dogs: Population Dynamics and Disease in Endangered African Wild Dogs

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Defending Wild Dogs: Population Dynamics and Disease in Endangered African Wild Dogs

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology

by

Elizabeth Arredondo
University of Arkansas
Bachelor of Science in Biology, 2011

May 2018
University of Arkansas

This thesis is approved for recommendation by the Graduate Council

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ABSTRACT

African wild dogs (*Lycaon pictus*) are endangered carnivores whose population is decreasing from habitat loss and fragmentation, interspecific competition, and disease. Survival rates are especially low in Kruger National Park (KNP), though it is unclear why. I estimated the abundance in KNP and survival rates over different time spans, six years and nine months, using public photographic survey data. In 2015, there were 298 (SE=12.1) individuals. Using a mark-recapture analysis in program R, I found that the survival rate between 2009-2015 was only 3.2%, and within the 9-month survey period (September 2014 – June 2015), monthly survival rates for the wild dogs varied by region of the park, with apparent survival (φ) at 0.807 (0.695-0.885 95%CI), 0.989 (0.852-0.999), and 0.975 (0.946-0.989) for dogs in the northern, central, and southern region of the park, respectively. I estimated mean lifespan to be .39 years, 7.2 years, and 3.3 years for the northern, central, and southern regions, respectively, and 1.41 years for all dogs combined. Recapture probability for the dogs varied by region and month, ranging between 0.07 and 0.828, highest in the south, followed by the north, then the central region, with an overall monthly recapture probability average in the park of 0.483 (SE=0.0148). Because disease is becoming an increasing threat to wild dogs and other wild canids, I also conducted review of the disease prevalence and vaccination strategy and efficacy in African wild dogs and Ethiopian wolves, focused on canine distemper and rabies. I found that vaccination with modified-live or recombinant vaccines, including annual boosters will be a key strategy in disease management going forwards. Vaccination of domestic dogs near wolf and wild dog populations, vaccination of wolves and wild dogs themselves, and a combination of the two, all appear to be viable management strategies in different scenarios. A greater understanding of population dynamics and disease dynamics from this study, in addition to more intensive

population and disease monitoring in the future, will help provide necessary information to guide successful management strategies of these two critically endangered species, and specifically wild dogs in Kruger National Park.

ACKNOWLEDGEMENTS

I would like to first and foremost thank my incredible husband, Devon Arredondo, for encouraging and supporting me. I could not have done it without your love and excitement for life pushing me on! Secondly I would like to thank my family, especially my parents, Dr. Gary and Catherine Templeton, for always telling me I could accomplish anything I dreamed of doing and be anyone I dreamed of being. Thanks for surrounding me with love and support all these years.

I would also like to thank Dr. Laurence Kruger for passing on his love of South Africa to me, his encouragement through the entire process, and his help in getting connected with the Endangered Wildlife Trust, without which this project never could have happened. Thanks also to Grant Beverley, of the Endangered Wildlife Trust. Thanks for providing guidance, knowledge, and the critical photographic data for this study; also, thanks for taking a chance on me. My sincerest thanks also goes out to the Sturgis Family, whose endowment through the Fulbright College at the University of Arkansas funded my research. I would also like to thank Dr. David Krementz for providing comments and suggestions for my project.

Additionally, I would like to thank my committee. Thank you, Dr. Steve Beaupre, for stepping up and taking over to help me finish, thank you, Dr. J.D. Willson for helping me understand RMark and the best way to analyze my data, and thank you Dr. Adam Siepielski for filling in last minute, amid hard circumstances.

I would also like to thank my epic lab mates and fellow students, who helped me get through during the times I felt like I never would. Mitchell, Alyssa, and Paul: thanks for the coffee, cocoa, and companionship in the lab. Phillip and Jake, thanks for always having an extra chair and listening ears when I needed it. Kelly and Jackie, thanks for helping me understand

MARK and R when I thought I might kill it. Alison, Anna, Evan, and Nora: Thanks for never being too tired of my thesis complaints to ignore them.

Last, but certainly not least, I would like to thank Dr. Kimberly G. Smith for taking me and my big dreams and pushing them forward into reality. I wouldn't be where I am without your help and encouragement, both in undergrad and graduate school, so thanks for always believing in me. You took me in and made Devon and I members of your graduate student family, something I will never forget. Even though you aren't here to watch me finish, this is for you. You were a one-of-a-kind advisor, and you will be forever missed.

DEDICATION

This thesis is dedicated to my late grandpa, Dr. George E. Templeton, and my late academic advisor, mentor, and friend, Dr. Kimberly G. Smith.

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INTRODUCTION

African wild dogs (*Lycaon pictus*) are large, social carnivores found in small, scattered populations throughout Africa. They are cooperative hunters and breeders, and almost all reproduction results from an alpha female. They live in highly cohesive packs that range from 2-28 adults, with a mean pack size between 5 – 9 adults (Creel 2002). Wild dogs are cursorial hunters that eat a variety of prey, focusing on ungulates ranging from 15-200kg (Creel and Creel 1995). High variation exists in home range sizes, but densities are lower than expected compared to other carnivores (Mills 1997a, Creel 2002, Creel, et al. 2004). Pomilia, et al. (2015) found the home range size for a pack in Kruger National Park (KNP), South Africa ranged from 150-1,110 km^2, with an average of 555 $km.^2$ Wild dogs' large space requirements result in small population sizes (Durant 1998, Creel 2001), even in large protected areas such as KNP (Woodroffe and Ginsberg 1998). This leads to the potential for rapid population decline under unfavorable conditions.

Disease, habitat fragmentation by humans, and interspecific competition are causing population decline for wild dogs throughout Africa (Palomares and Caro 1999, Creel and Creel 1996). They have been extirpated from many parts of Africa (Lindsey, et al. 2004, MacDonald and Sillero-Zubiri 2004) and have seen recent declines in KNP (Marnewick, et al. 2014), the one viable population remaining in South Africa (Fanshawe, et al.1997, Lindsey, et al. 2004). The extinction risk from stochastic demographic and environmental effects is higher in smaller populations (Lande 1993), and detecting risk and trends is extra challenging statistically (Ginsberg, et al 1995). Because of the continually decreasing population, extreme habitat fragmentation, and the extinction risk associated with small, isolated populations, the IUCN lists wild dogs as endangered.

Historically, conservation efforts for wild dogs have focused on monitoring rather than active management, but as wild dog numbers continue to decline, questions have been raised regarding the policies of hands-off monitoring. The Endangered Wildlife Trust (EWT) and managers of KNP are working to discover more about the survival of wild dogs in the park, including factors causing population decline. They are considering whether they should take specific actions, such as vaccination or relocation, to help mitigate negative impacts on wild dogs and increase the population. My study provides insight into numbers and survival patterns of wild dogs in KNP that will help managers know if this is a viable option.

I estimated survival rates of African wild dogs both between a 2009 and 2015 public photographic survey periods, and within the 9-month survey period ending in 2015. I analyzed the photographic data to determine the population count of dogs in 2015, and I estimated average survival rates in the park to provide a broader understanding of the wild dog population, including an up-to-date estimate of life expectancy for wild dogs in KNP. This will give managers a better idea of the population's health and threats for the future.

Ethiopian wolves (*Canis simensis*) are another highly endangered, social canid of Africa. The wolf is recognized as the most threatened African carnivore, and the rarest canid on the globe, with fewer than 500 individuals, in 7 small, isolated populations, remaining. (Sillero-Zubiri, et al. 2004). Stochastic events, (e.g. disease), can have large effects on small, widely spread populations, such as those found in wolves and wild dogs. Infectious disease, while a natural part of many ecosystems (Cleaveland 2009), has become a serious threat to endangered species. Because there is a close phylogenetic relationship between wild and domestic carnivores, and carnivores have a high susceptibility to domestic pathogens, domestic animals often serve as "reservoir" hosts for disease for wild canids (Cleaveland et al. 2002, Woodroffe and Donnelly 2011, Woodroffe, et al 2004, Cleaveland 2009). The social nature of wolves and wild dogs makes them even more susceptible to directly transmitted disease, such as canine distemper virus (CDV) and rabies (Mills 1993). For endangered canids, disease, particularly rabies and CDV have caused species decline (e.g. Ethiopian wolf *Canis simensis*) (Gordon, et al. 2015, Randall, et al. 2006, Sillero-Zubiri et al.1996) and even local extinction (e.g. African wild dog *Lycaon pictus*, Alexander, et al.1996, Gascoyne, et al. 1993, Tswalu Kalahari 2016). As protected space decreases and habitat fragmentation continues, endangered canids become increasingly prone to encounters with domestic dogs, especially near the edge of reserves (Breed, et al. 2009 and Sillero-Zubiri, et al. 2004). Contact with domestics greatly increases their chances to contract rabies or CDV, hindering conservation efforts for these two highly endangered carnivores.

Vaccination strategies in protected populations are becoming increasingly common in both wolves and wild dogs, as managers seek ways to protect these endangered canids from disease. For managers to make decisions that effectively manage disease in these critically endangered species, they must understand the context and history of CDV and rabies in wolves and wild dogs. I examined the research conducted on both diseases in both species, including outbreaks, antibody levels, and previous mitigation strategies. I sought to answer questions regarding disease prevalence and effectiveness of different mitigation techniques.

The purpose of these studies was to learn more about the survival of African wild dogs in Kruger National Park to help inform managers of population dynamics, analyze the effects of disease and disease management on African wild dogs and other African canids, and guide future management strategies.

LITERATURE CITED

Alexander KA, Kat PW, Munson LA, Kalake A, Appel MJG. 1996. Canine distemper-related mortality among wild dogs (Lycaon pictus) in Chobe National Park, Botswana. Journal of Zoo and Wildlife Medicine **27**:426–427.

Breed AC et al. 2009. Disease Management in Endangered Mammals. Pages 215–239 in R. J. Delahay, G. C. Smith, and M. R. Hutchings, editors. Management of Disease in Wild Mammals. Springer, Tokyo.

Cleaveland S, Hess GR, Dobson AP, Laurenson MK, McCallum H, Roberts MG, Woodroffe R. 2002. The role of pathogens in biological conservation. Pages 139–150 in P. J. Hudson, A. Rizzoli, B. Grenfell, and H. Heesterbeck, editors. The Ecology of Wildlife Diseases. Oxford University Press, Oxford.

Cleaveland S. 2009. Viral threats and vaccination: disease management of endangered species. Animal Conservation **12**:187–189.

Creel S, Creel NM. 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour **50**:1325–1339.

Creel S, Creel NM. 1996. Limitation of African Wild Dogs by Competition with Larger Carnivores. Conservation Biology **10**:526–538.

Creel S. 2001. Four Factors Modifying the Effect of Competition on Carnivore Population Dynamics as Illustrated by African Wild Dogs. Conservation Biology **15**:271–274.

Creel S. 2002. The African wild dog: behavior, ecology, and conservation. Princeton University Press, Princeton, N.J.

Creel S, Mills MGL, McNutt JW. 2004. Demography and population dynamics of African wild dogs in three critical populations. Pages 337–350 in D. W. Macdonald and C. Sillero-Zubiri, editors. The Biology and Conservation of Wild Canids. Oxford University Press, New York.

Durant SM. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology **67**:370–386.

Fanshawe JH, Ginsberg JR, Sillero-Zubiri C, Woodroffe R. 1997. The status and distribution of remaining wild dog populations. Pages 11-57 in R. Woodroffe, J.R. Ginsberg, and D.W. Macdonald, editors. The African wild dog: status survey and conservation action plan. IUCN Gland, Switzerland.

Gascoyne SC, King AA, Laurenson MK, 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. The Onderstepoort Journal of Veterinary Research **60**:415–420.

Ginsberg JR, Mace GM, Albon S. 1995. Local Extinction in a Small and Declining Population: Wild Dogs in the Serengeti. Proceedings of the Royal Society of London B: Biological Sciences **262**:221–228.

Gordon CH, Banyard AC, Hussein A, Laurenson MK, Malcolm JR, Marino J, Regassa F, Stewart A-ME, Fooks AR, Sillero-Zubiri C. 2015. Canine Distemper in Endangered Ethiopian Wolves. Emerging Infectious Diseases **21**:824–832.

Lande R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. American Naturalist **142**:911–927.

Lindsey P, du Toit JT, Mills MGL. 2004. The distribution and population status of African wild dogs (Lycan pictus) outside protected areas in South Africa. South African Journal of Wildlife Research **34**:143–151.

Macdonald DW, Sillero-Zubiri C, editors. 2004. The biology and conservation of wild canids. Oxford University Press, Oxford ; New York.

Marnewick K, Ferreira SM, Grange S, Watermeyer J, Maputla N, Davies-Mostert HT. 2014. Evaluating the Status of and African Wild Dogs Lycaon pictus and Cheetahs Acinonyx jubatus through Tourist-based Photographic Surveys in the Kruger National Park. PLoS ONE **9**:e86265.

Mills MG. 1993. Social systems and behaviour of the African wild dog Lycaon pictus and the spotted hyaena (Crocuta crocuta) with special reference to rabies. The Onderstepoort Journal of Veterinary Research **60**:405–409.

Mills MGL. 1997. Wild Dog, Lycaon pictus. Pages 192-193 in L. Hes and M.G.L. Mills, editors. The Complete book of southern African mammals. Struik Winchester, Cape Town, South Africa.

Palomares F, Caro TM. 1999. Interspecific Killing among Mammalian Carnivores. The American Naturalist **153**:492–508.

Pomilia MA, McNutt JW, Jordan NR. 2015. Ecological predictors of African wild dog ranging patterns in northern Botswana. Journal of Mammalogy **96**:1214–1223.

Randall DA, Marino J, Haydon DT, Sillero-Zubiri C, Knobel DL, Tallents LA, Macdonald DW, Laurenson MK. 2006. An integrated disease management strategy for the control of rabies in Ethiopian wolves. Biological Conservation **131**:151–162.

Sillero-Zubiri C, King AA, Macdonald DW. 1996. Rabies and mortality in Ethiopian wolves (Canis simensis). Journal of Wildlife Diseases **32**:80–86.

Sillero-Zubiri C, King AA, Macdonald DW. 2004. Afroalpine ecology, solitary foraging, and intense sociality amongst Ethiopian wolves. Pages 311–322 in D. W. Macdonald and C. Sillero-Zubiri, editors. The Biology and Conservation of Wild Canids. Oxford University Press, New York.

Tswalu Kalahari. 2016. "African Wild Dogs at Tswalu." http://www.tswalu.com/media/blog-article/african-wild-dogs-at-tswalu.

Woodroffe R, Ginsberg JR. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. Science **280**:2126–2128.

Woodroffe R, Cleaveland S, Courtenay O, Laurenson MK, Artois M. 2004. Infectious disease in the management and conservation of wild canids. Pages 123–142 in D. W. Macdonald and C. Sillero-Zubiri, editors. Biology and Conservation of Wild Canids. Oxford University Press, New York.

Woodroffe R, Donnelly CA. 2011. Risk of contact between endangered African wild dogs Lycaon pictus and domestic dogs: opportunities for pathogen transmission. Journal of Applied Ecology **48**:1345–1354.

CHAPTER 1- ESTIMATING ABUNDANCE AND SURVIVAL RATES OF AFRICAN WILD DOGS FROM PUBLIC PHOTOGRAPHIC CENSUS DATA IN KRUGER NATIONAL PARK, SOUTH AFRICA

ABSTRACT

African wild dogs (*Lycaon pictus*) (AWD) are endangered carnivores whose populations are decreasing from habitat loss and fragmentation, as well as interspecific competition with sympatric carnivores. Survival rates are especially low in Kruger National Park (KNP), though it is unclear why. I estimated survival rates in KNP over two different time spans that my data allowed, 6 years and 9 months, and recapture probability using photographic survey data and the program RMark. I found that the survival rate over six years (2009-2015) was 3.2%. Within the 9-month survey period (September 2014 – June 2015), monthly survival rates for the wild dogs varied by region of the park, with apparent survival (φ) at 0.807 (0.695-0.885 95%CI), 0.989 (0.852-0.999), and 0.975 (0.946-0.989) for dogs in the northern, central, and southern region of the park, respectively. The survival rate over the entire 9-month survey was estimated at 14.6%, 90.1%, and 79.8% for dogs in the northern, central, and southern regions, respectively. Extrapolating that to an annual survival rate, I estimated mean lifespan to be .39 years, 7.2 years, and 3.3 years for the northern, central, and southern regions, respectively, and 1.41 years for all regions combined. Recapture probability for the dogs varied by region and month, ranging between 0.07 and 0.828, with an overall monthly recapture probability average in the park of 0.483 (SE=0.0148). I also estimated abundance of African wild dogs in KNP in 2015, which I found to be 298 (SE=12.1) individuals. My population estimate showed an increase in wild dogs in KNP over the last 5 years, but my survival and life span estimates were lower than previously reported for the park. The population increase could be inflated from using a new estimation technique; I used the program SPECRICH to estimate abundance instead of POPAN in MARK to estimate number of packs and extrapolate abundance from there. Most likely, however, based on the size of the increase, the results are not artificial. The differences in survival rates by

region of the park can most likely be explained by difference in competitor density, but more work needs to be done to determine the factors influencing survival in each region. The especially low lifespan estimate in the northern region of the park could be the result of a lack of data, but needs to be examined further. Managers in KNP, and other protected areas, should be able to use these survival, lifespan, and detection estimates to better study and manage wild dogs.

INTRODUCTION

African wild dogs (*Lycaon pictus*) are large, social carnivores found throughout Africa. They are cooperative hunters and breeders, and almost all reproduction results from an alpha female. They live in highly cohesive packs that range from 2-28 adults, with a mean pack size between 5 – 9 adults (Creel 2002). Some packs in Kruger National Park (KNP), South Africa include over 30 dogs (personal observation). Wild dogs are cursorial hunters that eat a variety of prey, focusing on ungulates ranging from 15-200kg, including warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*), gazelle (*Eudorcas thomsonii*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and kudu (*Tragelaphus strepsiceros*) (Creel and Creel 1995). High variation exists in home range sizes, but densities are low compared to other carnivores (Mills 1997a, Creel 2002, Creel, et al. 2004). A pack may hunt a range as large as 2,000 km^2, and even in Kruger National Park, where prey is less mobile, Pomilia, et al. (2015) found the home range size for a pack ranged from 150-1,110 km^2, with an average of 555 km^2. Wild dogs' large space requirements result in small population sizes (Durant 1998, Creel 2001), even in large protected areas such as KNP (Woodroffe and Ginsberg 1998), a nearly 2 million ha reserve. This leads to the potential for rapid population decline under unfavorable conditions.

