

ABSTRACT

HARRIS, NYEEMA CHARMAINE. The Biogeography of Carnivore Hosts and their Parasites: Implications for Conservation in North America. (Under the director of Drs. Robert R. Dunn and Stacy A.C. Nelson.)

Much effort in ecology seeks to understand what processes maintain and erode patterns in biological diversity. However, little effort has focused on understanding determinants of species diversity for parasites; despite them being speciose and detrimental. Overall, my dissertation research aims to disentangle the mechanisms responsible for generating variation in parasite diversity across space and among species using carnivores as focal hosts.

Carnivores are a useful model group because the order Carnivora includes species that vary in their geographic extent as well as their rarity/abundance. As a consequence, the parasites of carnivores comprise both abundant species with potential as zoonotic vectors (e.g., raccoons and rabies) and parasites likely to be in need of conservation.

Chapter 1: Using host associations to understand spatial patterns of variation in parasites of North American Carnivores. I developed a parasite diversity model based on known host associations with 29 North American carnivores. Because wide-ranging hosts disproportionately contributed to total and specialist parasite diversity, conservation programs that focus on these common hosts may capture much biological diversity, but also unwittingly sources of human diseases. I supply the first parasite diversity model to understand broad scale patterns in species richness for North American carnivores, which can inform both future parasite conservation and disease management efforts.

Chapter 2: The influence of carnivore extinction on the composition and geography of zoonotic parasites. I used presence-absence matrices of host-parasite associations for 29

North American carnivore species and simulated the corresponding changes in parasite community composition and diversity with the random extinction of hosts. I also explored the spatial distribution of zoonotic parasite diversity under three carnivore host composition scenarios. I found that the composition of the parasite assemblage community changed independently across parasite groups with the proportion of zoonotic viruses markedly increasing with carnivore host extinctions. The loss of widespread carnivore hosts had the greatest impact by reducing overall zoonotic diversity and shifting the geographic distributions of parasite-rich areas. If high host diversity dilutes disease prevalence in humans, my findings demonstrate an added benefit of conserving widespread species for human health.

Chapter 3: Revisiting parasite conservation in endangered species. I explored whether endangered species have endangered parasites using one of the most endangered North American carnivore species - the black-footed ferret (*Mustela nigripes*). I sampled over 600 individuals and found that the most abundant ectoparasite is an important vector for plague, a flea *Oropsylla hirsuta*. I found that the extant parasite community on black-footed ferrets comprised species that are not host-specific, have low probabilities of extinction, and are found commonly in association with prey species. Black-footed ferrets like other endangered species undergo repeated parasite removal and vaccination efforts to facilitate population recovery, which may have unintentionally contributed to their depauperate ectoparasite community.

Chapter 4: Conserving endemic host-parasite interactions in rare species. I evaluated whether the role of an endangered species to supply habitat for ectoparasites varied across the

range of the host. I captured 234 island foxes (*Urocyon littoralis*), an endemic carnivore of the Channel Islands, from three populations: Santa Catalina (n=72), Santa Rosa (n=79), and San Miguel (n=83). I identified 8 ectoparasites species in total, but ectoparasite diversity varied among populations. Furthermore, I found there to be unique host-parasite associations in each island fox population. Given this information, I would be able to assign a fox of unknown origin to its respective population 70% of the time. My findings highlight the importance of conserving populations to maintain endemic interactions and emphasize always considering the role of a species in a local-specific context.

The Biogeography of Carnivore Hosts and their Parasites:
Implications for Conservation in North America

by
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DEDICATION

To Kevin and Phoenix Mclennon, my most pleasant distractions.

BIOGRAPHY

I was born to Linda Harris and Snelson Harris on the 29th day of April 1983. I spent the entirety of my youth in Philadelphia, Pennsylvania. I was raised by my mother in a household with my older brother and sister, Kibwe and Turiya, respectively.

Experiences early in my life confirmed my conviction to pursue a career in conservation and ecology, namely traveling to Kenya in East Africa at the age of 14 with a student group sponsored by the Philadelphia Zoo. I received a BS in Wildlife Science in 2004 from Virginia Tech in Blacksburg, Virginia. During this tenure, I participated in a study abroad program to Belize under the mentorship of my undergraduate advisor, Dr. Marcella Kelly. I was employed by the US Fish & Wildlife Service as a student trainee during the summers. However, the most influential experience as an undergraduate involved completing my first research project as a part of the Cooperative Allegheny Black Bear Study (CABS). Specifically, I explored the use of morpho-metrical indices to estimate the age of wild-born black bear cubs using growth metrics from captive-born cubs.

I completed a MS in Wildlife Biology from the University of Montana in Missoula, Montana in 2007. My project mixed theoretical population modeling and empirical vital rate estimation to understand population dynamics in elk and factors contributing to reduced recruitment. The mentorship provided by Drs. Daniel Pletscher and L. Scott Mills were monumental in framing how I approach science and the critical insights necessary to conduct research that matter to more than academicians. Moreover, being a city-girl, successfully

completing this project in a rural, agricultural community gave me to confidence to work anywhere and built “soft skills” that I can employ to work with diverse people.