Wild dog numbers declined by 70% in the 20th century due to culling practices by park managers. Managers believed wild dogs' cursorial hunting style to be savage and disruptive to ungulate populations, so dogs were hunted and killed (Childes 1988). Systematic culling ended in the 1970s (Rasmussen 1999), but now disease, habitat fragmentation by humans, and interspecific competition are causing population decline throughout Africa (Palomares and Caro 1999, Creel and Creel 2002). Wild dogs are limited by interspecific competition with more dominant carnivores, specifically lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*)

(Creel and Creel 1996, Durant 1998, Palomares and Caro 1999, Darnell, et al. 2014). Because wild dogs are now mostly limited to fenced reserves, the competition has gotten stronger. The have now been extirpated from many parts of Africa (Lindsey, et al. 2004, MacDonald and Sillero-Zubiri 2004) and have seen recent declines in KNP (Marnewick, et al. 2014), the one viable population remaining in South Africa (Fanshawe, et al.1997, Lindsey, et al. 2004). Global population numbers have dropped below 5,000, of which only around 1,400 are adults (Mills 1997a, Woodroffe and Sillero-Zubiri 2012) and the 2010 wild dog population estimate in KNP was 151 (Marnewick, et al. 2014). Outside of a few major reserves in Africa, including KNP, Selous Game Reserve in Tanzania, and Chobe National Park and Moremi Game Reserve in Botswana, the dogs currently exist in small, isolated populations, which greatly increases conservation challenges (Marnewick, et al. 2014). The extinction risk from stochastic demographic and environmental effects is higher in smaller populations (Lande 1993), and detecting risk and trends is extra-challenging statistically (Ginsberg, et al 1995). Because of the continually decreasing population, extreme habitat fragmentation, and the extinction risk associated with small, isolated populations, the IUCN lists wild dogs as endangered.

Historically, conservation efforts for wild dogs have focused on monitoring rather than active management, but as wild dog numbers continue to decline, more questions have developed regarding the policies of hands-off monitoring. The Endangered Wildlife Trust (EWT) and managers of KNP are working to discover more about the survivability of wild dogs in the park, including factors causing the decline. They are considering whether they should continue simply monitoring the KNP wild dog population or take specific actions, such as vaccination or relocation, to help mitigate negative impacts on wild dogs and increase the population size. A metapopulation of wild dogs has been established through reintroduction into smaller protected areas in South Africa (Davies-Mostert, et al. 2015), and managers have considered incorporating KNP into that system. My study provides insight into population sizes and survival patterns of wild dogs in KNP that will help managers determine if this is a viable option.

My first priority was to estimate survival rates of African wild dogs residing in KNP. Survival rates are lower in KNP than other areas of Africa (Mills 1997a, b, Creel 2002) for reasons that are not well known, though competition from high carnivore density has been suggested (Mills and Gorman 1997). To monitor the KNP wild dog population, EWT in South Africa has conducted a 9 to 12-month public photographic survey of wild dogs every 5-6 years over the past three decades (Endangered Wildlife Trust 2014). During this census, the EWT advertises a campaign calling for photos from tourists anytime they encounter wild dogs in KNP. They ask for photographs of as many dogs as possible, with metadata such as location, time of day seen, number of dogs seen, sex of dogs if possible. They offer prizes in different photograph categories to help incentivize submission. Wild dog coat patterns are individually unique, which allows photographs to be used for population estimations (Creel 2002). Photographic surveys have taken place in 1988/9 (June 1988–June 1989) (Maddock and Mills 1994), 1994/5 (June 1994–June 1995) (Wilkinson 1995), 1999/2000 (May 1999–June 2000) (Davies 2000), 2004/5 (October 2004–April 2005) (Kemp and Mills 2005), and 2008/09 (July 2008–April 2009) (Marnewick, et al. 2014), and most recently in 2014/15 (September 2014 – June 2015).

My study sought to build on the research of EWT by estimating survival rates of African wild dogs both between the 2009 and 2015 survey periods and within the 9-month survey period ending in 2015. I analyzed the photographic survey data to determine the population size of dogs in 2015, as was done in past surveys, but I also sought to determine average survival rates in the park to provide more understanding of the wild dog population, including an up-to-date estimate of life expectancy for wild dogs in KNP. A current estimation of the total wild dog population in KNP, along with recent survival rates, will give managers a better idea of the population's current health and help them understand how the population may change in the future. I also wanted to determine if the current methodology for surveys, especially timing, was the best way to estimate survival and population size; and if not, I sought to suggest improvements for future studies.

Previous studies have shown the average lifespan (length of existence) for African wild dogs is 6 - 10 years, depending on the region of Africa in which they live (Creel 2002), but in KNP, most dogs do not survive past 7 years of age (Mills 1997a). Based on these findings, I hypothesized that the 5-year survival rate would be very low (<15%). Most dogs identified in the 2008/2009 survey were already adults, and therefore I assumed most would not be alive in 2014/2015. However, I hypothesized that within the most recent 9-month survey period, from September 2014 to June 2015, the survival rate would be much higher, with at least 50% surviving the entire survey period.

METHODS

Study Site

I conducted my study in KNP, a partially fenced reserve in the northeast portion of South Africa bordering Mozambique and a few neighboring private reserves (Figure 1). KNP covers 1.9 million ha and is known for its heterogeneity – it straddles two climatic zones, the temperate south, and sub-tropic and tropical north (Mabunda et al. 2003). There are 35 recognized landscapes, but savanna dominates most of the park (Gertenbach 1983, Mabunda et al. 2003). Managers in KNP work to actively maintain natural heterogeneity in the system, both spatially and temporally (Rogers 2003). For part of this analysis, I examined three distinct regions in the park: the northern (north of the Olifants River), central (between the Sabie and Olifants River), and the southern region (south of the Sabie River) (Figure 2). The regions differ in density of roads and tourist camps, and therefore tourist volumes, which can lead to variation in sampling effort and detection probability, especially when using public sightings data (Marnewick, et al. 2014). The regions also differ in terms of prey biomass, which has been found to be positively correlated with lion densities in the park (Ferreira and Funston 2010), but Mills and Gorman (1997) found that wild dog density in KNP was not influenced by prey dispersal.

Sampling Methods

In 1988, EWT developed a public photographic survey, lasting 9-12 months, to better monitor the wild dog population in KNP (Maddock and Mills 1988). Photographic surveys have since occurred in the park every 5 or 6 years (Marnewick 2014). During the coordinated survey periods, EWT encouraged park visitors to send in photos when they encountered wild dogs by offering prizes for the best photographs submitted. Along with photographs, EWT asked tourists to submit the date and location of the sighting, total number of dogs seen, and age and sex of dogs seen, if known. These surveys were promoted to park visitors and staff using methods described by Marnewick et al. (2014), including posting advertisements for the survey around every rest camp and sightings boards in the park.

The two most recent surveys were completed from July 1, 2008 to April 30, 2009 and from September 21, 2014 to June 21, 2015. EWT chose this particular time of year for surveys because wild dogs breed at mid-year, and post-breeding is a good time to estimate their population size (Marnewick 2014). In each of the past two surveys, one observer (Grant Beverley of EWT) visually analyzed the submitted photos to determine how many individual dogs were seen over each 9-month period. The wild dogs were identified by Beverley by their coat patterns, which are unique to each dog, and each sighting location was georeferenced based on the location description given in the submission. Packs were easily distinguishable, and each pack was given a number and a name, usually based on locations in the park. Each dog was assigned to a pack, based on which pack it was seen with the most (it was not common for dogs to change packs).

Sampling distribution was limited in these surveys because members of the public are not allowed to travel off the designated roads in KNP, and therefore almost all the sightings came from locations along roadways (Figure 3). Park staff and researchers submitted photos as well, which accounts for the sightings not along the road. Uneven sampling also occurred between regions of the park, due to differences in number of visitors in each region (Marnewick 2014). I took this into account when building my population estimation models (see below).

Data Analysis

First, I worked to determine a population estimate for wild dogs alive during the 2014-15 survey period. For the 2008-2009 survey period, Marnewick, et al. (2014) estimated the population to be 151 dogs. They used a POPAN model in program MARK (White 1999) to estimate number of packs in the park, and multiplied that by the average pack size in KNP. However, this underestimated their population count, as they recorded sightings of 156 dogs, and there is a high probability they did not see every dog in the park. Pack size can vary greatly, and did not appear to give the most accurate estimation. Therefore, rather than calculate number of packs and an average pack size to get an abundance number for the dogs, I calculated an estimate of total number of dogs in KNP using a program that was originally made to calculate species richness in an area, SPECRICH (Hines 1996). This program uses methods described by

Burnham and Overton (1979), using the total number of species seen, and the number of species seen once, twice, 3x, 4x and then 5 or more times, to estimate the total number of species. While it was built to calculate species richness, I was able to use it in a similar manner to estimate dog abundance. I simply considered each dog its own species, and the program found an estimate of total dogs present during the survey.

To determine the survival rate between the 2008-09 and 2014-15 surveys, I visually compared the photographs of each dog in the 2008-09 survey to each dog in the 2014-15 survey. I attempted to find a program that would analyze and compare the photos for me, but none have been created that look at the entire individual rather than a certain spot on the body (e.g. a sea turtle's nose). I calculated the percentage of dogs seen in the first survey that were seen again in the second survey period as my survival rate, under the assumption that if a dog were still alive it would have been seen. To estimate the survival rate during the 2014-15 survey, I used open Cormack-Jolly-Seber (CJS), full-likelihood models using the package "RMark" (Laake 2013) in program R (version 3.2.3)(R Core Team 2013), which gave me estimates of apparent survival rate (ϕ) and recapture probabilities (p).

I divided the survey into 10 monthly encounter periods, beginning with September 2014 and ending in June 2015. If a dog was seen at any point during that month of the survey, it was considered "captured." I created mark-recapture encounter histories for each dog (n=233) for the 10 encounter periods. I also gave each dog its own group identifiers of sex, pack number, pack size, and park region. Pack size was assigned as small ($\leq$ 5 dogs), medium (>5 and <15 dogs), and large ($\geq$15 dogs), based on the number of dogs in the pack, and park region was decided based on where in the park the pack was most often encountered.

To ensure an accurate estimate of detection probability, I attempted to incorporate effort into my models, by considering the differentiation of sighting effort between time periods, or months. I chose to use the number of sightings divided by the number visitors in the park (Kruger National Park, *pers. comm.*) for each month as my measurement of effort, making three key assumptions: (1) all visitors are actively looking for wild dogs, (2) all visitors have an equal opportunity to see wild dogs, and (3) all visitors who saw wild dogs reported the sighting, or at least the percentage of those who did report sightings did not change over time. However, when I assigned each sampling occasion an effort coefficient as a covariate, it became too much data for the model and the models did not converge. I decided to drop the effort covariate for the formal modeling but keep it in mind for my interpreting the results.

After dropping the effort coefficient, I created CJS models in RMark using 3 covariates for apparent survival (φ) and recapture probability (p): time (month), pack size, park region. I evaluated 18 models (Table 1) in total: (1)p and φ constant, (2-16) each possible combination of p and φ varying by the 3 covariates and constant, and finally (17) p varying by time + region and φ varying by time and (18) p varying by time + region and φ varying by region. I did not test a model where p or ϕ varied with sex because behavior between males and females in packs does not differ enough to warrant different capture or survival probabilities (Marneweck 2014). Akaike Information Criterion (AIC; Akaike 1974) was used to select the most plausible model given the data (Burnam and Anderson 2002). I ranked the models according to AIC values adjusted for small sample sizes (AICc, Burnham and Anderson 2002) and used AICc weights to determine the strength of evidence for each of the models. Models with a higher weight (and lower AICc value) were better at explaining the variation in the data. Using my top model, I estimated survival and detection probabilities for all packs at all occasions, and then simplified the data and compared survival and detection among regions.

Finally, I extrapolated the apparent monthly survival rates through my survey to obtain an estimate of annual survival (S). I first found the 9-month survival rates for each region by multiplying the 9 monthly survival rates over the survey period. To get to annual survival (S) for each pack, I took the 9-month rate to the power of 1.33, assuming the 9-month rate gave a good estimate for the rest of the year. I then used the annual rate to estimate the mean life span (MLS) for each region separately and for dogs in the park as a whole using the equation MLS=1/-ln(S). I calculated a 95% confidence interval (CI) for the entire park MLS by finding the 95% CI for monthly survival, calculating a minimum and maximum annual survival rate and using the minimum and maximum S to get to minimum and maximum MLS.

RESULTS

Individuals Captured and Abundance

During the 9-month survey in 2014-2015, a total of 677 wild dog sightings were reported to EWT. A total of 233 individual wild dogs were seen: 109 (46.7%) male, 115(49.3%) female, and 9 (3.9%) unidentifiable. The dogs were seen in 22 different packs, and pack size varied greatly, ranging from 2 (usually a dispersal group) to 31 individuals with a mean pack size of 10.5 (SE=1.48). There were 8 packs in the south, 8 packs in the central region, and 5 packs in the north. One small pack of 2 female dogs, pack 19, was seen in all 3 regions of the park, most likely because it was a dispersal group and searching to find another pack to join. The mean pack size in the central and southern sections were larger (12.3 and 11.6) than the north (7.6), but the difference was not significant (ANOVA, F=0.721, p=0.50). Using the program SPECRICH, I estimated the population to be 298 dogs (SE=12.1). Only 33% (n=77) of the dogs were seen in at least half the survey months (5 or more), and some dogs went 4 months between sightings, proving the difficulty of detection in this species, at least while using public photographic surveys.

6-year Survival Rates

In the 2008-09 photographic survey, the public submitted pictures of 156 individual dogs. Another 165 dogs were seen by tourists and wildlife managers in the year that followed, bringing the total to 321 dogs to look for in the 2014-2015 survey. I compared all 233 of the dogs from the 2014-2015 survey to all 321 dogs in 2008-2010 study period and found that only 17 had survived over the 6 years, and only 5 of those were from the 2008-09 survey. The survival rate over the 6 years was 3.2%, and over the 5 years from 2010-2015 was 7.2%. Effectively, no dogs are surviving over a 6-year period in KNP.

2014-2015 Recapture Probability

CJS analysis of the census data favored a model where individual recapture probability (p) varied by time and region and apparent survival (φ) varied by park region (Table 2). The top model, φ(~region)p(region + time), had a AICc weight of 0.934, and the ΔAICc between it and the next highest model was greater than 5, so I chose to estimate the parameters using only the top model rather than model average. Individual recapture probabilities were estimated for each month in each region (Figure 4) and for the park as a whole (Figure 5). Each of the three regions followed a similar trend over time, starting low, increasing until December, then decreasing until the end of the survey, with a spike in recapture probability in April. December had the highest recapture probability for dogs in all regions, with the total park average at 0.698 (SE=0.025), and June, the last month of the survey, was the lowest, averaging 0.145 (SE=0.015). Dogs in the southern region had the highest recapture probability each month, ranging from 0.227 in June to 0.839 in December, followed by the northern region, 0.144 to 0.735, and the central had the lowest, 0.072 to 0.563.

2014-2015 Monthly Apparent Survival Rates

Model selection favored the CJS model where apparent survival varied by region (Table 2). The model yielded an estimate of apparent survival between survey periods (months) for dogs in each region (constant over each month), and I used a weighted average based on number of packs per region to determine an estimate for the entire park (Figure 6). Dogs in the central region of the park had the highest monthly apparent survival rate, at 98.9% with a 95% confidence interval of 85.2% to 99.9%, followed by the south at 97.5%, with a 95% CI of 94.6% to 98.9%, then the north at 81%, with a 95% CI of 69.5% to 88.5%. The average survival rate for all dogs in the park was a 94.2% (95% CI: 91.0% to 97.5%) from month to month.

2014-2015 9-month Apparent Survival Rates

Nine-month survival rate was 14.6% for the north, 90.1% for the central region, and 79.8% for the south. Using the average monthly survival rate across the park of 94.2% (SE=1.57%), I estimated the 9-month survival rate of dogs of all regions combined to be 58.7%. Using the standard error to set a minimum and maximum monthly rate gave a total park 9-month survival rate 95% CI of 42.7% to 79.7% (Table 3).

Mean Life Span

I used the 9-month survival rates to calculate an annual survival rate for each region. The central region again had the highest apparent survival. The annual survival rates were 7.71%

(95%CI 1.3% to 23.1%) for the north, 87.1% (14.7% to 99.1%) for the central region, and 74.1% (51.3% to 87.4%) for the south. The total park annual survival rate was 49.2%, with a 95% CI of 32.2% to 73.9% (Table 3).

Using the average annual survival rate for dogs in each region I estimated the mean life span (MLS) and found the life span to vary greatly between the regions. The MLS for dogs in northern packs was .39 years, or 3 months, for dogs in central packs it was 7.24 years, and for dogs in southern packs it was 3.33 years (Figure 7). Using the dogs' annual survival over the whole park I found the estimate for MLS for wild dogs in KNP to be 1.41 years, with a 95% (CI) of 0.88 and 3.31 years (Table 3).

Because so few dogs were seen in the north, the northern region survival rates are most likely under estimated. If dogs were truly only surviving three months, no population would persist in the north. Considering this, I also estimated the annual survival for dogs in the park without the two northern packs that were seen with only two or three dogs, as those were most likely dispersal groups and have a much smaller chance of survival. This left only three northern packs included in my weighted average for annual survival for the whole park. With this change, I estimated annual survival of dogs for the whole park to be 58.4% and the resulting MLS to be 1.85 years, with a 95% confidence interval of 39.7% to 84.6% and 1.08 years to 6 years.

DISCUSSION

The 2014-2015 survey was more successful in gathering data than the 2008-2009, with almost double the number of survey entries. This is probably due to several factors, including better advertising of the survey, the rising use of social media, and the ubiquity of smart phones with cameras. As the surveys continue to gain more traction with tourists, the data will hopefully continue to become more robust. A total of 233 dogs were seen in the 2014-15 survey, compared to only 156 in the 2008-09 survey. This could be because the population size is increasing, but it could also be because the number of entries increased.

The population estimate from the 2014-15 survey was 298, which was almost double the estimate in 2008-09. It is difficult to consider this a meaningful comparison, however, because the method of finding the park population size differed between the two surveys. If using the average pack size and number of packs in the 2014-15 survey, the population estimate is 231 (22 packs x 10.5 dogs/pack). Comparing that to the 151population size estimate in 2008-09, the number of dogs has increased in the last six years, but it would also be beneficial to go back and estimate the population size in 2008-09 using SPECRICH to get a more accurate estimate at that point, then compare it to the current estimate. Either way, however, it appears that the population of wild dogs in Kruger National Park has increased from 2008 to 2015. Population growth is important to see and sends a positive message to current managers that the dogs' status is improving in Kruger. Looking at the low survival between surveys, however, it is obvious that a lot can change in the population over six years, and surveying the population more often would be extremely beneficial.

The survival rate of wild dogs in KNP over a 5-year period was almost zero, suggesting the mean lifespan for the majority of dogs in the park is under 5 years. The estimated MLS of 1.41 years from the 2014-15 survey confirmed that many dogs are not making it to 2 years, much less 5 years. This lifespan is lower than most previous research has suggested. Mills (1997a) estimated mean lifespan for dogs in KNP to be around 4 years. However, one study found that the dogs' mean lifespan differed across Africa, and while MLS was estimated at 4.5 years in KNP, they found only 16% of dogs survive to age 2 (Creel, et al. 2004). These results support my findings of a mean lifespan of only 1.41 years in KNP. Because I had to extrapolate from the estimated 9-month apparent survival rate to get to an annual survival rate, my estimate could be lower than the actual MLS, but that is impossible to know with current survey methods. Monitoring the population over a shorter time interval, such as every 2 years, should help managers see if dogs are surviving that long, and get a more accurate estimate of lifespan. The differences in MLS between the regions was large, due to differences in monthly survival probability that became greater as I multiplied them out to a yearly rate.

The survival rate over the 9-month survey period was much higher than the 5 year, but varied among the three regions. This could be due to differences in vegetation structure, competitor density, or prey density, though the latter has not been true in Kruger previously. It could also be caused by a difference in available data, due to wild dog density and tourist density. The lower density of tourists and roads in the northern region of the park is likely contributing to the lower number of sightings of dogs in the region. The recapture probability for the dogs in the northern packs was higher than in the central packs, which suggests that at least some dogs that exist in the north are being seen repeatedly. It is possible, however, that a lower density of roads in the north limits access points for spotting dogs, causing the same packs to be repeatedly encountered, while others go un-sampled. It is important to consider that less data from the north could have produced artificial results, and until more data from the northern region is available, the results should be approached with caution. Dedicated research on dog occupancy and abundance in the northern region of the park will also give managers a better idea of survival rates.

Wild dogs in the central region are surviving longer than dogs in the south and much longer than dogs in the north. Determining why this is happening is key to managing the population in the future. Pack territories overlap more in the south and central regions, which on a basic level would suggest more wild dog competition and lower survival rates, however that is not the case. More knowledge of lion and other top competitor densities throughout the park could help explain the differences in survival in the different regions, and other possible causes such as vegetation and prey density should be explored as well. If vegetation resources are scarcer for wild dog prey species in the north, making prey species more scare, there could be increased intra and interspecific competition for resources, leading to a decline in survival.

One way to improve this study is to lengthen the survey time to examine how survival changes over an entire year. Surveying a population for a full year or 18 months would give a more accurate survival rate estimation, and more could be gleaned on how survival varies over time/season. As climate changes over time, and weather patterns such as El Niño cause variation in resources, researchers could get a clearer understanding of what factors affect survival more strongly. While longer and/or more common surveys would inevitably take more resources, specifically more people to visually analyze the pictures, it would be beneficial to determine if there is a certain point at which survival of dogs drops off or increases drastically. The previous study done in KNP, which showed only 16% of dogs survive to adulthood, found that adult survival rate is much higher, almost 80% (Creel, et al 2004). Gathering data through the winter, when pups emerge from the den and begin moving with the packs, with more frequent, yearlong surveys, could help managers track pup and adult survival separately, and determine if pup survival is still the population bottleneck (Creel and Creel 1996), or if survival declines at a steady rate from the first few months through five years out. Determining what life stage is experiencing the highest mortality rates will allow managers to make decisions that support survival at that life stage, increasing the population. I would also suggest further study on dog survival rates using more detailed spatial data, such as the GPS coordinates for each of the dog sightings in this study. The sightings could be mapped out over time and overlapped with vegetation structure and competitor densities. Lions and other large competitors have been known to influence wild dog movements and survival in other parks (Creel 1996, 2002, Darnell, et al. 2014), and mapping wild dog sightings over competitor densities could give managers a better idea of how competition is influencing wild dog survival.

The recapture probability for dogs differed by month and by region, with the highest recapture rates occurring in the month of December. One possible reason for this is the increase of tourists in the park during the Christmas holiday, increasing the amount of sighting effort and sightings. During December 2014, 184,256 guests visited Kruger, while only 120,507 visited in November and 111,534 visited in January (Kruger National Park, *pers. comm.*), and it was also the month with the highest number of sightings at 108. December could also be a period of more activity for dogs, resulting in higher visibility. The peak in recapture probability in April is intriguing, and there is no obvious reasoning that has been described in dog studies previously. One possible cause is another increased period of activity prior to the beginning of denning season, as dogs prepare to find a spot to settle in for a few months. April is also a time when yearlings will disperse from their packs prior to the new breeding season, causing more wild dog movement throughout the park. The sharp drop in recapture probability near the end of the survey could be explained by a few different reasons. Many of the dogs in the data were not seen for 3 or even 4 months and then seen again, so some of the drop off in survival in the last two months of the survey could be due to the survey ending and there being no chance to see the dogs again in the next month or two. In addition, May and June, the last two months of the survey, are the beginning of denning season, when dogs are rarely seen. The decrease in recapture probability during this time makes sense, as dogs spend most of the time at the den except for a few hours hunting at dawn and dusk.

Regionally, the south had the highest recapture probabilities, followed by the north, then the central region. I expected the southern region to have highest recapture probabilities because it has the highest density of roads and tourist camps; therefore, most tourists spend much of their time in the south, leading to increased effort in that area. In the north, there are usually fewer tourists, and according to the census, fewer dogs (38 in 5 northern packs compared to 93 in 9 central packs and 102 in 8 southern packs) than the other regions. The central region also has a larger average wild dog pack size and higher density of roads than the north (Figure 8), suggesting sightings should be easier. I therefore expected the lowest recapture rate in the north; however, the central region had the lowest estimated recapture rate. One possible explanation is that in the central region the dogs might not be spending as much time close to the road, where they are easily visible for tourists, due to lions. As home to almost half the park's lion population, the central region is known to be "big cat territory" (Images of a Great African Park). Studies show lion movement affects wild dog movement (Cozzi et al. 2012, Darnell, et al. 2014), and if lions are spending time close to roads, the wild dogs are most likely avoiding them. Another possible explanation is the vegetation structure of the central region. Wild dogs have been found to move along roadways more when the vegetation is thick (Abrahms, et al. 2016) because the clear path on the road requires less energy. Because the region's vegetation is more grassland than wooded savannah, if competitors (e.g. lions) are using the roads in the central region, the dogs may be avoiding the roads, making it harder for them to be seen by tourists.

My project is important for developing an effective management strategy for conservation of African wild dogs in reserves. The dogs appear to be dying sooner than expected or previously thought, which is important information for understanding population dynamics and implementing effective management strategies. My sampling procedure using the photographic census was affected by unequal sampling effort, which should be corrected as much as possible in future studies to more accurately estimate survival rates. With more work in this area, we can acquire better estimates of survival and work towards determining the factors currently lowering long-term survival rates. Once this information is known, park managers can adjust management strategies to increase the dogs' survival and/or manage the metapopulations in a way to increase the species' numbers even with low survival rates.

LITERATURE CITED

Abrahms B., Jordan N. R., Golabek K. A., McNutt J. W., Wilson A. M., Brashares J. S. 2016. Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. Animal Conservation **19**:247–255.

Anderson DR. 1975. Population ecology of the mallard: V. Temporal and geographic estimates of survival, recovery, and harvest rates. Federal Government Series 125, Resource Publication. U.S. Fish and Wildlife Service. Available from http://pubs.er.usgs.gov/publication/rp125 (accessed April 22, 2018).

Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag, New York.

Burnham KP, Overton WS. 1979. Robust Estimation of Population Size When Capture Probabilities Vary Among Animals. Ecology **60**:927–936.

Childes SL. 1988. The past history, present status and distribution of the Hunting dog Lycaon pictus in Zimbabwe. Biological Conservation **44:**301-316.

Cozzi G, Broekhuis F, McNutt JW, Turnbull LA, Macdonald DW, Schmid B. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology **93**:2590–2599.

Creel S, Creel NM. 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour **50**:1325–1339.

Creel S, Creel NM. 1996. Limitation of African Wild Dogs by Competition with Larger Carnivores. Conservation Biology **10**:526–538.

Creel S. 2001. Four Factors Modifying the Effect of Competition on Carnivore Population Dynamics as Illustrated by African Wild Dogs. Conservation Biology **15**:271–274.

Creel S. 2002. The African wild dog: behavior, ecology, and conservation. Princeton University Press, Princeton, N.J.

Creel S, Mills MGL, McNutt JW. 2004. Demography and population dynamics of African wild dogs in three critical populations. Pages 337–350 in D. W. Macdonald and C. Sillero-Zubiri, editors. The Biology and Conservation of Wild Canids. Oxford University Press, New York.

Darnell AM, Graf JA, Somers MJ, Slotow R, Szykman Gunther M. 2014. Space Use of African Wild Dogs in Relation to Other Large Carnivores. PLoS ONE **9**:1–9.

Davies, HT. 2000. The 1999/2000 wild dog photographic survey. South African National Parks unpublished report, South African National Parks, Skukuza.

Davies-Mostert HT, Mills MGL, Macdonald DW. 2015. The Demography and Dynamics of an Expanding, Managed African Wild Dog Metapopulation. African Journal of Wildlife Research **45**:258–273.

Durant SM. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology **67**:370–386.

Endangered Wildlife Trust. 2014. Conservation in Action: Integrated Report 2013-2014. <http://www.ewt.org.za/conreports/2014/book.swf >. Accessed 20 April 2016

Fanshawe JH, Fitzgibbon CD. 1993. Factors influencing the hunting success of an African wild dog pack. Animal Behaviour **45**:479–490.

Fanshawe JH, Ginsberg JR, Sillero-Zubiri C, Woodroffe R. 1997. The status and distribution of remaining wild dog populations. Pages 11-57 in R. Woodroffe, J.R. Ginsberg, and D.W. Macdonald, editors. The African wild dog: status survey and conservation action plan. IUCN Gland, Switzerland.

Ferreira SM, Funston PJ. 2010. Estimating lion population variables: prey and disease effects in Kruger National Park, South Africa. Wildlife Research **37**:194–206.

Ginsberg JR, Mace GM, Albon S. 1995. Local Extinction in a Small and Declining Population: Wild Dogs in the Serengeti. Proceedings of the Royal Society of London B: Biological Sciences **262**:221–228.

Gertenbach WPD. 1983. Landscapes of the Kruger National Park. Koedoe **26**:9–121.

Hines, JE. 1996. SPECRICH Software to compute species abundance from empirical species abundance distribution data. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/specrich.html.

Images of a Great African Park. The Central Region | Game Filled Savannas. n.d.. Siyabona Africa. Available from http://www.krugerpark.co.za/Kruger_National_Park_Regions-travel/Krugerpark-the-central-region.html (accessed April 12, 2018).

Kahle D, Wickham H. 2013. ggmap: Spatial Visualization with ggplot2. The R Journal **5**:144-161. URL

Kemp L, Mills MGL. 2005. The 4th Wild Dog and 2nd Cheetah Photographic Census in the Kruger National Park. South African National Parks. Unpublished report, South African National Parks, Skukuza.

Laake, JL 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. Alaska Fisheries Science Center, NOAA, National Marine Fish Services, Seattle, WA.

Lande R. 1993. Risks of Population Extinction from Demographic and Environmental Stochasticity and Random Catastrophes. American Naturalist **142**:911–927.

Lindsey P, du Toit JT, Mills MGL. 2004. The distribution and population status of African wild dogs (Lycan pictus) outside protected areas in South Africa. South African Journal of Wildlife Research **34**:143–151.

Mabunda D, Piennar D, Verhoef J. 2003. The Kruger National Park. Pages 3–21 in J. T. Du Toit, K. H. Rogers, and H. Biggs, editors. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, Washington D.C., USA.

Macdonald DW, Sillero-Zubiri C, editors. 2004. The biology and conservation of wild canids. Oxford University Press, New York.

Maddock AH, Mills MGL. 1994. Population characteristics of African wild dogs Lycaon pictus in the Eastern transvaal lowveld, South Africa, as revealed through photographic records. Biological Conservation **67**:57–62.

Marnewick K, Ferreira SM, Grange S, Watermeyer J, Maputla N, Davies-Mostert HT. 2014. Evaluating the Status of and African Wild Dogs Lycaon pictus and Cheetahs Acinonyx jubatus through Tourist-based Photographic Surveys in the Kruger National Park. PLoS ONE **9**:e86265.

Mills MGL. 1997. Wild Dog, Lycaon pictus. Pages 192-193 in L. Hes and M.G.L. Mills, editors. The Complete book of southern African mammals. Struik Winchester, Cape Town, South Africa.

Mills MGL, Gorman ML. 1997. Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park. Conservation Biology **11**:1397–1406.

Palomares F, Caro TM. 1999. Interspecific Killing among Mammalian Carnivores. The American Naturalist **153**:492–508.

Pomilia MA, McNutt JW, Jordan NR. 2015. Ecological predictors of African wild dog ranging patterns in northern Botswana. Journal of Mammalogy **96**:1214–1223.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. (Accessed 20 April 2016).

Rogers KH. 2003. Adopting a heterogeneity paradigm. Pages 41–56 in J. T. Du Toit, K. H. Rogers, and H. Biggs, editors. The Kruger Experience: Ecology and Management of Savanna Heterogeneity. Island Press, Washington D.C, USA.

White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46**:S120–S139.

Wilkinson I. 1995. The 1994/1995 wild dog photographic survey. South African National Parks, unpublished report, South African National Parks, Skukuza.

Woodroffe R, Ginsberg JR. 1998. Edge Effects and the Extinction of Populations Inside Protected Areas. Science **280**:2126–2128.

Woodroffe R, Sillero-Zubiri C. 2012. *Lycaon pictus*. The IUCN Red List of Threatened Species 2012: e.T12436A16711116. (Accessed 08 April 2016).

Table 1. The 18 models tested in RMark. Phi represents apparent survival and p represents recapture probability.

Model	Model Parameters
1	Phi(.)p(.)
2	Phi(.)p(~time)
3	Phi(.)p(~packsize)
4	Phi(.)p(~region)
5	Phi(~time)p(.)
6	Phi(~time)p(~time)
7	Phi(~time)p(~packsize)
8	Phi(~time)p(~region)
9	Phi(~packsize)p(.)
10	Phi(~packsize)p(~time)
11	Phi(~packsize)p(~packsize)
12	Phi(~packsize)p(~region)
13	Phi(~region)p(.)
14	Phi(~region)p(~time)
15	Phi(~region)p(~packsize)
16	Phi(~region)p(~region)
17	Phi(~time)p(~region+time)
18	Phi(~region)p(~region+time)

Table 2. Top 6 Cormack Jolly Seber models produced from running RMark.

Model	npar	AICc	DeltaAICc	Weight
Phi(~region)p(~region + time)	14	1602.68	0	0.933688729
Phi(~time) p(~region + time)	20	1607.99	5.307429068	0.065721662
Phi(~time) p(~region)	12	1617.42	14.73487611	0.000589609
Phi(~region) p(~time)	12	1667.12	64.43977611	9.49E-15
Phi(~packsize) p(~time)	12	1683.85	81.16407611	0
Phi(~time) p(~packsize)	12	1689.76	87.07347611	0

Table 3. The one, nine, and 12-month wild dog survival rates for the packs in north, central, and south regions, and in the entire park (SE), as well as the mean life span (MLS) for dogs in each region.

	Survival Rates (Phi)			MLS (years)
Region	1 month	9 month	12 month	
North (95% CI)	0.8072 (0.6947-0.8852)	0.1456 (0.0377-0.3336)	0.0766 (0.0126-0.2313)	0.3901 (0.23-0.68)
Central (95% CI)	0.9885 (0.8523-0.9992)	0.9013 (0.2374-0.9930)	0.8706 (0.1470-0.9907)	7.237 (0.52-107.15)
South (95% CI)	0.9752 (0.9459-0.9888)	0.7978 (0.6062-0.9039)	0.7400 (0.5130-0.8739)	3.329 (1.49-7.42)
Total (95% CI)	0.9452 (0.9099-0.9751)	0.5868 (0.4273-0.7971)	0.4912 (0.3219-0.7390)	1.410 (0.88-3.31)

Figure 1. A map of the study site, Kruger National Park, shown in relation to the rest of southern Africa.

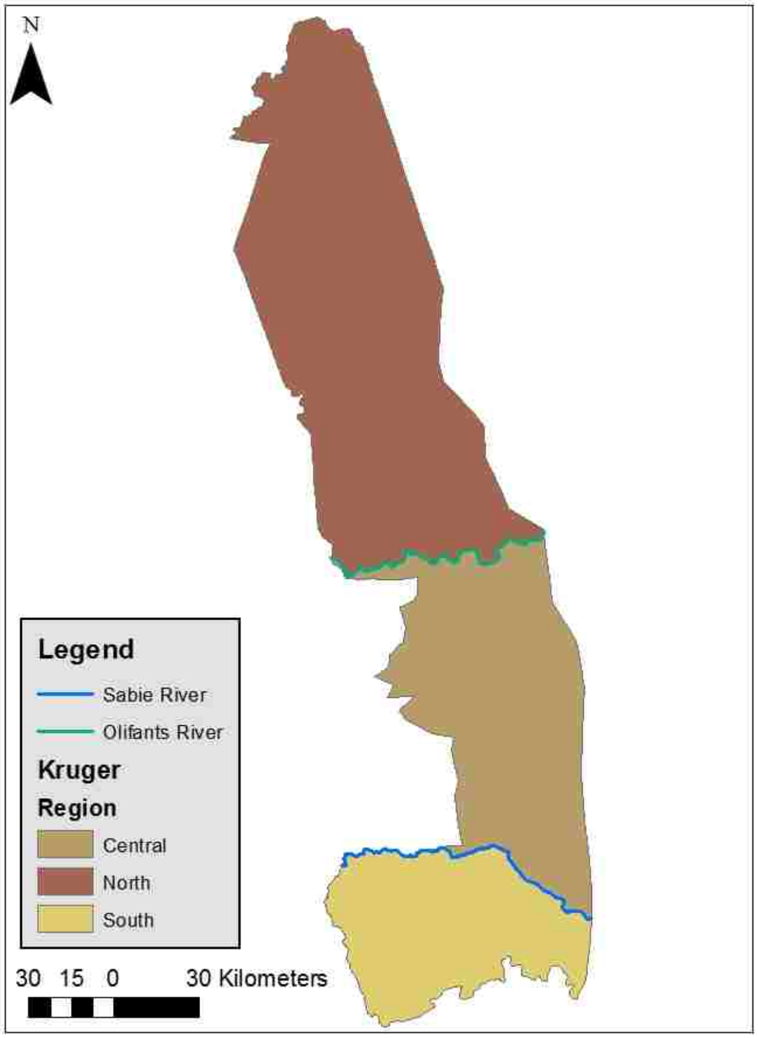

Figure 2. A map of KNP showing the regions, north, central, and southern, as divided by the Olifants and Sabie River.