Now, having completed my dissertation exploring patterns of species diversity in threatened and endangered carnivores and their associated parasites, I have added to my diverse trainings. I have been invited to present my novel and exciting research at conferences in Mexico, China, and Greece. And was the 2010 recipient of the Emerging Conservation Leader award from the Philadelphia Zoo. I gained additional experiences during my employment was the US Forest Service; evaluating the effects of habitat modifications and climate on plant and animal species of conservation concern. In addition to my scholastic achievements, I remain active in mentoring and recruiting efforts aimed to increase minority participation in ecology. I know my passion for conserving biological diversity will continue as I travel the world, study rare species, and broadly disseminate information to the public.

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I am extremely grateful for the opportunities that I have been given and created during my tenure at North Carolina State University and have lots of people to thank. I am so grateful for the mentorship and guidance that I have received from so many individuals both in formal and informal capacities. I want to start by acknowledging my amazing committee, made of diverse and successful professors.

Dr. Robert Dunn (co-advisor) took the brunt of the responsibility in advising me during the course of my doctoral program. Having been introduced to the field of biogeography through his course my first semester, I can honestly say that Rob has changed my life. I have gained much more from our interactions and by watching his example than I had ever anticipated. He has been extremely tolerant of my “sass” and supportive of all my aspirations. I learned a different approach to scientific inquiry and the magnitude of his impact on me will manifest in the many years to come. I have felt a flurry of emotions through my interactions with him. Specifically, I thank him for giving me a broader appreciation of species big and small, demonstrating the qualities of an effective collaborator, and valuing the diverse dissemination of information. I know I have not been an easy student, but now feel like I will be a good colleague, given the personal and professional growth I have experienced during this journey.

I thank Dr. Stacy Nelson (co-advisor) who graciously accepted his role and the challenge of working with me. Stacy has helped to keep my eyes on the finish line and worked diligently on my behalf to help secure future employment opportunities. I thank Dr.

Charles Apperson (Committee member) for his leadership in Entomology and providing helpful guidance as I tried to navigate this new discipline for myself. He spent time under the microscope, put me in contact with others that became collaborators, explained life-history traits of ticks and other parasites. He was a great resource. And finally, Dr. Nick Haddad (Committee Member) has been influential in both the completion of my research project, but also in my overall professional development. I have the opportunity to develop a new course for the Biology curriculum and Nick served as my teaching mentor for the Preparing the Professoriate Program. Through our interactions, this is the first time I felt that a professor could actually be a productive contributor to science and an influential teacher. He takes both of these roles seriously and motivated me to do so as well.

In addition to the training I received through the Preparing the Professoriate program, I received much insight about pedagogical practices through the Certificate of Accomplishment in Teaching (COAT) in life sciences led by Dr. Miriam Ferzli. Because I had no experience teaching prior to the start of my teaching assistantship, the mentorship I received from Dr. Ferzli has been invaluable. I learned the importance of asking the right question to facilitate discussion among numerous other skills that translate beyond just the classroom directly to real-world interactions.

Dr. Barry Goldfarb, the current department head for Forestry and Environmental Resources has also been quite influential in my professional development. Numerous candid conversations aided in the preparation of my career trajectory. I truly value all the insight he provided during impromptu meetings and the thoughtful ear he provided me to question “the

system”. I also thank Lisa Schabenburger, who initially recruited me to Virginia Tech and remains one of my biggest supporters. Now, in an administrative role in the Department of Forestry and Environmental Resources, Lisa continued to motivate me throughout my doctoral program. It was absolutely amazing to have a constant spirit of cheer surrounding me.

Given the interdisciplinary nature of my dissertation, it was particularly necessary to expand my training and secure collaborators outside my area of expertise. I started my training in entomology and parasitology through formal courses and workshops; Medical and Veterinary Entomology taught by Wes Watson, Diagnostic Parasitology administered by the Center for Disease Control and Prevention, and Introductory Acarology by Ohio State University. I have the opportunity to visit the US National Tick Collection in the Institute of Arthropodology and Parasitology at Georgia Southern University. There I obtained confirmation of my prior tick and louse specimens from Drs. Lorenzi Beati and Lance Durden. Additionally, Gabrielle Dietrich and John Montenieri at the Center for Disease Control at the Fort Collins, Colorado office provided training in the identification of tick and louse specimens. Erica Mize at the University of South Dakota also provided assistance in the identification of fleas.

I thank my family and friends for all their encouraging words throughout this journey. I recognize that I have missed a lot of birthday celebrations and holidays due to my traveling schedule, field work, and school demands. But despite, this time apart, I still felt all of their love and support.

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CHAPTER 1: USING HOST ASSOCIATIONS TO PREDICT SPATIAL PATTERNS IN THE SPECIES RICHNESS OF THE PARASITES OF NORTH AMERICAN CARNIVORES

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Abstract

Despite the central theme in ecology of evaluating determinants of species richness, little effort has focused on parasites. Here, we developed a parasite diversity model based on known host associations with 29 North American carnivores to investigate the spatial heterogeneity of parasite richness, its relationship to carnivore richness, and how host composition and specificity influenced these patterns. Patterns in parasite species richness closely tracked carnivore species richness across space and this relationship was robust to deviations from the assumption that parasites match the distribution of their hosts. Because wide-ranging hosts disproportionately contributed to total and specialist parasite species richness, conservation programs that focus on these common hosts may capture much of biological diversity, but also unwittingly sources of human diseases. We supply the first parasite diversity model to understand broad scale patterns in species richness patterns for North American carnivores, which can inform both future parasite conservation and disease management.