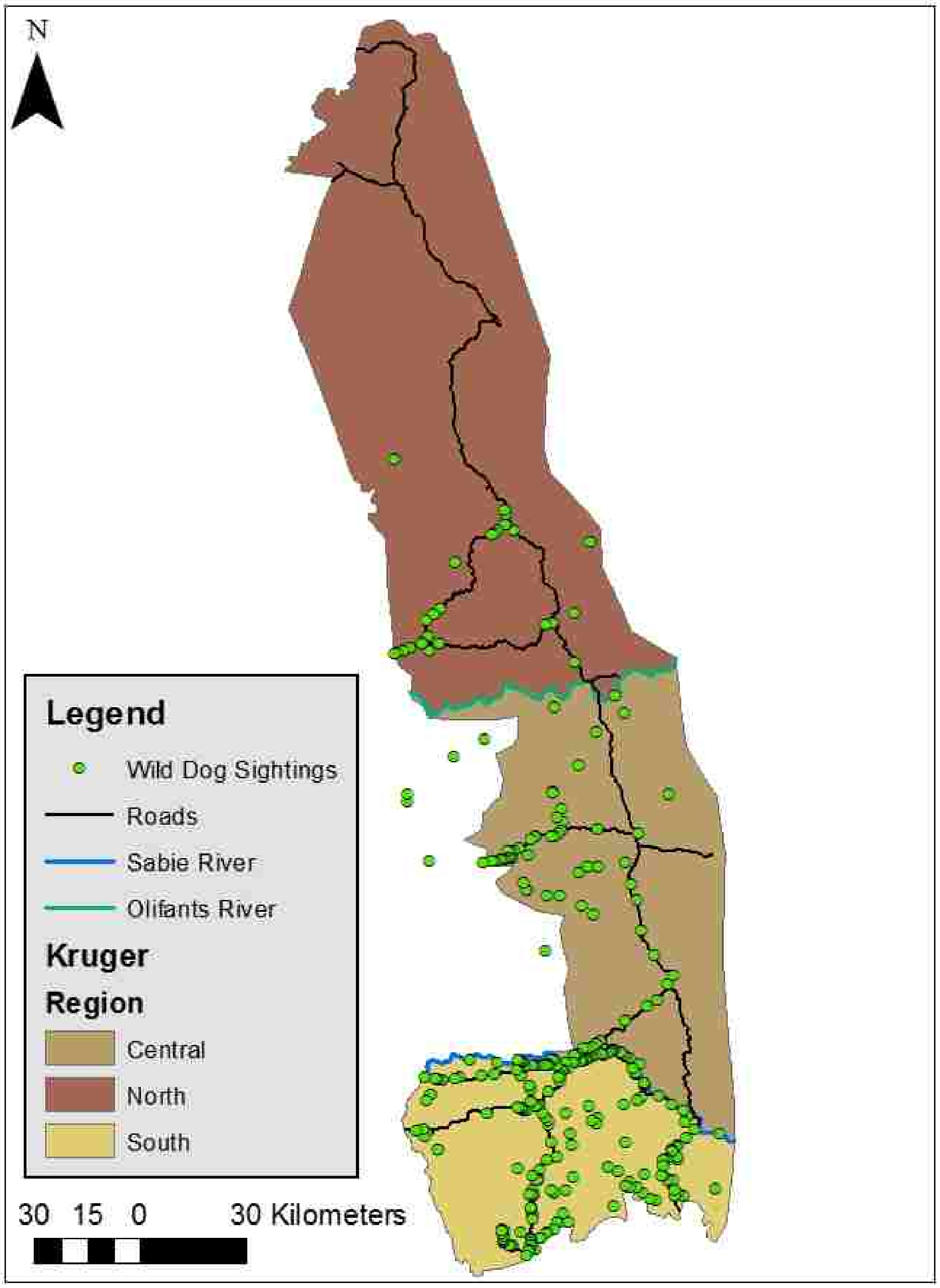

Figure 3. Map of Kruger National Park with main roads in black and African wild dog sightings from the 2014-2015 survey in green. Most sightings were along the roads due to lack of off-road access for tourists.

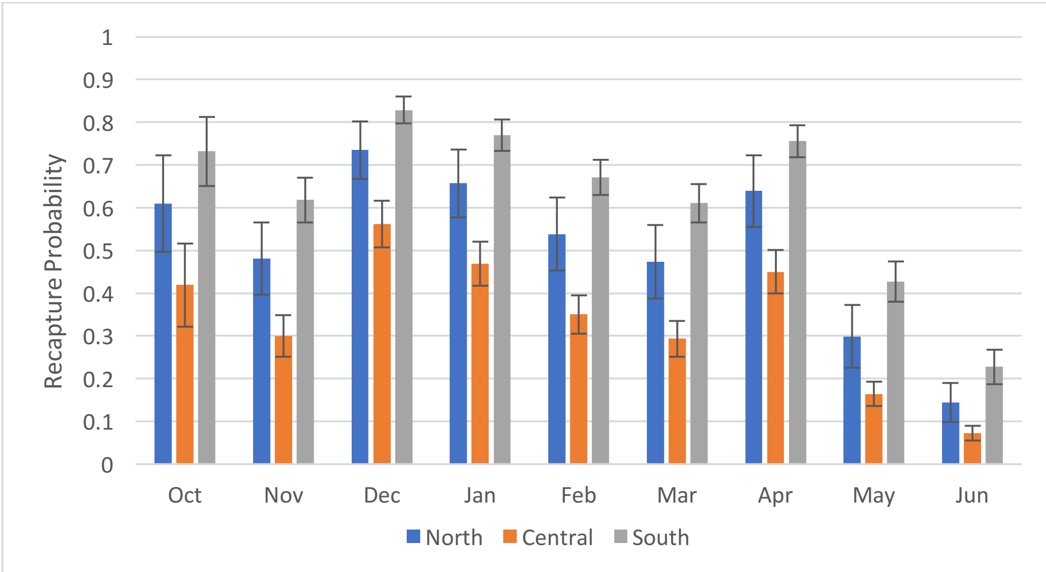

Figure 4. Monthly recapture rates of dogs in each region during the 2014-15 survey, whiskers denote one standard error. Each region followed a similar trend over time, increasing in December, then decreasing until March, increasing again in April, then dropping off quickly near the end of the survey.

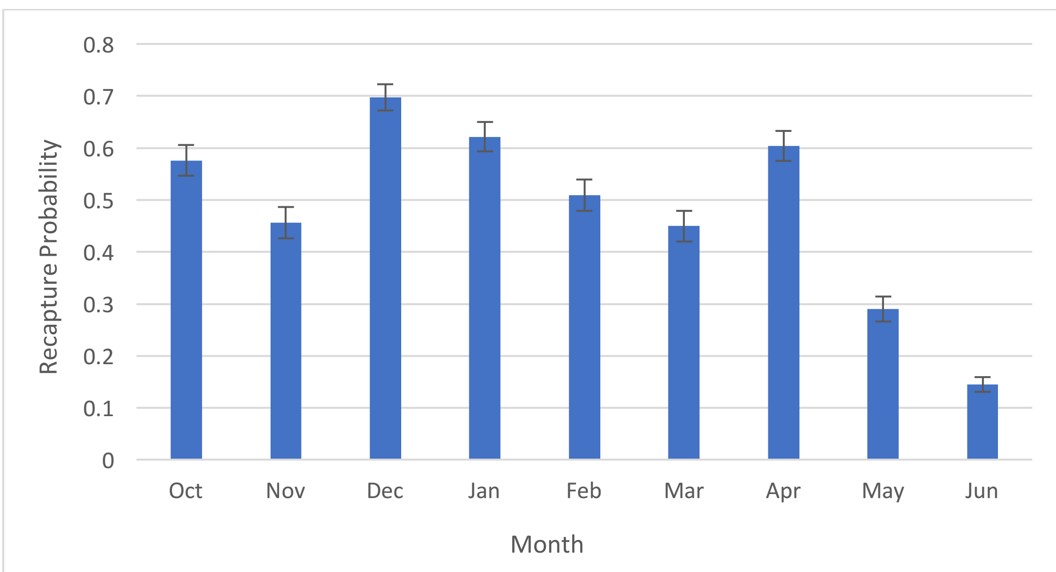

Figure 5. Average monthly recapture probabilities of African wild dogs in all of Kruger National Park; whiskers denote one standard error.

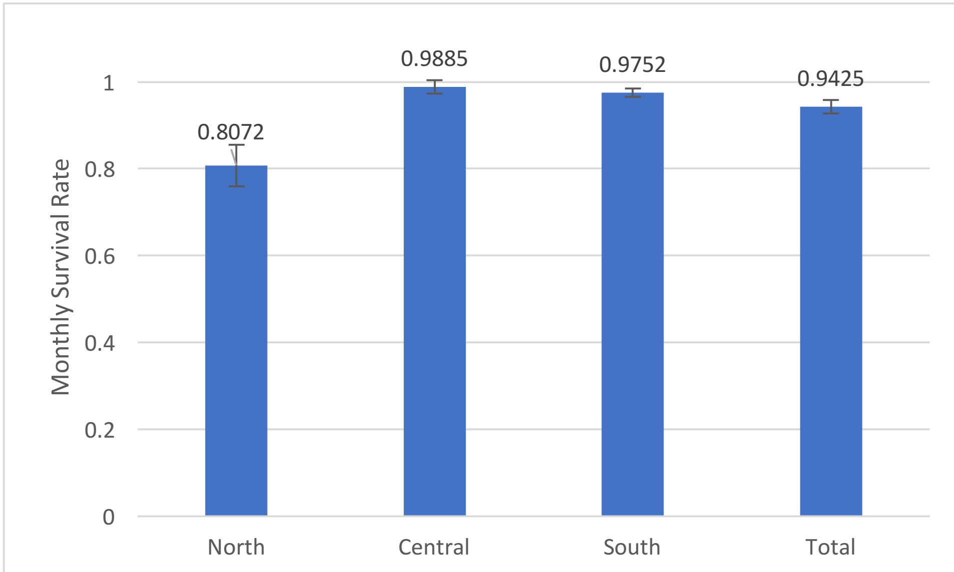

Figure 6. Monthly apparent survival rates (φ) of African wild dogs for each region and the total park during the 2014-15 survey, based on the top model. The total park estimate is a weighted average based on number of packs in each region; whiskers denote one standard error.

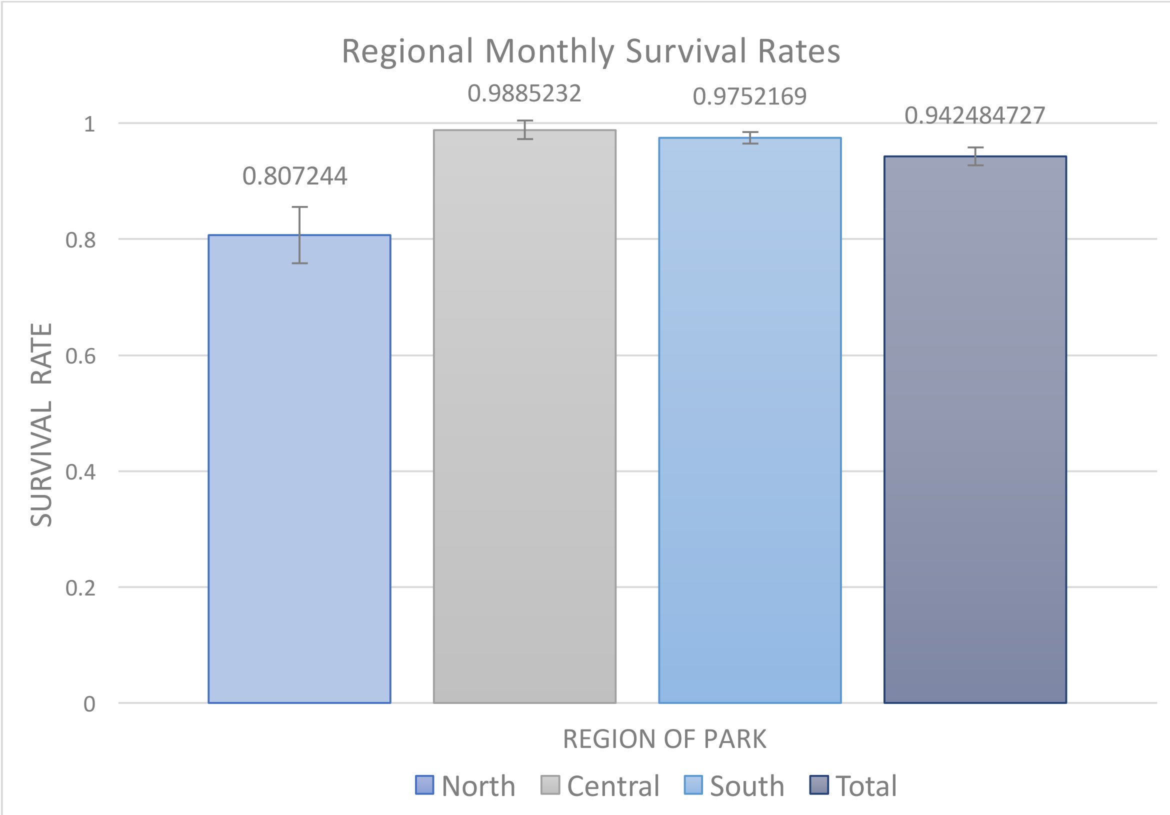

Figure 7. Annual survival of African wild dogs in Kruger National Park by park region; whiskers denote one standard error.

Figure 8. Map of Kruger National park showing roadways and rest camps. The density of roads and camps is much higher in the southern and central region than in the northern region.

CHAPTER 2 – DISEASE PREVALENCE AND VACCINE EFFICACY IN ETHIOPIAN WOLVES AND AFRICAN WILD DOGS: A REVIEW

ABSTRACT

The African wild dog (*Lycaon pictus*) and Ethiopian wolf (*Canis simensis)* are the two most highly endangered African carnivores. As human population growth fragments habitat for these species, both wild dog and wolf populations experience more negative population pressures. One such threat is disease. Two major infectious disease threats for wolves and wild dogs are canine distemper and rabies, both of which can be transferred across domestic and wild canid species. In the last 35 years, disease has had an increasing impact on both species, in part due to increased exposure through domestic dogs roaming near protected areas. Many cases of rabies or canine distemper have been reported for wolves and wild dogs, resulting in population decline and even local extirpation. Mitigation strategies have focused on vaccination, but methods and type of vaccine have varied, as has mitigation success. After multiple local outbreaks reduced crucial populations of Ethiopian wolves in the Bale Mountains and African wild dogs in and around Kruger National Park in 2016 and 2017, proactive vaccine programs were initiated. To help inform management strategies involving disease in these two species, I conducted a systematic review of the literature and unpublished information surrounding canine distemper and rabies for Ethiopian wolves and African wild dogs in the last 35 years. Vaccination with modified-live or recombinant vaccines, including annual boosters will be a key strategy in disease management going forwards. Vaccination of domestic dogs near wolf and [redacted] dog populations, vaccination of wolves and wild dogs themselves, and a combination of the two, all appear to be viable management strategies in different scenarios. More intensive population and disease monitoring in the future will help provide necessary information to guide successful management strategies of these two critically endangered species.

INTRODUCTION

Endangered African Canids: Ethiopian Wolves and African Wild Dogs

The Ethiopian wolf (*Canis simensis*) and African wild dog (*Lycaon pictus*) are both highly endangered social carnivores found solely in Africa. The wolf is recognized as the most threatened African carnivore, and the rarest canid on the globe, with fewer than 500 individuals, in seven small, isolated populations, remaining. (Sillero-Zubiri, et al. 2004, Strategic planning for the Ethiopian wolf conservation 2011). They exist only in the Afro-alpine habitat in Ethiopia, at altitudes above 3000m. Wolves live in packs of up to 13, with an adult sex ratio biased towards males 1.8:1, but are solitary diurnal hunters with a diet consisting mostly of rodents. Their main prey item is the giant mole rat (*Tachyoryctes macrocephalus*, Gottelli and Sillero-Zubiri 1992, Sillero-Zubiri, et al. 2004). All pack members work together to mark and defend territory and contribute to pup-rearing, and the average wolf pack home range size is 6.4 km^2 (Gottelli and Sillero-Zubiri 1992).

African wild dogs (*Lycaon pictus*) are even more intensely social than wolves, and distributed more widely across Africa. They are cooperative hunters and breeders, and almost all reproduction results from an alpha female. They exist in a variety of habitats, but prefer deciduous woodlands and wooded grasslands (Creel, et al. 2004). Wild dogs are cursorial hunters that eat a wide range prey, focusing on ungulates ranging from 15-200kg. They live in highly [redacted]esive packs that range from 2-30 adults, with a mean pack size between 4.8-8.9 adults (Creel 2002). Their home ranges are large and vary greatly in extent (150-1318km^2, Fuller, et al. 1992, Woodroffe et al., 1997, Pomilia, et al. 2015). Because wild dogs require a lot of space, populations are often small (Durant 1998, Creel 2001), even in large protected areas such as

KNP (Woodroffe and Ginsberg 1998), a nearly 2 million ha reserve. Wild dogs' small, scattered populations lead to the potential for rapid population decline under unfavorable conditions.

Threat of Disease in Endangered Social Canids

Stochastic events, (e.g. disease outbreaks), can have large effects on small, widely spread populations, such as those found in wolves and wild dogs. Infectious disease, while a natural part of many ecosystems (Cleaveland 2009), has become a serious threat to endangered species, especially carnivores (Cleaveland 2009, Randall et al. 2006) through suppression of population growth rates, and increased vulnerability to extinction, especially in small populations (Breed et al. 2009). While small, endangered populations usually cannot maintain virulent viral pathogens due to die out (Cleaveland 2009), threats lie in diseases that find "reservoir hosts" in another species (Cleaveland et al. 2002, Woodroffe and Donnelly 2011, Woodroffe, et al 2004). Because there is a close phylogenetic relationship between wild and domestic carnivores, and carnivores have a high susceptibility to domestic pathogens, domestic animals often serve as these hosts. This may explain why carnivores, within mammals, are particularly threatened by infectious disease (Cleaveland 2009, Pedersen, et al. 2007). Within carnivores, canids seem to have more trouble with disease than felids, possibly because there is usually a smaller presence of domestic cats than dogs near wildlife-protected areas, and contact rates between domestic cats and wild felids is most likely lower than that of domestic dogs and wild canids (Cleaveland 2009). The [redacted]al nature of wolves and wild dogs makes them even more susceptible to directly transmitted disease such as canine distemper virus (CDV) and rabies (Mills 1993). For endangered canids, disease, particularly rabies and CDV have caused species decline (e.g. Ethiopian wolf *Canis simensis*) (Gordon, et al. 2015, Randall, et al. 2006, Sillero-Zubiri et al.1996) and even local extinction (e.g. African wild dog *Lycaon pictus*, Alexander, et al.1996, Gascoyne, et al. 1993, Kat, et al. 1995, Tswalu Kalahari 2016). As protected space decreases and habitat fragmentation continues, endangered canids have become increasingly prone to encounters with domestic dogs, especially near the edge of reserves (Breed, et al. 2009 and Sillero-Zubiri, et al. 2004). Contact with domestics greatly increases their chances to contract rabies or CDV, hindering conservation efforts for these two highly endangered carnivores.

Canine Distemper Virus

Canine distemper virus is a single-stranded RNA virus, a member of the *Morbillivirus* genus in the family *Paramyxoviridae* (Green, G.E. and M.J. Appel 1990), and has been reported in all terrestrial carnivore families (Deem, et al. 2000). It is in the same genus as other well-known morbilliviruses, including measles and rinderpest. It has a wide host range, occurring in five mammalian orders, and has a propensity for switching hosts (Viana, et al. 2015). Canine distemper is primarily transmitted through the respiratory system as small particles are aspirated, but other body excretions can also pass the virus if they are aerosolized and inhaled. It is a highly contagious virus that begins with a systemic infection that enters the bloodstream and moves into other organ systems (Deem, et al. 2000, Green, G.E. and M.J. Appel 1990). In most species that contract CDV, the virus begins in the respiratory system, moves to the lymph nodes and then the gastrointestinal system, and finally, the central nervous system (CNS, Deem, et al. 2000). In nondomestic canids, the clinical signs are similar, but susceptibility varies. Not all mammalian [redacted]ies exhibit the same clinical signs, if any, which makes it hard to detect in some hosts.

Rabies Virus

The rabies virus is a fatal encephalomyelitis belonging to the genus *Lyssavirus*, in the *Rhabdovirus* family. It is one of the oldest known infectious diseases, and can be contracted by all mammals, including humans (Rupprecht, et al 2001). It is an important zoonosis that is usually transmitted through bites, as the viral agents are passed to the salivary glands and saliva after reproducing in the central nervous system (Rupprecht, et al. 2001). It has been monitored throughout history because of its implications in public health, and it is becoming increasingly important in wildlife ecology (Dazak, et al. 2000, Rupprecht, et al. 2001). Rabies is distributed throughout Africa in domestic dogs (*Canis lupus familiaris*), which are considered a key reservoir host of the virus. Rabies has also been reported in African wildlife, including many wild canid species (Rupprecht, et al 2001, Breed, et al 2009).

Endangered Canids and Disease: Current Status

In recent years, there have been increased reports of CDV in wild animals, but the origin and maintenance in the wild dog, as well as other wild carnivores, is not well understood (Martinez-Gutierrez and Ruiz-Saenz 2016, Viana, et al. 2015, Goller, et al. 2010.) The proximity of human settlements near the borders of KNP and other protected areas in Africa, as well as the close taxonomic relationship between domestic and wild canids, suggest that spillover transmission from domestic dogs could be a major cause of wild dog infection (Breed, et al. 2009, Woodroffe and Donnelly 2011, Woodroffe, et al. 2004, Woodroffe, et al. 2012). However, CDV infection and mortality has occurred even when transmission from domestic dogs was impossible (Tswalu Khalari 2016), suggesting other exposure sources. It has been shown that asymptomatic circulation of CDV in wildlife has become asynchronous with domestic dog [redacted]ctions, which points toward a wildlife cycle (Viana, et al. 2015), possibly in other wild canids such as jackals. In addition, CDV antibodies have been found in wild dogs without coinciding evidence of mortality or influence on pup survival (Alexander, et al. 2010 and Creel, et al. 1997), which suggests not all exposure to CDV results in death. However, in the past ten years alone, CDV has resulted in death of entire packs and/or populations of wild dogs across

Africa (Goller, et al. 2010, Van de Bilt, et al. 2012, Tswalu Kalahari 2016, G. Beverley, *pers. comm.*).

The rabies virus has been a known threat to African wildlife for many decades. It is especially threatening to social endangered canids, such as the wolf and wild dog, because of the various communal interactions in which pack members engage, including mouth-licking and food regurgitation for pups (Skinner and Smithers, 1990). Rabies is the most significant threat for the wolf (Haydon, et al. 2002), even though there have been a few episodes of CDV. In the last few decades, rabies has been responsible for significantly reducing the population of wolves in the Bale Mountains of Ethiopia (Haydon, et al. 2002, Randall, et al. 2004, Randall, et al. 2006, Stewart, et al. 2012). With multiple rabies outbreaks, some coming in successive years, the wolf population is struggling as numbers dwindle to around 400 (Marino, et al. 2017). Wild dogs have also suffered from rabies in recent years throughout Africa, including back – to – back outbreaks in Madkiwe Reserve in South Africa (Hofmeyr, et al. 2002, Hofmeyr, et al. 2004).

Disease, specifically canine distemper and rabies, have become a more noticeable threat to wolves and wild dogs, especially as their populations dwindle from habitat fragmentation and other competitive factors. Vaccination strategies in protected populations are becoming increasingly common in both wolves and wild dogs, as managers seek ways to protect these endangered canids from disease. In the last few years, an oral vaccination strategy study for [redacted]ves was started in the Bale Mountain population that shows initial promise (Sillero-Zubiri, et al. 2016). A vaccination and disease survey study was also launched in Kruger National Park in 2016 after an entire pack was decimated by CDV in just two weeks (G. Beverley, *pers. comm.*). For managers to make decisions that effectively manage disease in these critically endangered species, they must understand the context and history of CDV and rabies in wolves and wild dogs. In order to gain a more comprehensive view, I examined the research done on both diseases in both species, including outbreaks, antibody levels, and previous mitigation strategies. In the process, I sought to answer seven main questions: (1) What type of research has been done on rabies and CDV in wolves and wild dogs? (2) In the past 35 years, how prevalent was CDV and rabies in wild dogs and wolves? Is one disease more common, and does it differ by species? (3) Does disease prevalence vary by country? (4) Does disease prevalence vary with weather patterns? (5) Does disease prevalence or natural seroprevalence change across land use or management type? Does this differ by disease or by species? (6) What are the exposure routes for disease? Are any more common than another, and does that differ by disease, species, or land use/management? (7) What are the mortality rates for disease, and does that differ by disease, species, or land use/management? (8) How effective are vaccines in mitigating disease for wild dogs and wolves? Does it differ by disease, species, vaccine type, or vaccine administration technique? By answering these questions, I hope to provide a framework for managers to help guide future disease management strategies for both the wolf and the wild dog.

METHODS

Disease Research

To begin the analysis of the impact of CDV and rabies on the wolf and wild dog, including how effective vaccination strategies have been at mitigating disease risk, I examined [redacted]vailable articles related to the disease in each species from 1980 to present. I searched for studies of disease outbreaks, studies testing seroprevalence for the diseases, and vaccination studies. After a systematic review of the literature and personal interviews with researchers, I found 39 cases/studies of CDV and/or rabies in African wild dogs and Ethiopian wolves. I separated the studies into four distinct categories: Disease Outbreak, Natural Seroprevalence, Vaccination Seroconversion, and Vaccination Administration Techniques to help systematically analyze the studies. I then determined the basic qualities of each study, starting with the basics such as study year, location, and species and disease studied, as well the presence of certain weather patterns. I also noted the land use type of the study location and the management level of the population studied. From there, I noted more specific qualities for each of the four types of studies, including suspected source of infection, vaccination type and vaccination effectiveness. A complete record of studies and their extracted qualities is included in the Appendix. I used these notes and distinctions to find trends to answer my study questions.

Prevalence of Disease

To begin, I looked at the prevalence of disease, which was the focus of my first five study questions. I first determined the percentage of cases, both in total and within each of the four study types, that involved CDV and rabies, as well as the percentage of studies on wild dogs versus wolves. To examine if one disease was more prevalent for each species, I found the percentage of outbreaks for each disease within each species. I also looked at the percentage of vaccination and natural seroconversion studies done within each species to see if there was a difference in research focus and in disease incidence. To determine if disease prevalence varied among African countries, I found the percentage of disease outbreak cases found in each country, both in total and by disease and species. Next, I examined if weather patterns played a role in [redacted]ase prevalence, as some researchers have suggested (Beverley, G. *pers. comm.*), by determining the percentage of disease outbreaks that occurred during an El Niño year, as El Niño-caused drought patterns have been suggested to affect disease outbreaks.

Prevalence of Disease and Natural Seroprevalence in Different Land Use Types

After establishing the prevalence of CDV and rabies by species, country, and weather, I looked at how disease differed among different land use and management types. I broke studies into two land-use groups, unprotected and protected, and also labeled each study population as either managed, unmanaged, or captive. I found the percentage of disease outbreaks that occurred in each type of environment in total, for each species, and for each disease. I also found the percentages of cases that showed natural seroprevalence by environment in total, and by disease and species.

Disease Exposure

To determine the most common paths of disease exposure for wild dogs and wolves, I calculated the percentage of studies that found different origins of the infection, i.e. domestic dogs, another wild canid or another mammal, and the percentage of cases where the origin of disease was unknown. I did this in total, for both diseases and species combined, and then for each disease within each species. I also compared the exposure sources among land use/management types.

Mortality Rates

To examine the virulence of the two diseases, I determined the percent mortality in each disease outbreak case, divided the cases into four groups (<10%, <50%, >50%, >90% mortality), [redacted] found the percentage of cases that occurred in each subgroup. Again, I found these percentages for all cases combined, and then compared difference between diseases, species, and land use/management types.

Vaccination Effectiveness

Finally, to help determine effective management strategy for the future, I examined vaccine effectiveness within the studies. For this analysis, I considered any study where an animal had been vaccinated, including studies classified as disease outbreak, vaccine seroconversion, and vaccine administration. I determined the types of vaccines used in each case (i.e. inactive, modified-live, recombinant, combination or singular) and the method of vaccine administration (i.e. oral or intramuscular (IM)). I compared vaccine effectiveness (i.e. survival or successful seroconversion) among these vaccine types in total and by disease in each species by finding the percentage of cases with successful vaccination in each scenario.

Management Strategy Implications

After analyzing the data, I compiled my results to give a succinct analysis of the status of disease for each species. I developed a general framework for what I believe to be an effective management strategy, including where to focus research efforts and where vaccination might be most effective, for the future of the Ethiopian wolf and the African wild dog.

RESULTS

Compilation of Studies

After a thorough search of the literature and unpublished data, I found 39 separate studies/cases involving canine distemper and/or rabies in wild dogs and wolves, which I [redacted]rated into four categories (Appendix). I found 19 studies of disease outbreak, detailing 22 separate occurrences of disease. I also discussed with researchers two recent unpublished disease outbreaks in wild dogs in South Africa in Tswalu Kalahari Reserve (Tswalu Kalahari 2016) and Kruger National Park (Beverley, G. *pers. comm.*), which brought the total number of disease outbreak cases to 24 within the last 40 years. I found only five published studies testing the natural seroprevalence of either disease, two of which looked at both CDV and rabies (Prager, et al. 2012a, Prager, et al. 2012b). For vaccine cases, I found eight published studies examining seroconversion after vaccination for CDV and rabies, including one study which tested both CDV and rabies vaccines in wild dogs (Van Heerden, et al. 2002). Finally, I found two published studies testing oral rabies vaccine administration techniques in wild dogs (Figure 1).

Context of Disease

Among all 39 studies, 18 (46.2%) pertained to canine distemper, 14 (35.9%) pertained to rabies, and 7 involved study of both diseases (17.9%). I discovered the wolf was less studied than the wild dog, with 31 (79.5%) of the cases focused on wild dogs and only eight (20.5%) focused on wolves. Among the 24 disease outbreak cases, 12 (50%) cases were strictly CDV, eight (33.3%) were rabies, and four (16.7%) discussed the possibility of both diseases. Seventeen (70.8%) of the disease outbreak cases involved wild dogs, and seven (29.2%) involved disease in wolves. Among the five studies of natural seroprevalence, three studies were focused only on CDV (60.0%), and two examined seroprevalence of CDV and rabies (40.0%); all five of the studies were done with wild dogs. Among the eight studies testing seroconversion post-vaccination, three (37.5%) were done on CDV vaccines, four (50.0%) on rabies vaccines, and one looked at seroconversion of vaccinations for both diseases (12.5%). Finally, the two studies on vaccination administration techniques involved rabies vaccinations in wild dogs.

[redacted]*cies Disease Prevalence*

In wolves, rabies was slightly more prevalent than CDV. Four studies reported rabies in wolves, 2 CDV outbreaks, and one reported death from both diseases. In wild dogs, CDV was more common, with 10 studies reporting CDV outbreaks, four reporting rabies outbreaks, and three detailing cases of both (Figure 3). After determining there were slight differences in prevalence between species, I totaled the number of cases on seroprevalence, seroconversion, and vaccination administration for each disease in each species to examine if research followed the same trend. In wild dogs, 17 cases were split in half by disease: eight on rabies, nine on CDV. There was, however, only one study focused on vaccination in Ethiopian wolves, looking at rabies seroconversion. Just as disease is occurring more often in wild dogs than Ethiopian wolves, disease research is also occurring at a disproportionate level.

Disease Outbreak Location

Looking at the spatial context of disease, I found that disease outbreaks occurred in five different countries in Africa: Botswana (2 cases, 8.3%), Ethiopia (7, 29.2%), Kenya (2, 8.3%), South Africa (7, 29.2%), and Tanzania (4, 16.7%) (Figure 2). Only one case (4.1%), a vaccine-induced infection, occurred outside of Africa, in a zoo in the United States. South Africa was the country with the most CDV cases, with 5 (31% of CDV cases), and Kenya was the least, with only 1 (6.3%). Ethiopia was the country with the most rabies cases, with 5 (41.7% of rabies cases), and Kenya was again the country with the least, with only 1 (6.3%) (Figure 2).

Climate/Weather Related Disease

When I examined weather pattern associations with the disease cases, I found that more cases of disease occurred during an El Niño year than did not, for each disease separately and combined (Figure 4). Upon running a binomial test of significance, however, I found the results [redacted] not statistically significant ($p>0.1$) for either disease or both combined.

Land Use and Management

I originally sought to compare the prevalence of each disease in wild dogs and wolves in protected versus unprotected areas; however, I only found one (4.1%) case of disease reported in an unprotected area. A population of wild dogs contracted CDV outside of protected reserves in

Kenya, and the population experienced 90% mortality as two known packs completely disappeared. The remainder of the 23 diseases outbreaks occurred in protected areas, so I decided to compare captive, managed, and unmanaged populations instead, including the unprotected area as unmanaged. Twelve (50%) cases of disease occurred in unmanaged populations, eight (33.3%) in managed populations, and 4 (16.7%) in captive population (zoos). CDV and rabies both occurred most in unmanaged populations (7 cases each), followed by managed populations (5 cases each). There were no cases of rabies in captive populations, and all four cases of CDV in captive populations were thought to be vaccine-induced infections. Breaking it down by species, all seven cases of disease in wolves occurred in unmanaged populations. In 17 wild dog cases, almost half (8 cases) occurred in managed populations, and four cases each (25%) occurred in unmanaged and captive populations.

There was an uneven distribution between captive, managed, and unmanaged populations in the vaccination seroconversion studies. Seven of the eight studies occurred in captive populations and the other in an unmanaged population. Six (86%) of the studies in captive environments were successful, resulting in seroconversion of over 70% of vaccinated dogs, and the one vaccination study in the unmanaged population resulted in successful seroconversion as well.

Five studies examined the natural seroprevalence of CDV, one in a managed population [redacted]s, three in an unmanaged population, and one in both. The study done on a managed population found wild dogs had no natural seroprevalence of CDV. The studies on the unmanaged populations differed: one found no natural seroprevalence and two found that seroprevalence was present but fluctuated with time. The study done on both a managed and unmanaged population found that wild dogs had antibodies to CDV, but noticeably more in unmanaged populations. Only two studies examined the seroprevalence of rabies; one was done with an unmanaged population and one was conducted on both managed and unmanaged populations. In the unmanaged population, in Kenya, the seroprevalence of rabies fluctuated. The study done over multiple populations found little to no seroprevalence in any of them.

Disease Exposure Routes

Between wolves and wild dogs, there were three known paths of exposure to disease: either domestic dogs, another wild canid (usually a jackal), or vaccination. In all cases combined, domestics dogs were the most common source of infection, occurring in 13 (54.2%) of the studies. Wild canids were the source of disease exposure in three of the cases (12.5%), vaccination in four (16.7%), and in four (16.7%) cases the exposure source was unknown. All four vaccine-induced disease outbreaks occurred in captive zoo populations. Exposure did not differ greatly when comparing CDV and rabies cases, both followed the same pattern as the overall results, except that vaccination was never the source of a rabies infection, only CDV infections. Between species there was a greater distinction in exposure, as the only known source for the wolf was domestic dogs, while wild dogs experienced infection from domestic dogs, other wild canids, and vaccines, as well as four outbreaks with unknown causes. There was also a noticeable difference in exposure source between managed and unmanaged populations. Exposure was spread evenly though the sources in managed populations, but in unmanaged [redacted]ulations, domestic dogs accounted for 11 of 12 (91.7%) disease cases, and the twelfth came from an unknown source. In the 23 disease cases reported in protected areas, domestic dogs were again the most common source of disease with 12 cases (52.2%).

Mortality Rates

To compare mortality rates among the 24 disease outbreaks, I used statistics given in each study to determine the mortality rate, using the number of individuals who died divided by the total number of individuals in the population (estimated or known). The mortality rate ranged from 6% (one wild dog pack died in 2016 in the large Kruger population, Beverley, G. *pers. comm.*) to 100% (two vaccine-induced outbreaks, Durchfield, et al. 1990 and Van Heerden, et al. 1989), with an average of 70% mortality and a median of 77% mortality. When looking at both CDV and rabies together, only the aforementioned outbreak that caused one pack's death in Kruger, experienced a mortality rate of less than 10%, two had a mortality rate of 10% to 50%, 15 had a rate of 50% to 90%, and five cases had a mortality rate of over 90% (Figure 5). Looking at just cases of CDV, the 50% to 90% mortality rate range had the most cases at 10 and the average and median mortality rate were 68% and 72%, respectively. For rabies cases, again the 50%-90% mortality rate range had the highest number of cases, with six. The average and median mortality rate for rabies cases were 66% and 73%, respectively (Figure 5). In disease outbreaks in wild dogs, mortality rates were distributed across the groups, but almost half the cases (47%) resulted in 50-90% mortality. The mean mortality rate was 73% and the median was 69%. In cases with Ethiopian wolves, mortality rates were much less varied; all 7 cases resulted in 50-90% mortality, with a mean of 67% and median of 77% (Figure 6).

Mortality rates did not vary much among managed, unmanaged, and captive populations. [redacted]und two-thirds of cases in both managed and unmanaged population types experienced between 50 and 90% mortality, with the rest split somewhat evenly between < 50% and > 90%. The minimum and maximum mortality rate for disease cases in managed populations was 30% and 92%, respectively, with an average of 66% and a median of 61%. The minimum and maximum mortality rate for cases in unmanaged populations were 6% and 95%, respectively, with an average of 67% and median of 73% (Figure 7). One disease outbreak study within a managed population did not yield sufficient data to accurately calculate a mortality rate, so I gave it a designation of “unknown” and did not use it to calculate any percentages). The captive population mortality rates were higher than the managed and unmanaged, with all four cases above 50% and two at 100%. The minimum and maximum were 67% and 100%, with an average of 88% and a median of 92% (Figure 7).

Vaccination Effectiveness

Finally, I examined the vaccine effectiveness between species and diseases. In the 24 cases of disease outbreak, more cases detailed outbreaks in unvaccinated populations than vaccinated. Fourteen (58%) occurred in wild dogs and wolves that had not been vaccinated and ten (42%) occurred in populations that had been vaccinated. In five outbreaks of non-vaccinated individuals, the population was vaccinated during the outbreak to control the spread of disease. Canine distemper occurred equally in populations that had and had not been vaccinated against the disease (n=8 for both), but rabies occurred more often in unvaccinated populations (vaccinated n=8, unvaccinated n=4).