Introduction

Much research in biogeography and ecology has sought to understand the processes that determine and erode spatial patterns in biological diversity, particularly at large spatial scales. As a result, although the mechanisms underlying correlations between diversity and climate or geography remain contentious, the correlates of patterns in the diversity of key vertebrate taxa are now relatively well-resolved¹. With a handful of recent exceptions²⁻⁴, smaller organisms such as invertebrates, which arguably represent most of the biodiversity on Earth e.g.,^{5,6}, have played a more minor role in discussions of large-scale patterns of diversity. For most invertebrate taxa, it is unlikely that we will ever know patterns in distribution of species in sufficient detail to map global patterns in species richness.

Estimates of the total species richness of invertebrates globally still range from three million to a hundred million⁷⁻⁹. In this context, it is unlikely that continental or global species richness patterns and their correlates for invertebrates will be understood simply by mapping geographic ranges one species at a time. Fortunately, because the majority of invertebrate taxa depend on hosts for at least one of their life stages, we may be able to indirectly understand a great deal about invertebrate species richness patterns by understanding the distribution of hosts and incorporating information on host associations into species distribution models e.g.,¹⁰. A key question in this regard is the extent to which patterns in parasite species richness track those of their hosts.

Parasitism is the most common species interaction¹¹, with estimates of the total number of animal parasites in the hundreds of thousands¹² and plant parasites in the millions to tens of millions^{13,14}. To date, studies of large-scale patterns of species richness in terrestrial

parasites of animals most often focus on species problematic to humans¹⁵⁻¹⁷, such as those that cause emerging infectious diseases although see¹⁸ for a marine context. A number of studies have now shown that plant species richness adequately explains patterns of richness for some herbivorous insects^{19,20}, as well as other less plant-dependent taxa such as terrestrial vertebrates²¹. Employing the same logic from animals to parasites, perhaps the simplest expectation for spatial patterns of parasite species richness is that they track their hosts. However, whether or not this is the case is likely to depend on several features of host and parasite distribution that have not yet been well characterized.

Here, we explore spatial patterns in species richness for carnivore parasites based on known parasite-host association and the geographic ranges of North American carnivore species (Order Carnivora). We begin with the simplifying assumption that the entire parasite community occurs throughout the geographic range of their host, much in the way that species richness patterns are derived from bioclimatic models that assume the presence of species based on their fundamental niche. This assumption could be true on average even if it is wrong in specific cases and is amenable to empirical tests in the future. Carnivores are a useful focal group because the parasites of carnivores are relatively well-studied^{22,23}. Carnivores can also serve as key reservoirs for an array of parasites that are associated with domestic animals and humans, given high rates of exposure through predation and movement²⁴. Additionally, the order Carnivora contains species that vary in their geographic extent as well as their rarity/abundance, including wide-ranging species such as raccoon (*Procyon lotor*) as well as endangered species, with incredibly reduced modern distributions such as black-footed ferret (*Mustela nigripes*) and red wolf (*Canis rufus*). As a consequence, the

parasites of carnivores include both abundant species with potential as zoonotic reservoirs (e.g., raccoons and rabies) and parasites likely to be in need of conservation^{25,26}.

Where they have been considered, diversity patterns of plant parasites appear to track patterns in diversity of their hosts; where there are more hosts, as in the tropics, there should be more parasites²⁰. We explore whether this assumption also holds for the parasites of mammals by considering North American carnivores. We begin by conducting a systematic review of the literature to obtain a list of parasites for 29 terrestrial, mammalian carnivores of North America. We calculate parasite species richness per grid cell to evaluate patterns of species richness across space. We then partition the data to explore whether spatial patterns in parasite species richness differ when only specialist parasites or narrow-ranging hosts are considered. Because wide-ranging species often drive species richness patterns^{27,28}, wide-ranging carnivore hosts may similarly drive spatial patterns of parasite species richness. We also use a simple set of simulations to explore how differences between host and parasite distribution patterns, such as those that might occur if parasites are more directly influenced by climate than their hosts, could affect patterns in parasite richness and the relationship between host and parasite richness across space. Finally, we discuss the significance of our findings in the context of host-based and parasite conservation planning and disease management.