All ten CDV vaccination cases were wild dog studies; I found no instance of CDV vaccination in Ethiopian wolves. Three types of CDV vaccinations were given among the studies: inactive, modified-live, and recombinant. Modified-live vaccines were the most [redacted]mon, given in six cases, inactive in three, recombinant in one, and one case did not specify vaccine type. No type of vaccination was effective in 100% of the studies. The modified-live vaccinations were only 33% effective, with only 2 cases resulting in seroconversion, and four resulting in vaccine-induced infection in the wild dogs. The inactive vaccinations were also only effective in 33% of the cases; in one case the dogs seroconverted, in another the dogs contracted the disease around a year post-vaccination, and in the final case the dogs did not seroconvert. The recombinant vaccine study showed partial success. Connelly, et al. (2013) tested an oral and parenteral administration of a recombinant CDV vaccination, which produced successful seroconversion only in the dogs that received the vaccination parenterally (Figure 8). After successful seroconversion, however, titers declined (around 6.5 months post-vaccination).

Comparing oral and parenteral vaccinations was difficult as only one study evaluated oral administration. The oral vaccination did not produce successful seroconversion, and parenteral vaccinations did so in only four of the ten studies. More parenteral vaccinations were effective immediately after vaccination, but eventually, 6-12 months later, titers declined and wild dogs were susceptible to disease again.

Of the fifteen rabies vaccination cases, five involved the Ethiopian wolf and ten involved African wild dogs. Eleven (69%) of the cases showed rabies vaccinations to be effective in either preventing disease spread or leading to seroconversion. Rabies vaccines were either modified-live or killed vaccines and could be administered orally or parenterally. I found six cases involving modified-live vaccines, which were all effective, and ten cases of killed vaccines, which were effective against disease 40% of the time. Parenteral vaccines were more common than oral, used in 75% of the cases, and they were also slightly more effective (Figure 9).

Within the Ethiopian wolf rabies vaccination studies, all five cases, whether killed or live, [redacted]n parenterally or orally, were effective against disease. In the wild dog rabies vaccination cases, all three live vaccinations studies were effective, but only 57% of the seven cases with killed vaccines showed effective disease protection. Parenteral rabies vaccinations were much more common, and more effective, than oral vaccinations in wild dogs (Figure 9).

DISCUSSION

General Disease Threat Conclusions

It is apparent that both canine distemper and rabies are a threat for wild dogs and wolves in Africa. Based on the disease outbreaks studied for this review, it appears that canine distemper is more of a threat in South Africa than other countries; however, that could merely be a product of a large meta-population of wild dogs in South Africa, a result of more individuals, and more focused research. Rabies outbreaks were less common than distemper outbreaks across Africa, but were most common in Ethiopia, suggesting rabies needs to remain a key focus of wolf population managers in that country.

Unmanaged populations appear to be more susceptible to disease than managed populations, but managed populations still had high incidence of disease. This trend was not surprising, as unmanaged populations often have not been vaccinated and are more susceptible to disease. However, it was obvious that managed populations of wolves and wild dogs cannot be considered safe from disease from an initial vaccination. Managers of protected areas must pay careful attention to disease prevalence in and around the protected area, whether their population is highly managed our not. It will be particularly important for managers to stay aware of disease trends in domestic dogs and other wild canids. While domestic dogs are the most common source of disease in both species, wild canid species (e.g. jackals) also exposed wild dogs to disease in outbreaks that wiped out entire packs (Hofmeyr, et al. 2000, 2004, Tswalu Kalahari 2016). This [redacted] be especially important during times of increased physiological stress that could weaken the immune system (e.g. lower prey concentration due to drought).

While there was no statistical difference in disease cases that occurred during El Niño years and non- El Niño years, it is plausible that a relationship could emerge in the future as El Niño weather patterns cause warmer, drier summers in southern Africa. As human activity, including the domestic dogs that come with it, moves closer to protected areas, and as drought becomes more common with climate change, disease will continue to become a stronger threat to wolves and wild dogs inside parks and reserves and managers must remain engaged and informed on the subject (Woodroffe, et al. 2004).

General Vaccination Conclusions

In general, vaccines provided some protection against disease for both wild dogs and Ethiopian wolves; however, it was not uncommon for a population that had been vaccinated over 6 months prior to exposure to succumb to a disease outbreak, either rabies or distemper. Based on the vaccination seroconversion studies for both diseases, it is possible for individuals to not seroconvert to a level of true immunity until given a booster vaccination (Spencer and Burroughs 1992, Van Heerden, et al. 2002). In other cases, specifically with inactive CDV vaccines, even a booster did not always produce immunity. In one seroconversion study, multiple inactive CDV vaccinations did not produce immunity in wild dogs (Van Heerden, et al. 2002), and in 2000 the entire population of wild dogs (49 of 52 wild dogs) in Tanzania succumbed to CDV despite annual vaccination with an inactive vaccine (Van de Bilt, et al. 2002). While modified-live CDV vaccines did lead to vaccination-induced infection in a few cases (Durchfield, et al. 1990, McCormick 1983, Van Heerden et al. 1989), modified-live vaccines have also been shown to be effective in wild dogs while having have no ill effects (Spencer and Burroughs 1992, Van [redacted]rden, et al. 2002, Woodroffe 2001, Woodroffe, et al. 2004). Woodroffe, et al. (2004) suggest that because modified-live vaccines for CDV have a better success rate in providing immunity, they may be worth the risk in some cases. Another option to consider for CDV vaccination is the recombinant vaccine form. This has been shown to be effective in the Island fox (*Urocyon littoralis catalinae*), another wild canid, with no ill effects (Timm, et al. 2009), and in one vaccination study with a recombinant CDV vaccine in wild dogs, the parenteral form produced effect titer levels (Connolly, et al. 2013). More studies are needed before results can be considered conclusive, but the recombinant CDV vaccination is a promising mitigation frontier.

For rabies, a smaller percentage of disease outbreaks occurred in vaccinated populations, suggesting that rabies vaccination is more effective than CDV vaccination. The studies on seroconversion supported this theory, as a higher percentage (80%) showed effective seroconversion as compared to the CDV studies (40%). In Ethiopian wolves, all the rabies vaccination attempts resulted in immunity in the majority the population, even when the vaccination program began post-outbreak. Oral rabies vaccination strategies are currently being tested in Ethiopian wolf populations as a proactive vaccination measure, and preliminary results suggest sufficient pack coverage and successful immunity (Sillero-Zubiri, et al. 2016). This is encouraging because oral vaccination in bait requires far fewer resources, and stress on the animals, than trapping and sedating individuals for vaccination (Laurenson, et al. 2001). The amount of "handling" required by a typical sedation vaccination program has been suggested to cause immune-suppression in wild dogs (Burrows 1992), and despite refutation from other studies (Ginsberg, et al. 1995, Kat, et al. 1995), it remains probable that less active intervention put less stress on the packs and individuals. Knobel, et al. (2002, 2003) tested oral rabies vaccination in captive and free-ranging wild dogs with similar success, suggesting oral [redacted]cination in bait is the future of rabies vaccination for both species. Again, more research is needed before firm conclusions can be drawn, but initial results show promise.

Another important factor to consider in vaccination strategies for these two species is that herd-immunity, which would require vaccination of 70-80% of individuals, is not the necessary solution to this disease threat. The goal is not to eradicate the disease completely; that proves virtually impossible as it persists in other species. Instead, a population viability strategy, which suggests vaccination of only 20-40% of individuals, is desired. This strategy, while conserving resources, greatly reduces a population's chance of extinction (Haydon, et al. 2002), which is the true end goal.

Ethiopian Wolf Conclusions

Rabies appears to be a larger threat to Ethiopian wolves than canine distemper, with only three canine distemper outbreaks compared to five rabies outbreaks, and the mortality rate in rabies cases was higher. However, all three CDV cases occurred in the last decade, suggesting that CDV is becoming an increasing threat for wolves that managers must address. All disease outbreaks in the cases reviewed listed domestic dogs as the source of disease exposure for Ethiopian wolves, which indicates domestic dog vaccination for rabies and CDV in neighboring areas of wolves could be an effective mitigation strategy. This is a strategy currently being implemented by the Ethiopian Wolf Conservation Project (Stewart, et al. 2012, Marino, et al. 2017b), with encouraging success. Because rabies is also a threat to humans, it is easier to convince neighboring communities to participate in local vaccination programs (Marino, et al. 2017b) than with other diseases. In addition, with in an increase in oral vaccination use and success in Ethiopian wolves, it should become more feasible to proactively vaccinate individuals in especially small and threatened populations. A combination of proactive wolf vaccination [redacted]gram and a local domestic dog vaccination program should greatly increase the chance for species' survival.

African Wild Dog Conclusions

Canine distemper seems to be a more common threat, especially as domestic dog exposure increases. In Kruger National Park, South Africa, while fences help keep out most domestic dogs, managers have found an increasing number of domestic dogs brought into the park illegally for poaching rhino, and they often have rabies or distemper (Beverley, G, *pers.comm*). The increase of poaching has increased wild dogs' and other susceptible species exposure to rabies and canine distemper within the park, and a more proactive vaccination strategy may be necessary. The wild dog population has never been vaccinated, but as mentioned earlier, after the collapse of two packs in the park and its surrounding reserves, a small disease survey and vaccination program has commenced. Managers and researchers from the Endangered Wildlife Trust in South Africa have implemented a vaccination goal of 30-40% per pack for this project, which follow the population viability model. This is one of the first CDV and rabies vaccination studies in free-ranging wild dogs, and as this project continues, it will add to the limited knowledge of disease prevalence in Kruger National Park. Managers in other reserves should use the knowledge gained from this project as it emerges to more effectively implement their own management strategies as they combat an increasing disease threat.

Recommendations for Managers

Managers of wolves and wild dogs should work proactively to establish mitigation strategies to initiate in case of a disease outbreak, especially in areas where disease has occurred [redacted]iously. With a plan in place, when an outbreak does occur, they can react quickly and efficiently to minimize the effects. In some parks and reserves, it might even be necessary to proactively vaccinate, such as the dwindling Ethiopian wolf populations in the Bale Mountains and the staple wild dog population in Kruger National Park. These populations are critical for the survival of their species, and special caution should be taken when it comes to disease.

Disease mitigation could look different for wolves and wild dogs, but effective vaccination strategies ensuring population viability will be critical for both. For Ethiopian wolves, a strategy should focus on three main solutions, some of which are discussed in Randall, et al. 2006: (1) proactive oral rabies vaccination in 20-40% of the population, making sure a booster is given 6 months to a year later; (2) local vaccination programs covering CDV and rabies in domestic dogs; and (3) an emergency response vaccination strategy to employ when an outbreak occurs, vaccinating all individuals in the affected population.

For African wild dogs, a similar strategy should be employed, but more focused on canine distemper. The main elements of a population-viability vaccination strategy for a population of wild dogs should include: (1) proactively vaccinating for canine distemper and rabies; and (2) an emergency response vaccination strategy to employ in a disease outbreak, vaccinating all individuals in the affected and surrounding packs that could become exposed. For canine distemper vaccination, either a modified-live or parenteral recombinant vaccine should be used. As more information is gathered about the efficacy of the recombinant vaccination, if it continues to prove effective it could become the preferred vaccine. Individuals that are vaccinated should receive boosters one to three months after the first vaccination, and then annually to further continue immunity. For rabies vaccinations, using oral vaccination appears to be a good strategy, however if individuals are already being handled for CDV vaccinations, they [redacted]ld be vaccinated with a modified-live version parenterally. Again, a booster vaccination one to three months after initial vaccination will increase immunity, but yearly vaccinations may not be necessary as rabies immunity appeared to continue longer than distemper immunity. Currently, in domestic dogs, a three-year vaccination schedule is pursued. This could be an effective strategy for African wild dogs as well, but more research is needed to determine the best vaccination schedule. For an emergency outbreak response to rabies, a baited oral vaccination could be employed for a quick, wide-covering strategy.

Following these strategies regarding disease threat mitigation should help managers effectively maintain and grow Ethiopian wolf and African wild dog populations. If resources permit, employing a mix of these strategies would help curtail disease effects even more than employing just one mitigation strategy. Both rabies and canine distemper fit well into the SEIR epidemiological model, which models disease viability by breaking up the population into susceptible, exposed, infected, and recovered individuals (exposed being an individual that has been exposed to infection yet not infectious due to a lag period) (Ellner, Guckenheimer 2006). In this model, limiting susceptibility and exposure rates is key to reducing the reproductive number of the disease (R_0: the number of secondary infections arising from an initial infection). Because wolves and wild dogs are often exposed to rabies and CDV through domestic dogs, the best approach to limiting the disease threat is limiting the number of susceptible and exposed domestic dogs in addition to the susceptible and exposed wolf and wild dogs. In the past 15 years, management strategies of endangered species derived from mathematical modeling of disease have slowly begun to emerge. Randall, et al. (2006) presented a similar vaccination strategy involving both domestic dogs and Ethiopian wolves, based on mathematical modeling of rabies in the wolf. This modeling was only possible due to diligent wolf population monitoring [redacted] an extended period (Haydon, et al. 2006, Randall, et al. 2006); therefore, in order to accurately predict the effective vaccination rates for domestic hosts and the endangered species, intensive disease monitoring must take place.

The endangered Ethiopian wolf and African wild dog will continue to experience an increasing load of threats from humans in different ways, and in the future, more intensive monitoring and management will be increasingly necessary to protect their populations. Managing for disease is one opportunity to help reduce stochastic negative pressures on already small, scattered populations, helping to ensure their survival into the future.

LITERATURE CITED

Alexander KA, Conrad PA, Gardner IA, Parish C, Appel M, Levy MG, Lerche N, Kat P. 1993. Serologic Survey for Selected Microbial Pathogens in African Wild Dogs (Lycaon pictus) and Sympatric Domestic Dogs (Canis familiaris) in Maasai Mara, Kenya. *J ZOO Wildlife Med* 24:140–144.

Alexander KA, Appel MJG. 1994. African wild dogs (Lycaon pictus) endangered by a canine distemper epizootic among domestic dogs near the Masai mara national reserve, Kenya. *J Wildlife Dis* 30:481–485.

Alexander KA, Kat PW, Munson LA, Kalake A, Appel MJG. 1996. Canine distemper-related mortality among wild dogs (Lycaon pictus) in Chobe National Park, Botswana. *J Zoo Wildl Med* 27:426–427.

Alexander KA, McNutt JW, Briggs MB, Standers PE, Funston P, Hemson G, Keet D, van Vuuren M. 2010. Multi-host pathogens and carnivore management in southern Africa. *Comp Immunol Microb* 33:249–265.

Berentsen AR, Dunbar MR, Becker MS, M'soka J, Droge E, Sakuya NM, Matandiko W, McRobb R, Hanlon CA. 2013. Rabies, Canine Distemper, and Canine Parvovirus Exposure in Large Carnivore Communities from Two Zambian Ecosystems. *Vector-Borne Zoonot* 13:643–649.

Breed AC, Plowright RK, Hayman DTS, Knobel DL, Molenaar FM, Gardner–Roberts D, Cleaveland S, Haydon DT, Kock RA, Cunningham AA, et al. 2009. Disease Management in Endangered Mammals. In: *Management of Disease in Wild Mammals*, R. J. Delahay, G. C. Smith, and M. R. Hutchings, editors. Springer, Tokyo. pp. 215–239.

Burrows R. 1992. Rabies in wild dogs. *Nature* 359:277.

Burrows R, Hofer H, East ML. 1994. Demography, Extinction and Intervention in a Small Population: The case of the Serengeti wild dogs. *P Roy Soc Lond B Bio* 256:281–292.

Cirone F, Elia G, Campolo M, Friedrich K, Martella V, Pratelli A, Buonavoglia C. 2004. Immunogenicity of an Inactivated Oil-Emulsion Canine Distemper Vaccine in African Wild Dogs. *J Wildlife Dis* 40:343–346.

Cleaveland S, Hess GR, Dobson AP, Laurenson MK, McCallum H, Roberts MG, Woodroffe R. 2002. The role of pathogens in biological conservation. In: *The Ecology of Wildlife Diseases*, P. J. Hudson, A. Rizzoli, B. Grenfell, and H. Heesterbeck, editors. Oxford University Press, Oxford. pp. 139–150.

Cleaveland S. 2009. Viral threats and vaccination: disease management of endangered species. *Anim Conserv* 12:187–189.

Connolly M, Thomas P, Woodroffe R, Raphael BL. 2013. Comparison of oral and intramuscular recombinant canine distemper vaccination in African wild dogs (Lycaon pictus). *J Zoo Wildlife Med* 44:882–888.

Connolly M, Thomas P, Woodroffe R, Raphael BL. 2015. Single- versus double-dose rabies vaccination in captive African wild dogs (Lycaon pictus). *J Zoo Wildlife Med* 46:691–698.

Creel S, Creel NM, Munson L, Sanderlin D, Appel MJG. 1997. Serosurvey for selected viral diseases and demography of African wild dogs in Tanzania. *J Wildlife Dis* 33:823–832.

Creel S. 2001. Four Factors Modifying the Effect of Competition on Carnivore Population Dynamics as Illustrated by African Wild Dogs. *Conserve Biol* 15:271–274.

Creel S, Mills MGL, McNutt JW. 2004. Demography and population dynamics of African wild dogs in three critical populations. In: *The Biology and Conservation of Wild Canids*, D. W. Macdonald and C. Sillero-Zubiri, editors. Oxford University Press, New York. pp. 337–350.

Daszak P, Cunningham AA, Hyatt AD. 2000. Emerging Infectious Diseases of Wildlife--Threats to Biodiversity and Human Health. *Science* 287:443–449.

Deem SL, Spelman LH, Yates RA, Montali RJ. 2000. Canine distemper in terrestrial carnivores: a review. *J Zoo Wildlife Med* 31:441–451.

Durchfeld B, Baumgärtner W, Herbst W, Brahm R. 1990. Vaccine-associated canine distemper infection in a litter of African hunting dogs (Lycaon pictus). *J Vet Med B* 37:203–212.

Flacke G, Becker P, Cooper D, Szykman Gunther M, Robertson I, Holyoake C, Donaldson R, Warren K. 2013. An Infectious Disease and Mortality Survey in a Population of Free-Ranging African Wild Dogs and Sympatric Domestic Dogs. *Int J Biodivers* 2013:e497623.

Fuller TK, Kat PW, Bulger JB, Maddock AH, Ginsberg JR, Burrows R, McNutt JW, Mills MGL. 1992. Population Dynamics of African Wild Dogs. In: *Wildlife 2001: Populations*, D. R. McCullough and R. H. Barrett, editors. Elsevier Science Publishers LTD, Essex, England. pp. 125–139.

Gascoyne SC, King AA, Laurenson MK, 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. *Onderstepoort J Vet Res* 60:415–420.

Gascoyne SC, Laurenson MK, Lelo S, Borner M. 1993. Rabies in African wild dogs (Lycaon pictus) in the Serengeti region, Tanzania. *J Wildlife Dis* 29:396–402.

Ginsberg JR, Mace GM, Albon S. 1995. Local Extinction in a Small and Declining Population: Wild Dogs in the Serengeti. *P Roy Soc Lond B Bio* 262:221–228.

Gordon CH, Banyard AC, Hussein A, Laurenson MK, Malcolm JR, Marino J, Regassa F, Stewart A-ME, Fooks AR, Sillero-Zubiri C. 2015. Canine Distemper in Endangered Ethiopian Wolves. *Emerg Infect Dis* 21:824–832.

Gordon CH, Banyard AC, Hussein A, Laurenson MK, Malcolm JR, Marino J, Regassa F, Stewart A-ME, Fooks AR, Sillero-Zubiri C. 2015. Canine Distemper in Endangered Ethiopian Wolves. *Emerg Infect Dis* 21:824–832.

Greene CE, Appel MJ. 2012. Canine Distemper, 4th edition. In: *Infectious Diseases of the Dog and Cat*, C. E. Green, editor. W.B. Saunders, Philadelphia. pp. 226–241.

Haydon DT, Laurenson MK, Sillero-Zubiri C. 2002. Integrating Epidemiology into Population Viability Analysis: Managing the Risk Posed by Rabies and Canine Distemper to the Ethiopian Wolf. *Conserv Biol* 16:1372–1385.

Haydon DT, Cleaveland S, Taylor LH, Laurenson MK. 2002. Identifying reservoirs of infection: a conceptual and practical challenge. *Emerging Infect Dis* 8:1468–1473.

Hofmeyr M, Bingham J, Lane EP, Ide A, Nel L. 2000. Rabies in African wild dogs (Lycaon pitus) in the Madikwe Game Reserve, South Africa. *Vet Rec* 146:50–52.

Hofmeyr M, Hofmeyr D, Nel L, Bingham J. 2004. A second outbreak of rabies in African wild dogs (Lycaon pictus) in Madikwe Game Reserve, South Africa, demonstrating the efficacy of vaccination against natural rabies challenge. *Anim Conserv* 7:193–198.

Kat PW, Alexander KA, Smith JS, Munson L. 1995. Rabies and African Wild Dogs in Kenya. *P Roy Soc Lond B Bio* 262:229–233.

Knobel D L, Fooks A R, Brookes S M, Randall D A, Williams S D, Argaw K, Shiferaw F, Tallents L A, Laurenson M K. 2007. Trapping and vaccination of endangered Ethiopian wolves to control an outbreak of rabies. *J Appl Ecol* 45:109–116.

Knobel DL, du Toit JT, Bingham J. 2002. Development of a bait and baiting system for delivery of oral rabies vaccine to free-ranging African wild dogs (Lycaon pictus). *J Wildl Dis* 38:352–362.

[redacted] Knobel DL, Liebenberg A, Du Toit JT. 2003. Seroconversion in captive African wild dogs (Lycaon pictus) following administration of a chicken head bait/SAG-2 oral rabies vaccine combination. *Onderstepoort J Vet Res* 70:73–7.

Knobel DL, Toit JT du. 2003. The influence of pack social structure on oral rabies vaccination coverage in captive African wild dogs (Lycaon pictus). *App Anim Behav Sci* 80:61–70.

Laurenson MK, Cleaveland S, Artois M, Woodroffe R. 2004. Assessing and managing infectious disease threats to canids. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, UK. pp. 246–256.

Laurenson K, Van Heerden J, Stander P, Van Vuuren M. 1997. Seroepidemiological survey of sympatric domestic and wild dogs (Lycaon pictus) in Tsumkwe District, north-eastern Namibia. *Onderstepoort J Vet Res* 64:313–316.

Marino J, Sillero-Zubiri C, Deressa A, Bedin E, Bitewa A, Lema F, Rskay G, Banyard A, Fooks AR. 2017. Rabies and Distemper Outbreaks in Smallest Ethiopian Wolf Population., Rabies and Distemper Outbreaks in Smallest Ethiopian Wolf Population. *Emerg Infect Dis* 23:2102–2104.

Marino J, Bedin E, Sillero-Zubiri C. 2017. EWCP Annual Report. Ethiopian Wolf Conservation Program. p. 34.

Martinez-Gutierrez M, Ruiz-Saenz J. 2016. Diversity of susceptible hosts in canine distemper virus infection: a systematic review and data synthesis. *BMC Vet Res* 12:78–88.

McCormick AE. 1983. Canine Distemper in African Cape Hunting Dogs (Lycaon pictus): Possibly Vaccine Induced. *J Zoo Wildlife Med* 14:66–71.

McNutt, J.W. Sociality and dispersal of African wild dogs (Lycaon pictus). PhD Dissertation. University of California, Davis, CA.

Prager KC, Mazet JAK, Munson L, Cleaveland S, Donnelly CA, Dubovi EJ, Gunther MS, Lines R, Mills MGL, Davies-Mostert HT, et al. 2012. The effect of protected areas on pathogen exposure in endangered African wild dog (Lycaon pictus) populations. *Biol Conserv* 150:15–22.

Prager KC, Mazet JA, K, Dubovi EJ, Frank LG, Munson L, Wagner AP, Woodroffe R. 2012. Rabies Virus and Canine Distemper Virus in Wild and Domestic Carnivores in Northern Kenya: Are Domestic Dogs the Reservoir? *EcoHealth* 9:483–98.

Pomilia MA, McNutt JW, Jordan NR. 2015. Ecological predictors of African wild dog ranging patterns in northern Botswana. *J Mammal* 96:1214–1223.

Randall DA, Marino J, Haydon DT, Sillero-Zubiri C, Knobel DL, Tallents LA, Macdonald DW, Laurenson MK. 2006. An integrated disease management strategy for the control of rabies in Ethiopian wolves. *Biol Conserv* 131:151–162.

Rupprecht CE, Stöhr K, Meredith C. 2001. Rabies, 3rd edition. In: *Infectious Diseases of Wild Mammals*, E. S. Williams and I. K. Barker, editors. Iowa State University Press, Ames, IA. pp. 4–37.

Sillero-Zubiri C, King AA, Macdonald DW. 1996. Rabies and mortality in Ethiopian wolves (Canis simensis). *J Wildl Dis* 32:80–86.

Sillero-Zubiri C, King AA, Macdonald DW. 2004. Afroalpine ecology, solitary foraging, and intense sociality amongst Ethiopian wolves. In: *The Biology and Conservation of Wild Canids*, D. W. Macdonald and C. Sillero-Zubiri, editors. Oxford University Press, New York. pp. 311–322.

Spencer J, Burroughs R. 1992. Antibody Response to Canine Distemper Vaccine in African Wild Dogs. *J Wildlife Dis* 28:443–444.

Stewart A-ME, Gordon CH, Marino J, Sillero-Zubiri C. 2012. EWCP Annual Report. Ethiopian Wolf Conservation Program.

Marino J, Stewart AE, Gordon CH, Gottelli D, Tefera Z, Laurenson MK, Sillero-Zubiri C. 2011. Ethiopian wolf status review. In: *Strategic planning for Ethiopian wolf conservation,* IUCN/SSC Canid Specialist Group, editors, Oxford, United Kingdom. pp. 1-50.

Timm SF, Munson L, Summers BA, Terio KA, Dubovi EJ, Rupprecht CE, Kapil S, Garcelon DK. 2009. A suspected canine distemper epidemic as the cause of a catastrophic decline in Santa Catalina Island foxes (Urocyon littoralis catalinae). *J Wildl Dis* 45:333–343.

Tswalu Kalahari. 2016. "African Wild Dogs at Tswalu." http://www.tswalu.com/media/blog-article/african-wild-dogs-at-tswalu.

van de Bildt MWG, Kuiken T, Visee AM, Lema S, Fitzjohn TR, Osterhaus ADME. 2002. Distemper outbreak and its effect on African wild dog conservation. *Emerg Infect Dis* 8:212–213.

Van Heerden J, Bainbridge N, Burroughs REJ, Kriek NPJ. 1989. Distemper-like disease and encephalitozoonosis in wild dogs (Lycaon pictus). *Journal of Wildlife Diseases* 25:70–75.

Van Heerden J, Mills MG, Van Vuuren MJ, Kelly PJ, Dreyer MJ. 1995. An investigation into the health status and diseases of wild dogs (Lycaon pictus) in the Kruger National Park. *J S Afr Vet Assoc* 66:18–27.

Van Heerden J, Bingham J, Van Vuuren M, Burroughs REJ, Stylianides E. 2002. Clinical and serological response of wild dogs (Lycaon pictus) to vaccination against canine distemper, canine parvovirus infection and rabies. *J S Afr Vet Assoc* 73:8–12.

Viana M, Cleaveland S, Matthiopoulos J, Halliday J, Packer C, Craft ME, Hampson K, Czupryna A, Dobson AP, Dubovi EJ, et al. 2015. Dynamics of a morbillivirus at the domestic–wildlife interface: Canine distemper virus in domestic dogs and lions. *Proc Natl Acad Sci USA* 112:1464–1469.

Woodroffe R. 2001. Assessing the risks of intervention: immobilization, radio-collaring and vaccination of African wild dogs. *Oryx* 35:234–244.

Woodroffe R, Cleaveland S, Courtenay O, Laurenson MK, Artois M. 2004. Infection Disease in the managment and conservation of wild canids. In: *Biology and Conservation of Wild Canids*, D. W. Macdonald and C. Sillero-Zubiri, editors. Oxford University Press, New York. pp. 123–142.

Woodroffe R, Donnelly CA. 2011. Risk of contact between endangered African wild dogs Lycaon pictus and domestic dogs: opportunities for pathogen transmission. *J Appl Ecol* 48:1345–1354.

Woodroffe R, Prager KC, Munson L, Conrad PA, Dubovi EJ, Mazet JAK. 2012. Contact with Domestic Dogs Increases Pathogen Exposure in Endangered African Wild Dogs (Lycaon pictus). *PLOS ONE* 7:e30099.

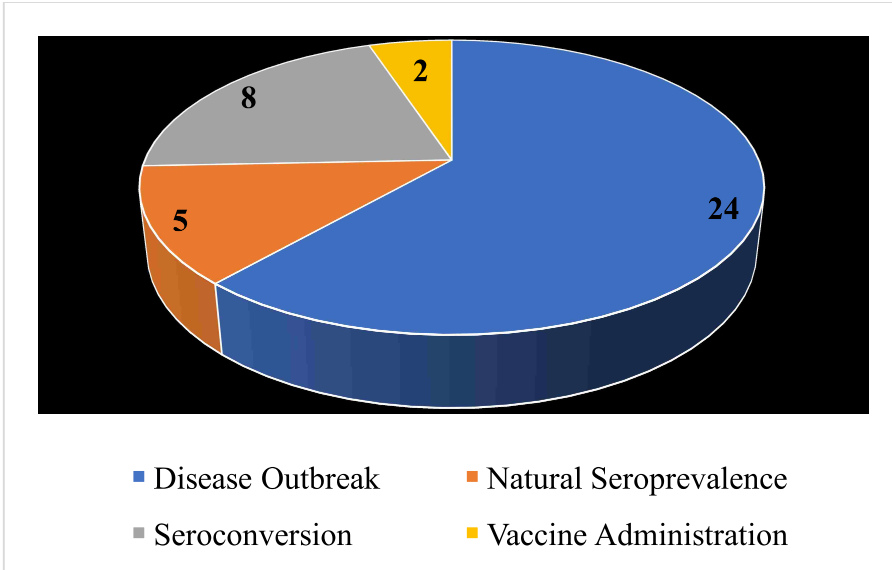

Figure 1. The breakdown of study type among all 39 studies reviewed

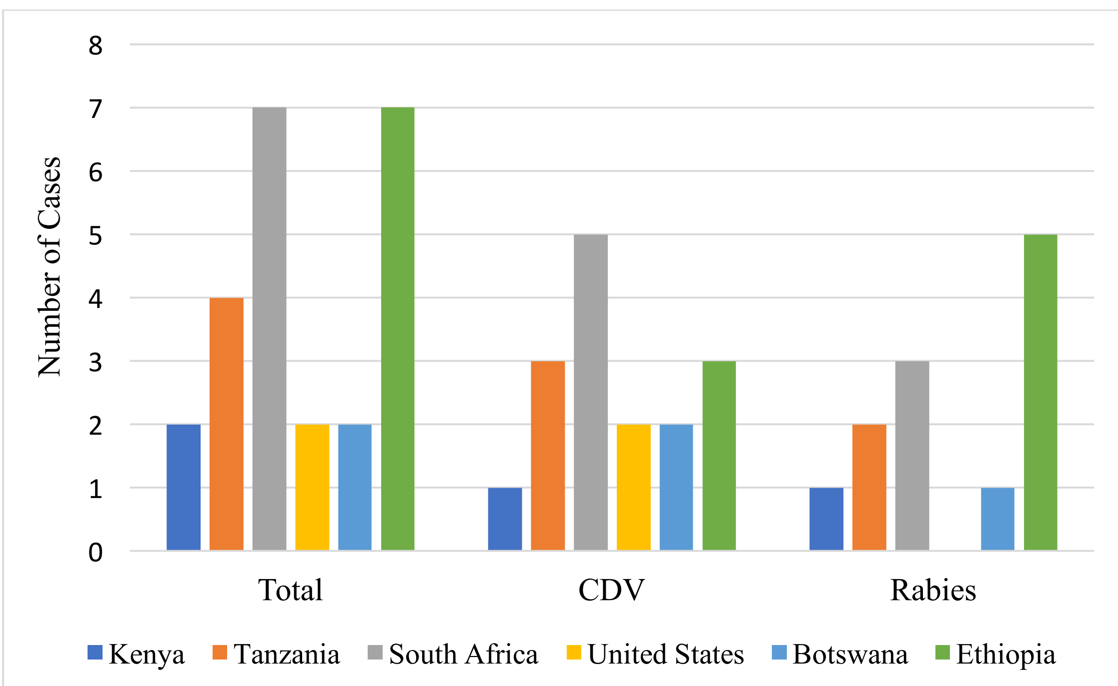

Figure 2. Distribution of 24 disease outbreaks across countries, in total and by disease.

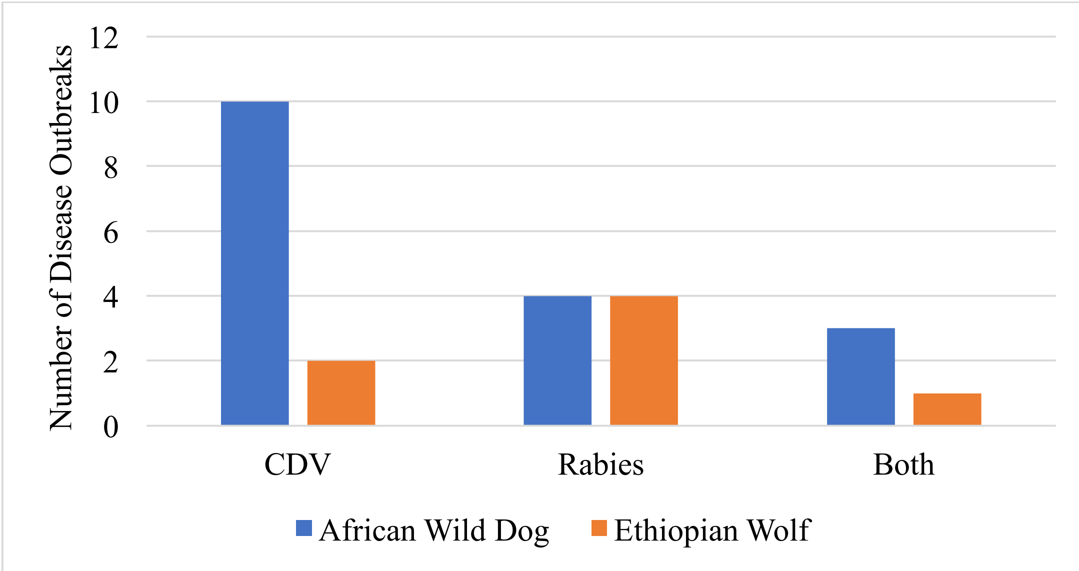

Figure 3. Distribution of disease outbreak by disease for each species.

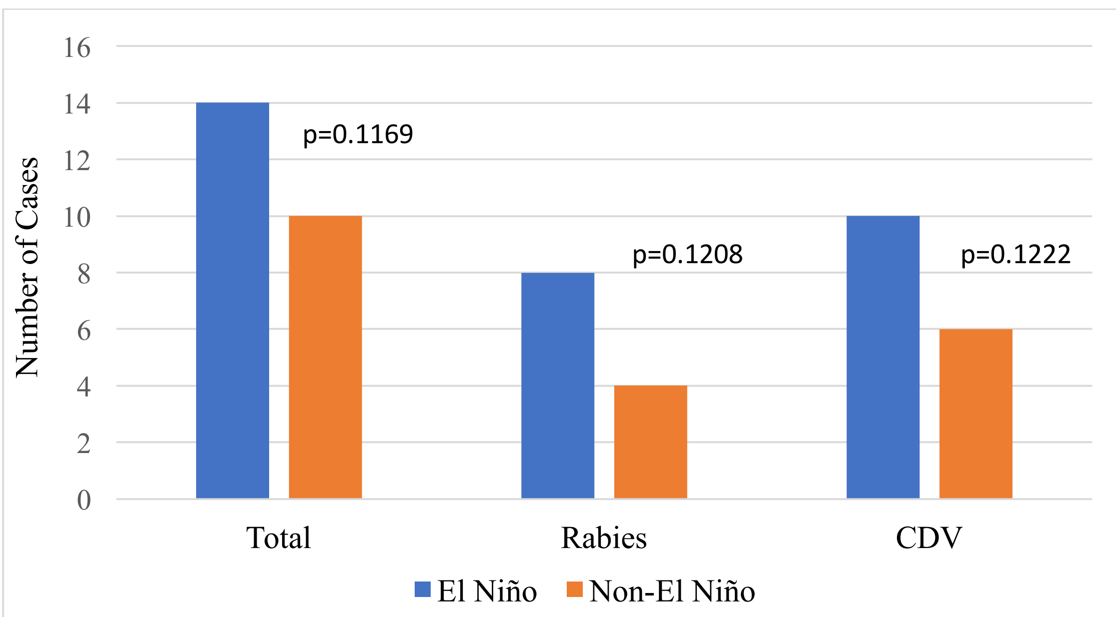

Figure 4. Number of disease outbreaks in El Niño year versus non-El Niño year, in total and by disease. A binomial test revealed there was no significant difference (all $P > 0.05$) in disease occurrence in total or for either disease.

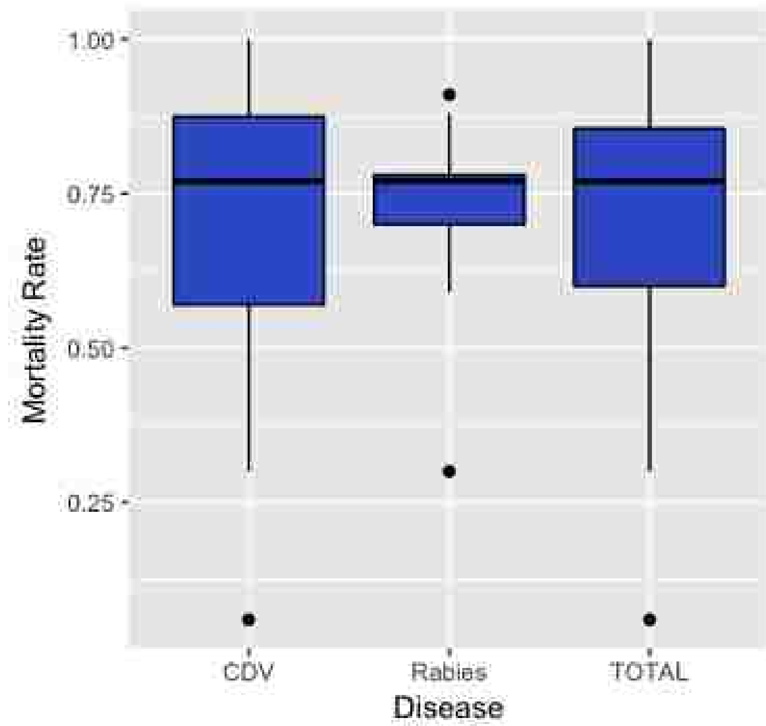

Figure 5. Box plots showing distribution of mortality rates across all disease cases and by each disease; horizontal lines represent the median.