Methods

Parasite species richness relative to carnivore hosts

We included 29 terrestrial, mammalian carnivore species (Order Carnivora) in North America, which encompassed 17 genera and 6 families in our analyses of parasite species richness. This includes all terrestrial carnivore species in North America and roughly one in ten species globally. We compiled a list of naturally occurring parasites in wild carnivore populations reported in North America using the Natural History Museum host-parasite (www.nhm.ac.uk) and the Global Mammal Parasites www.mammalparasites.org,²⁹ databases. In an attempt to obtain the most comprehensive dataset on parasites for these carnivore species, we supplemented these data with a systematic literature search of published books and peer-reviewed articles using the Zoological Record database, which nearly doubled the number of records. We used the common or scientific name of the carnivore hosts and either parasite or disease as keywords in the search and included studies published from January 1965 – August 2009. We inclusively defined parasites any infectious organism that uses host resources for food or shelter and included microparasites (e.g., viruses, bacteria, and protozoa), macroparasites (e.g., helminthes), and ectoparasites (e.g., arthropods) following Anderson and May³⁰. Parasites reported from experimental manipulations or captive individuals were not included in our analyses. For studies that only identified parasites to the genus level, such parasites were included only if they represented unique genera for a particular carnivore host.

Projected spatial patterns in parasite species richness

In addition to documenting the pattern in parasite richness across host, we also explored how several attributes of that pattern may translate across space. We modeled the parasite richness pattern that would emerge if every parasite species occurred throughout the entire

range of its hosts. We also used simulations along 1-dimensional latitudinal domain bounded at 82.5° in the north and 7.5° in the south to explore how deviations from this assumption might influence patterns of species richness.

We overlaid distribution maps for all carnivore species (obtained from NatureServe; www.natureserve.org) using ArcMap (ESRI, version 9.2) to calculate carnivore species richness in each 1° latitude x 1° longitude grid cell. Again, we begin with the assumption that wherever a carnivore occurs in space so does all of those parasite species capable of living on it. This approach is analogous to the fundamental niche concept³¹ in that the primary condition governing the presence of a parasite is the availability of suitable habitat, though it focuses on just one aspect of habitat, the host.

For each grid cell, we calculated total parasite species richness and then, separately, specialist parasite species richness. We narrowly defined specialist parasites as those occurring in a single carnivore host, realizing these parasites, while known from a single carnivore, may also be found on other mammals outside the Order Carnivora including humans. All estimates of parasite and carnivore species richness were log-transformed before analyses.

Given possible biases in parasite species richness due to uneven sampling effort across carnivore hosts, we examined the relationship between sampling effort and various measures of species richness at two scales. We first regressed parasite diversity on range size and found a modest correlation ($r^2 = 0.302$) across carnivore hosts. We then examined the relationship between the residuals of this relationship and sampling effort and found no relationship ($r^2 = 0.002$, $P = 0.79$). In other words, once the direct effects of range size on

parasite diversity are accounted for, we find no effect at all of sample size on parasite diversity. Second, we tested whether a relationship existed between the mean number of studies conducted on host species within a grid cell and the parasite richness expected in that grid cell across space. One might expect grid cells with better sampled hosts to artificially have more parasite species. However, the effect of sampling effort on total ($r^2 = 0.07$; $P = 0.08$) or specialist ($r^2 = 0.07$; $P = 0.15$) parasite species richness were not significant. As such, we used uncorrected estimates of parasite species richness in all analyses.

We examined whether parasite species richness followed the “canonical” latitudinal pattern, with more species at lower latitudes, as has been documented for free-living and parasitic organisms alike³²⁻³⁴, but has gone unexplored for the parasites of carnivores, whether wild or domestic. We also used nonlinear regression to explore the relationship between parasite and carnivore species richness and mapped the residuals to evaluate where deviations from expected relationships occurred across space.

We also tested whether the patterns in parasite species richness on wide-ranging hosts differ from those of parasites on narrow-ranging hosts, where narrow-ranging carnivore species were defined as those below the 50th percentile (n=15) and wide-ranging carnivore species as those above the 50th percentile (n=14). We then tested a more specific prediction (by analogy from Jetz and Rahbek²⁸), that patterns of parasite species richness are driven by patterns in richness not of all hosts, but instead primarily of wide-ranging hosts. In general, wide-ranging species tend, statistically, to drive patterns of diversity because they “count” in many cells. In addition, wide-ranging species have been shown, in several cases, to host more parasites^{22, 35, 36}. And so, a-priori, we predict that patterns of parasite species richness should

be influenced primarily by the patterns in the richness of these wide-ranging hosts, which both are counted in more cells and likely have more parasites to be counted. To test this prediction, we compared variation in total and specialist parasite species richness explained by patterns of richness in narrow- and wide-ranging host species separately.

Relaxing the assumption that parasites occur everywhere their hosts occur

Our original model assumes that every parasite occurs throughout in the geographic range of each of its hosts. In practice, nearly all parasite species seem likely to deviate from this assumption and exhibit spatial variation in their distribution because of additional abiotic and biotic requirements, or behavioral variations that influence the susceptibility of their hosts e.g.,^{37, 38}. Ideally, one would like to be able to model the distribution of each parasite species, but even for a well-studied group such as carnivores this is unlikely to be possible for many years to come. To better understand the consequences of adding more biological realism into our original model, we simulated four forms of deviation from host-parasite distributional matching along a 1-dimensional latitudinal domain.