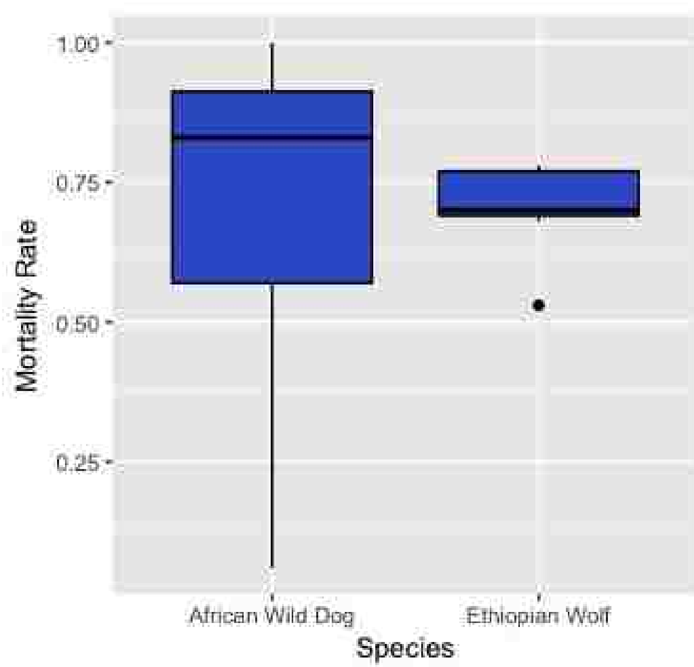

Figure 6. Box plots showing distribution of mortality rates in disease cases by species; horizontal lines represent the median.

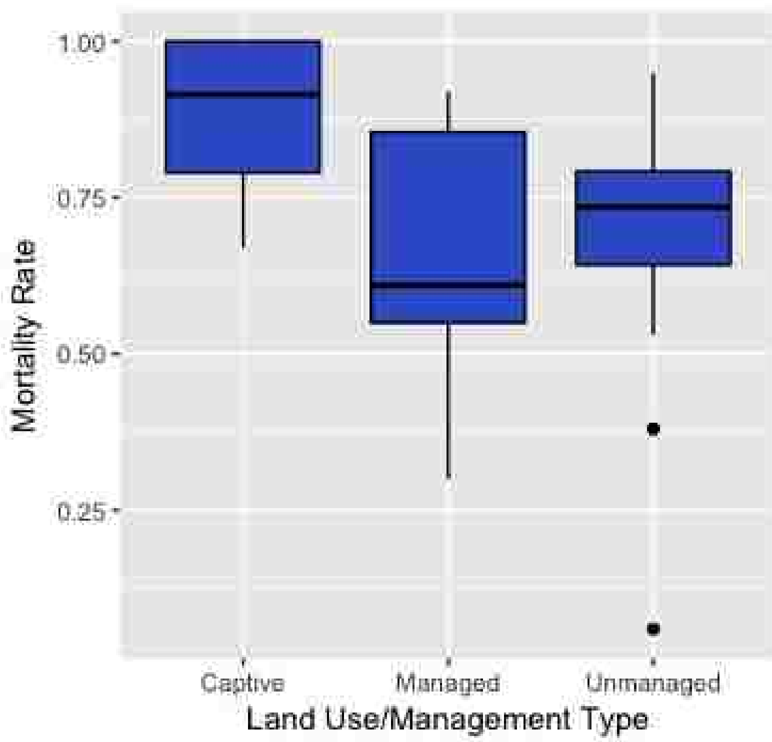

Figure 7. Box plots showing the distribution of mortality rates in disease cases by land use/management; horizontal lines represent the median.

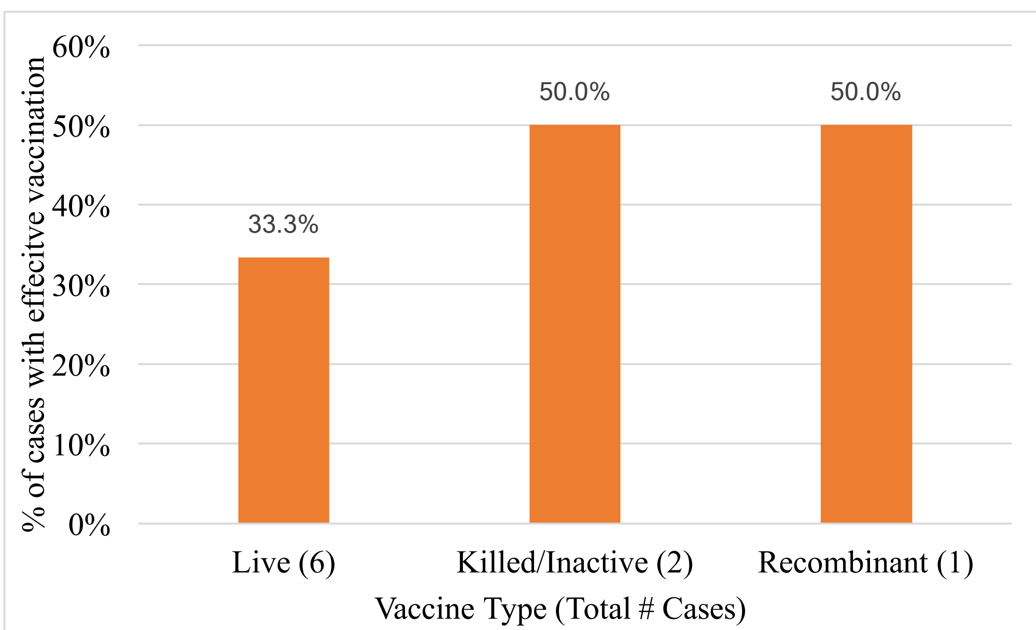

Figure 8. Percentage of cases with effective canine distemper vaccination in African wild dogs by vaccine type.

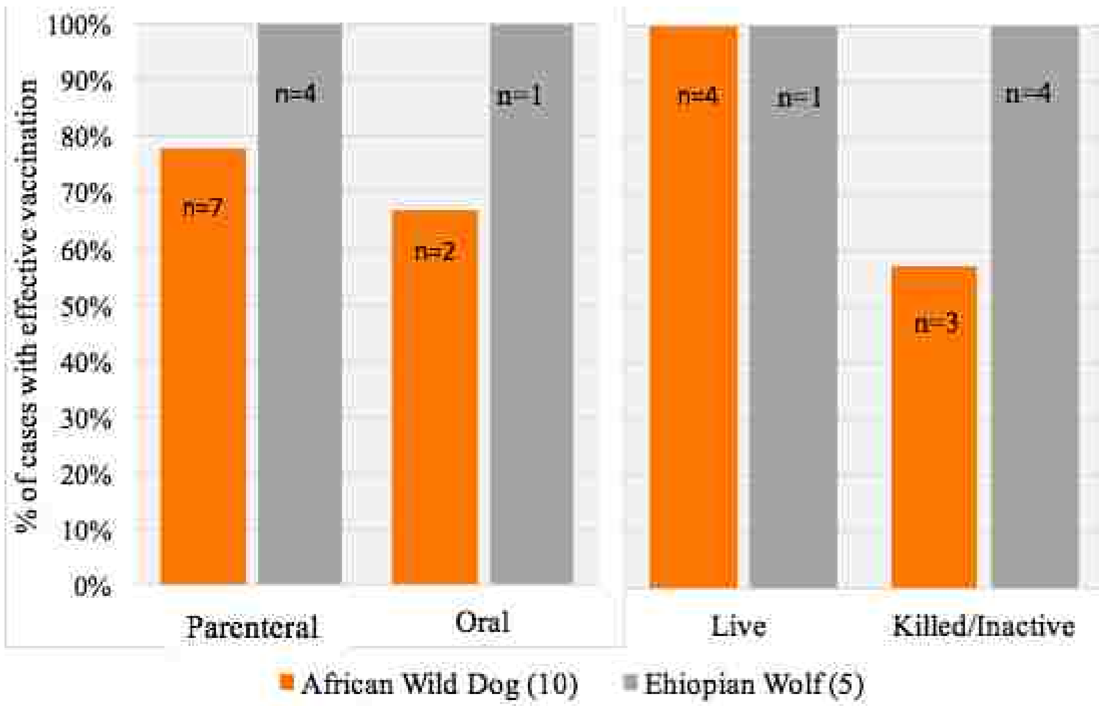

Figure 9. Percentage of cases with effective rabies vaccination by species and vaccine type, n=number of effective cases.

Appendix A: Studies Reviewed. Grouped studies in gray denote one study with multiple outbreaks or diseases covered.

Case	Author	Case Type	Study Date	Species	Location	El Niño	Captive	Protected	Managed
1	Alexander and Appel, 2014	Disease Outbreak	1989-1991	AWD	Kenya	N	N	N	N
2	Alexander, *et al.* 1993	Natural Seroprevalence	1989-1990	AWD	Kenya	N	N	Y	Y
3	Alexander, *et al.* 1996	Disease Outbreak	1994	AWD	Botswana	Y	N	Y	N
4	Alexander, *et al.* 2010	Disease Outbreak	1992-1993	AWD	Botswana	Y	N	Y	Y
5	Berensten, *et al.* 2013	Natural Seroprevalence	2009-2011	AWD	Zambia	Y	N	Y	N
6	Burrows, *et al.* 1994	Disease Outbreak	1965-1993	AWD	Tanzania	Y	N	Y	Y
7	Cirone, *et al.* 2004	Seroconversion Post-vaccination	2003	AWD	Rome (zoo)	Y	Y	Y	Y
8	Connolly, *et al.* 2013	Seroconversion Post-vaccination	2005-2007	AWD	Bronx zoo	Y	Y	Y	Y
9	Connolly, *et al.* 2015	Seroconversion Post-vaccination	2005-2007	AWD	Bronx zoo	Y	Y	Y	Y
10	Durchfeld, *et al.* 1990	Disease Outbreak	1989	AWD	Zoo	N	Y	Y	Y
11	Flacke, *et al.* 2013	Disease Outbreak	2006-2007	AWD	South Africa (KZN)	Y	N	Y	N
12	Gascoyne, *et al. 1993*	Disease Outbreak	1990-1992	AWD	Tanzania	N	N	Y	Y
13	Gascoyne, *et al.* 1993b	Seroconversion Post-vaccination	1975	AWD	Frankfurt zoo	N	Y	Y	Y
14	Goller, *et al*. 2010	Disease Outbreak	2007	AWD	Tanzania	Y	N	Y	Y
15	Gordon, *et al.* 2015	Disease Outbreak	2005-2007	Ethiopian Wolf	Ethiopia	Y	N	Y	N
16	Gordon, *et al*. 2015	Disease Outbreak	2010	Ethiopian Wolf	Ethiopia	N	N	Y	N
17	Hofmeyr, *et al*. 2000	Disease Outbreak	1997	AWD	South Africa	Y	N	Y	Y
18	Hofmeyr, *et al.* 2004	Disease Outbreak	2000	AWD	South Africa	N	N	Y	Y

Appendix (cont.)

Case	Disease	Exposure	Vaccination	Live/Inactive CDV	Live/Killed Rabies	Combo vs Single	Oral vs Parenteral (IM)	>70% Seroconversion?	Mortality rate
1	CDV	domestic dogs	N	NA	NA	NA	NA	NA	95%
2	CDV	none	N	NA	NA	NA	NA	NA	NA
3	CDV	domestic dog	N	NA	NA	NA	NA	NA	83%
4	Both	unknown	N	NA	NA	NA	NA	NA	30%
5	CDV	domestic dogs, other mammals	N	NA	NA	NA	NA	NA	NA
6	both	unknown	y	NA	Killed	Single	IM	NA	51%
7	CDV	none	y	inactive	NA	Single	IM	yes	NA
8	CDV	none	Y	recombinant	NA	Single	Mixed	no	NA
9	Rabies	none	Y	NA	modified live	Single	IM	yes	NA
10	CDV	vx	Y	live	NA	Combination	IM	NA	100%
11	Both	domestic dog	Y	NA	Killed	Unknown	Mixed	NA	38%
12	Rabies	domestic dog	Post outbreak	NA	Killed	Single	IM	NA	unsure
13	Rabies	NA	Y	NA	Killed	Single	IM	yes	NA
14	CDV	domestic dog	N	NA	NA	NA	NA	NA	61%
15	CDV	domestic dog	N	NA	NA	NA	NA	NA	53%
16	CDV	domestic dog	N	NA	NA	NA	NA	NA	68%
17	Rabies	jackals	Y	NA	Killed	Single	IM	no	88%
18	Rabies	jackals	Y	NA	Killed	Single	IM	no	59%

[redacted]

[redacted] [redacted]

Appendix (cont.)

Case	Author	Case Type	Study Date	Species	Location	El Niño	Captive	Protected	Managed
19	Johnson, *et al.* 2010	Disease Outbreak	2007	Ethiopian Wolf	Ethiopia	Y	N	Y	N
20	Johnson, *et al.* 2010	Disease Outbreak	2008	Ethiopian Wolf	Ethiopia	N	N	Y	N
21	Kat, *et al.* 1995	Disease Outbreak	1989	AWD	Kenya	N	N	Y	N
22	Knobel, *et al.* 2002	Vaccination Administration	2001	AWD	South Africa		N	Y	N
23	Knobel, *et al.* 2003	Seroconversion Post-vaccination	2002/3	AWD	South Africa	Y	Y	Y	Y
24	Knobel, *et al.* 2003b	Vaccination Administration	2001	AWD	South Africa		Y	Y	Y
25	Laurenson, *et al.* 1997	Natural Seroprevalence	1993-94	AWD	Namibia	Y	N	both	N
26	Marino, *et al.* 2017	Disease Outbreak	2016	Ethiopian Wolf	Ethiopia	Y	N	Y	N
27	McCormick 1983	Disease Outbreak	1983	AWD	New York zoo, from Namibia	Y	Y	Y	Y
28	Prager, *et al.* 2012	Natural Seroprevalence	1988-2009	AWD	Kenya, South Africa, Tanzania, Zambia, Zimbabwe, Botswana	Y	N	Both	N
29	Prager, *et al.* 2012	Natural Seroprevalence	1988-2009	AWD	Kenya, South Africa, Tanzania, Zambia, Zimbabwe, Botswana	Y	N	Both	N
30	Prager, *et al.* 2012b	Natural Seroprevalence	2000-2009	AWD	Kenya	Y	N	N	N
31	Prager, *et al* . 2012b	Natural Seroprevalence	2000-2010	AWD	Kenya	Y	N	N	N
32	Randall, *et al.* 2004	Disease Outbreak	2003-04	Ethiopian wolf	Ethiopia	Y	N	Y	N
33	Sillero-Zubiri, *et al.* 1996	Disease Outbreak	1991-92	Ethiopian wolf	Ethiopia	Y	N	Y	N
34	Sillero-Zubiri, *et al.* 2016	Seroconversion Post-vaccination	2014	Ethiopian wolf	Ethiopia		N	Y	N
35	Spencer and Burroughs 1992	Seroconversion Post-vaccination	1991	AWD	South Africa	Y	Y	Y	Y

Appendix (cont.)

Case	Disease	Exposure	Vaccination	Live/Inactive CDV	Live/Killed Rabies	Combo vs Single	Oral vs Parenteral (IM)	>70% Seroconversion?	Mortality rate
19	Rabies	domestic dog	Post outbreak	NA	killed	Single	IM	no	70%
20	Rabies	Domestic dog	Post outbreak	NA	killed	Single	IM	no	70%
21	Rabies	domestic dog	N	NA	NA	NA	NA	NA	91%
22	Rabies	NA	Y	NA	modified live	Single	Oral	yes	NA
23	Rabies	NA	Y	NA	modified live	Single	Oral	yes	NA
24	Rabies	NA	Y	NA	modified live	Single	oral	yes	NA
25	CDV	domestic dog	N	NA	NA	NA	NA	NA	NA
26	Both	domestic dog	Post outbreak	NA	killed	Single	IM	yes	77%
27	CDV	Vaccination	Y	live	Killed	Combination	IM	no	83%
28	CDV	Domestic dog, wild canids	N	NA	NA	NA	NA	NA	NA
29	Rabies	unknown	N	NA	NA	NA	NA	NA	NA
30	CDV	domestic dog, wild carnivores	N	NA	NA	NA	NA	NA	NA
31	Rabies	domestic dog	N	NA	NA	NA	NA	NA	NA
32	Rabies	domestic dog	Post outbreak	NA	Killed	Single	IM	yes	78%
33	Rabies	domestic dog	N	NA	NA	NA	NA	NA	77%
34	Rabies	NA	Y	NA	Live	Single	Oral	yes	NA
35	CDV	NA	Y	live	NA	Combination	IM	yes	NA

Appendix (cont.)

Case	Author	Case Type	Study Date	Species	Location	El Niño	Captive	Protected	Managed
36	Van de Bilt, *et al.* 2002	Disease Outbreak	2000-2001	AWD	Tanzania	N	N	Y	Y
37	Van Heerden, et al. 1989	Disease Outbreak	1989	AWD	South Africa Zoo	N	Y	Y	Y
38	Van Heerden, et al. 1989	Disease Outbreak	1989	AWD	South Africa Zoo	N	Y	Y	Y
39	Van Heerden, et al. 2002	Seroconversion Post-vaccination	2001	AWD	South Africa	N	Y	Y	Y
40	Van Heerden, *et al.* 2002	Seroconversion Post-vaccination	2001	AWD	South Africa	N	Y	Y	Y
41	Unpublished report	Disease Outbreak	2016	AWD	South Africa	Y	N	Y	Y
42	Unpublished report	Disease Outbreak	2016	AWD	South Africa	Y	N	Y	N

Case	Disease	Exposure	Vaccination	Live/Inactive CDV	Live/Killed Rabies	Combo vs Single	Oral vs Parenteral (IM)	>70% Seroconversion?	Mortality rate
36	CDV	Unsure	Y	inactive	NA	Combination	IM	no	92%
37	CDV	VX	Y	live	NA	Combination	IM	no	67%
38	CDV	VX	Y	live	NA	Combination	IM	no	100%
39	CDV	NA	Y	live	NA	Combination	IM	no	NA
40	Rabies	NA	Y	NA	modified live	Combination	Mixed	yes	NA
41	CDV	Wild canid	Y	unknown	NA	NA	IM	no	83%
42	CDV	Unknown	N	NA	NA	NA	NA	NA	6%