First, we simulated a scenario in which climate would limit the northern distribution of parasites relative to their hosts. Because colder climates occurring in the northern regions of North America could hinder the parasite's life cycle³⁹, we correspondingly reduced the occurrence of parasites from 20% in their northern-most latitudes despite the presence of suitability hosts, creating a southern bias in total parasite species richness across latitudes. Second, we considered a scenario in which interspecific competition among parasites would be higher in southern regions, as is commonly theorized and reported in free-living species e.g.,⁴⁰. We did so by limiting the occurrence of parasites from 20% in the southern-most

latitudes, creating a northern bias in total parasite species richness across latitudes. Third, we considered an effect of the absence of competent vectors from the range margins in parasite distribution. We created this central bias in parasite species richness by reducing parasite occurrence by 10% at each of the range margins in each carnivore hosts. Fourth, we considered the possibility of intermediate hosts being absent from the middle of parasite distributions. By reducing the parasite distributions by 20% in the middle of the range, this scenario creates an increase in parasite diversity at the periphery of the carnivores' distribution. Again, we acknowledge that any of a variety of mechanisms may underlie these deviations in nature. Our goal is to simulate a range of potential mechanisms, but also, more broadly, to understand the extent to which deviations between host and parasite diversity patterns are possible. We also evaluated how alternative deletions of 5% and 50% to parasite distributions and random deletions of 20% altered spatial patterns of parasite species richness (Fig. S1). Because these variations only altered the magnitude of deviation from the original model and not any conclusions, we present results for 20% deviations for the various scenarios.

Results

Parasite species are an order of magnitude more diverse than hosts

The final data set included 1344 records of host-parasite combinations, representing 579 parasite species across 29 North American carnivore species with 313 unique combinations (Table S1). Parasite species richness per carnivore species ranged from 8 to 153 (mean = 46, SE = 7), with the black-footed ferret and coyote (*Canis latrans*) representing the two

extremes. Specialist (found on only one host) parasite species richness per carnivore species ranged from 0 to 67 (mean = 11, SE = 3) and accounted on average for 19% of the diversity of the parasite community for a given host.

Parasite species richness is more spatially variable than is host species richness

The number of carnivores ranged from 1 to 18 per 1° x 1° grid cell across North America. The estimated total number of parasites per grid cell ranged from 12 to 532 species (mean = 336, SE = 2; Fig 1a) and specialist parasites ranged from 3 to 268 per grid cell (mean = 142, SE = 1). Thus, the variation in parasite species richness at the community level was estimated to be an order of magnitude greater than variation in carnivore species richness. Total and specialist parasite species richness were highest at mid-latitudes and were highly correlated with each other across space ($r^2 = 0.99$).

Even after incorporating deviations from the original model by inducing a northern, central or southern bias in parasite distributions; the spatial patterns in parasite species richness remained consistent (Fig. S2). Each of these scenarios reduced parasite richness for a given host richness across the range of latitudes, but the patterns in parasite richness did not change appreciably. Those deviations we did see between scenarios reflected the directional limitations we introduced. For example, where a southern bias was induced, parasite species richness decreased slightly for northern latitudes.

Parasite species richness per grid cell tracks carnivore species richness

Both total and specialist parasite species richness patterns closely tracked those of carnivores (Fig. 2a). Qualitatively, the strong relationship between parasite and carnivore species richness was maintained even when we simulated deviations in the assumptions of

our original model by not allowing all parasites to occur throughout the geographic distribution of each carnivore hosts (Fig. 3).

Nonetheless, in several geographic areas, host and parasite species richness patterns were discordant. Northern portions of North America outside the United States had fewer parasites per grid cell than expected given the number of carnivore host species present; while southern regions in the south-eastern United States and Central America had more parasites per grid cell than would be expected given the number of carnivore species present (Fig. 2b).

Wide-ranging hosts govern spatial patterns in parasite species richness

Partitioning carnivore species according to their geographic ranges revealed the substantial contribution of wide-ranging host species to both total and specialist parasite species richness patterns (Fig. 4, Table S1). This effect is due both to the fact that wide-ranging host species and their associated parasite communities are “counted” in more grid cells, but also to the reality that wide-ranging carnivore species have on average twice as many total parasites ($t = 2.17, P = 0.04$) and almost four times the number of specialist parasites as narrow-ranging carnivore species ($t = -2.47, P = 0.03$). The geographic ranges of wide-ranging carnivore species ranged from approximately 379 - 544 km², whereas range sizes of the narrow-ranging carnivore species ranged from approximately 26 - 370 km².

Discussion

With the exception of human diseases, there has been little effort to characterize the geographic variation in the diversity of parasites for mammalian groups. Even for humans,

geographic data on parasites are typically analyzed coarsely at the spatial scale of political regions e.g.,¹⁷. Here we take a first step in understanding the geographic distribution of the parasites for one North American clade, the carnivores. We began with the simplest possible model, one that assumes that all parasites occur everywhere their hosts occur. This assumption appears to hold, in the few cases where it has been empirically investigated, for example for fleas on mammals⁴¹. Because spatially-explicit host-parasite data at large scales are sparse, with very few exceptions see^{11, 42, 43}, such a simple model provides a useful starting point from which to begin to explore consequences of deviations.

It is likely that many parasites differ in one regard or another from our starting assumption of perfect host/parasite distributional matching. However, whether this leads to a systematic bias is unknown. Fortunately, we can explore the extent to which biologically plausible deviations from this assumption influence the relationship between host and parasite species richness and these patterns across space. In doing so, we found that while the magnitude of parasite species richness is altered by such deviations, they have only weak influences on the geographic patterns of parasite species richness, at least for the species considered along a 1-dimensional domain. Clearly, a major challenge for the future is to understand what the most consistent deviations from host/parasite distributional matching are and where these deviations occur.

In understanding broad-scale patterns of species diversity, latitude has long been known to be a key correlate for vertebrate and plant diversity³³. For carnivores and primates, hosts with ranges closer to the equator had higher parasite species richness^{22, 34}, but this result does not necessarily indicate that total parasite species richness is also higher in the tropics. Total

parasite diversity depends on the diversity of parasites per host, but also the diversity of hosts. We found that parasite species richness was highest in the mid-latitudes of the domain we studied, North America. We also found that there was an influence of latitude on where carnivore and parasite species richness were discordant in space (see Fig. 2b), demonstrating the geographic variability in species interactions see review by ⁴⁴.

Both mechanistically and statistically, it is perhaps not surprising that parasite species richness covaries geographically with carnivore host species richness as also appears to be the case with consumer diversity relative to producer diversity- ^{45, 46, 47}; where species richness of hosts is zero, species richness of parasites must also be zero. However, this perhaps intuitive result has less than intuitive consequences for large-scale conservation, and animal and human health.

For the species we considered, rare hosts tended to have relatively few and mostly generalized parasites, a result similar to those of Altizer *et al.* ⁴⁸ who found that threatened primate species had fewer parasite species than their non-threatened counterparts. Therefore, the presence or addition of a rare carnivore species will import few new parasites to a given area. This implies that reintroduction efforts of carnivores to ecosystems is unlikely to increase the risk of disease to humans or our domesticates, a concern often raised in species translocation and reintroduction studies ⁴⁹. Interestingly, although rare carnivores receive, for obvious reasons, a large proportion of conservation funding, we show they are relatively unimportant for parasite conservation or, for that matter, human health. If our results generalize, there exists an obvious conflict between parasite conservation and host conservation, at least as long as conservation remains species rather than habitat based. This

conflict exist because those interested in parasite conservation and those interested in reducing threats from zoonotic parasites, need to both focus on wide-ranging hosts, given these hosts had more specialists, and overall more parasites. Our study illuminates this interesting dichotomy. On the one hand, geographically widespread carnivores and their parasites can (and do) raise safety and human health concerns. On the other hand, those same carnivores include species of great conservation concern (e.g., *Lynx canadensis* and *Gulo gulo*), but more germane to our work here, play host to both zoonotic pathogens and parasites that seem likely to be of conservation concern. We do not propose to resolve this conundrum here, but highlight it as a major concern for the future of conservation.

When beginning with the assumption that parasites occur everywhere their hosts occur, the richness patterns of hosts and parasites were highly correlated. This correlation persisted even when we simulated deviations between host and parasite distributions like those that might be expected from differences in host and parasite climatic tolerances. These correlations were strong, though importantly imperfect. For example, the most diverse grid cells for parasites were not always the same as the most diverse grid cells for hosts. Given the importance of abiotic conditions to parasite life history^{43, 50}, a key next step is to understand when climate and landscape features constrain parasite distributions using specimen records from well-studied parasites. The differences between host and parasite richness patterns are significant in the context of climate change (if parasites and hosts do not move in lock-step, for example), but also for conservation. We found twenty times as many species of carnivore parasites as there are carnivores. As such, understanding the distribution

of these diverse species is a first step toward knowing how to manage and conserve, for the good, bad, or otherwise; a management that, to date, we have largely ignored.

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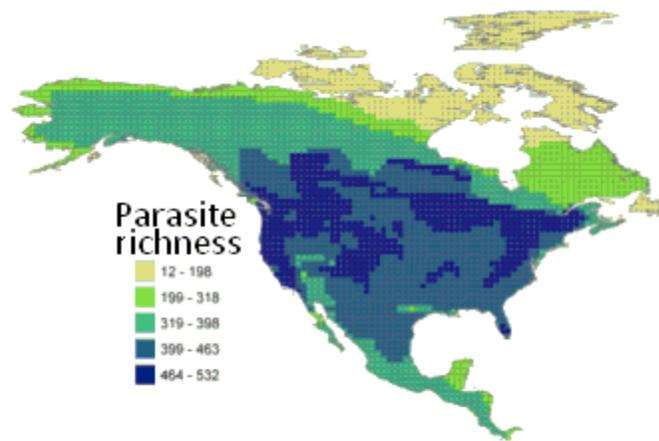
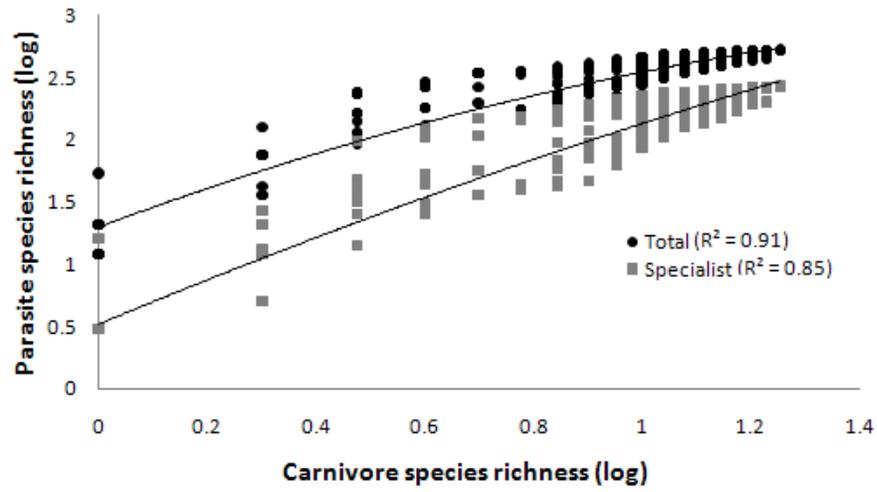


Figure 1.1. Spatial variation in parasite species richness (total number of parasites per 1° lat/long grid cell) for North American carnivore

(a)



(b)

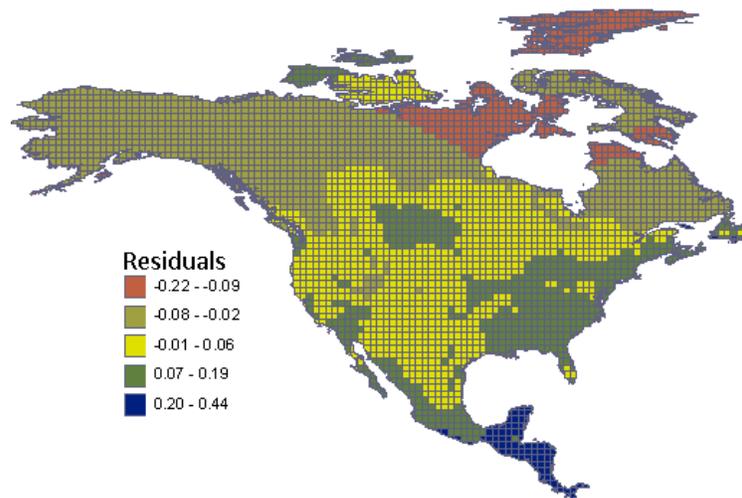


Figure 1.2. (a) Total and specialist parasite species richness plotted against carnivore species richness (total number of carnivores per lat/long grid cell). (b) Residuals map of total parasite species richness vs. carnivore species richness based on a polynomial model with variables log transformed from Fig 2a

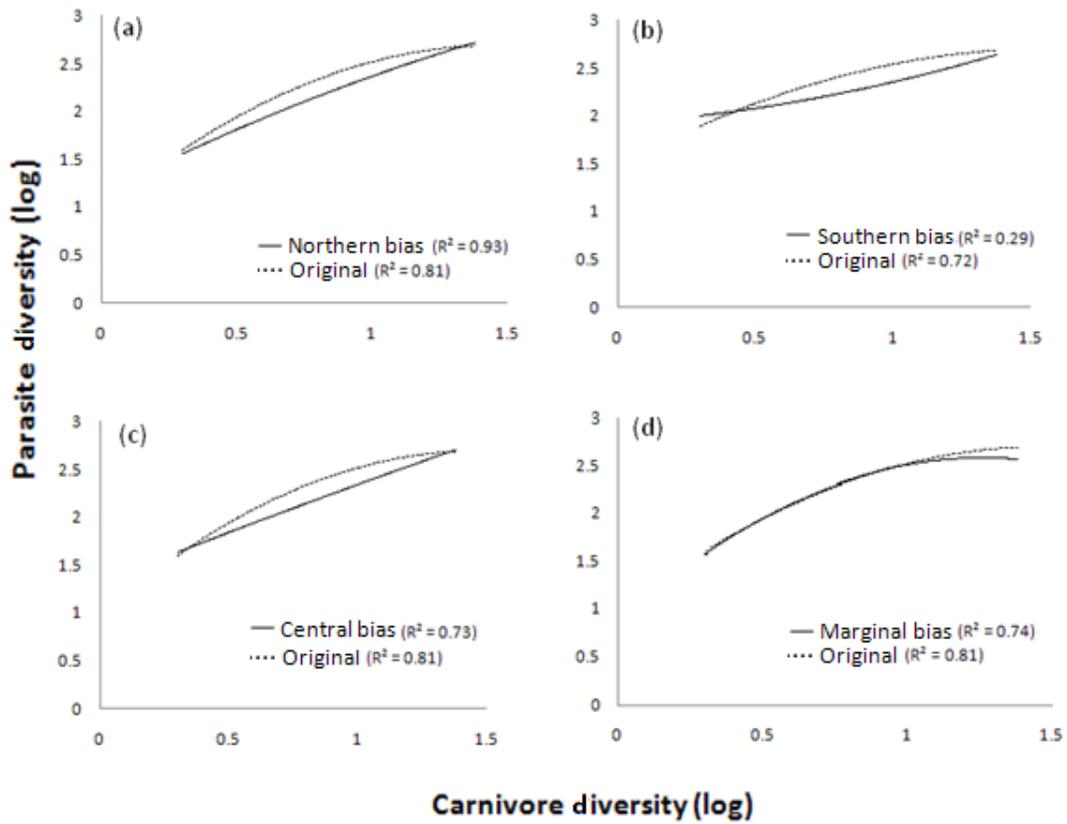


Figure 1.3. The relationship between parasite species richness and carnivore species richness compared between a model in which parasite and host distributions match (dashed line) and four scenarios in which parasite ranges have a northern (a), southern (b), central (c) or marginal bias (d) relative to the distributions of their hosts (solid line)

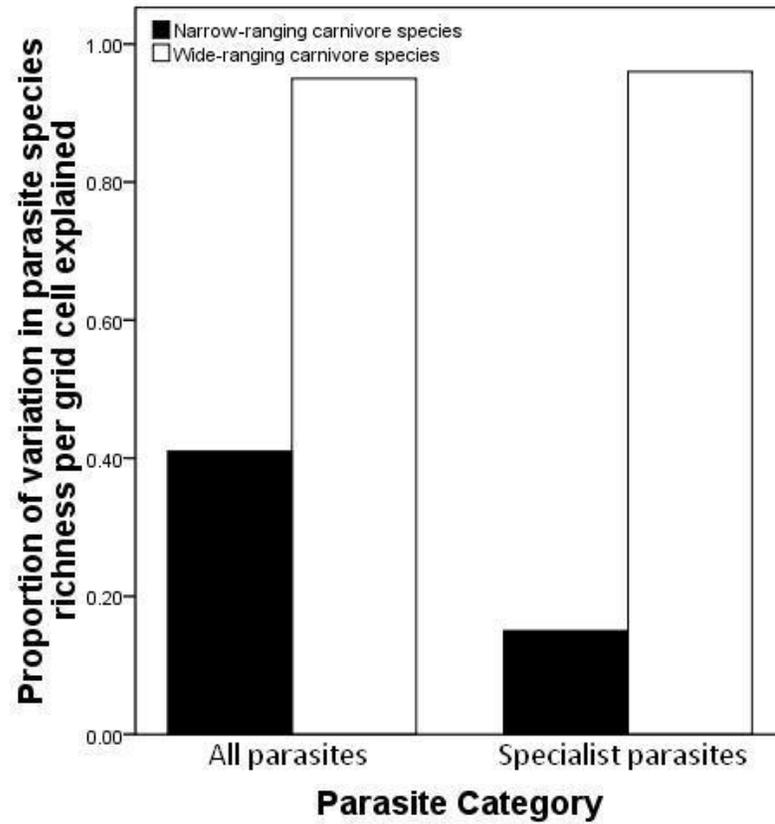


Figure 1.4. Proportion of variation in total and specialist parasite species richness explained by parasite community in narrow-ranging ($n = 15$) and wide-ranging ($n = 14$) carnivore species

Table S1.1. Parasite species richness for 29 North American carnivores. Parasites include bacteria, viruses, protozoa, helminthes, and arthropods. Species with geographic ranges below and above the median were classified as narrow-ranging (N) and wide-ranging (W).

Scientific Name	Range	Total Parasites	Specialist Parasites
FAMILY CANIDAE			
<i>Canis latrans</i>	W	153	44
<i>Canis lupus</i>	W	62	9
<i>Canis rufus</i>	N	11	0
<i>Urocyon cinereoargenteus</i>	N	67	7
<i>Urocyon littoralis</i>	N	16	0
<i>Vulpes lagopus</i>	W	31	13
<i>Vulpes macrotis</i>	N	25	4
<i>Vulpes velox</i>	N	26	4
<i>Vulpes vulpes</i>	W	83	11
FAMILY FELIDAE			
<i>Lynx canadensis</i>	W	32	4
<i>Lynx rufus</i>	N	94	18
<i>Puma concolor</i>	N	63	7
FAMILY MEPHITIDAE			
<i>Conepatus leuconotus</i>	N	14	3
<i>Mephitis macroura</i>	N	9	2
<i>Mephitis mephitis</i>	W	60	14
<i>Spilogale gracilis</i>	N	35	7
<i>Spilogale putorius</i>	N	35	5
FAMILY MUSTELIDAE			
<i>Gulo gulo</i>	W	21	3
<i>Martes americana</i>	W	31	5
<i>Martes pennanti</i>	N	30	6
<i>Mustela erminea</i>	W	12	0
<i>Mustela frenata</i>	W	57	24
<i>Mustela nigripes</i>	N	8	2
<i>Mustela nivalis</i>	W	26	7
<i>Mustela vison</i>	W	54	16
<i>Taxidea taxus</i>	N	35	7
FAMILY PROCYONIDAE			
<i>Procyon lotor</i>	W	151	67
FAMILY URSIDAE			
<i>Ursus americanus</i>	W	88	24
<i>Ursus arctos</i>	N	15	0

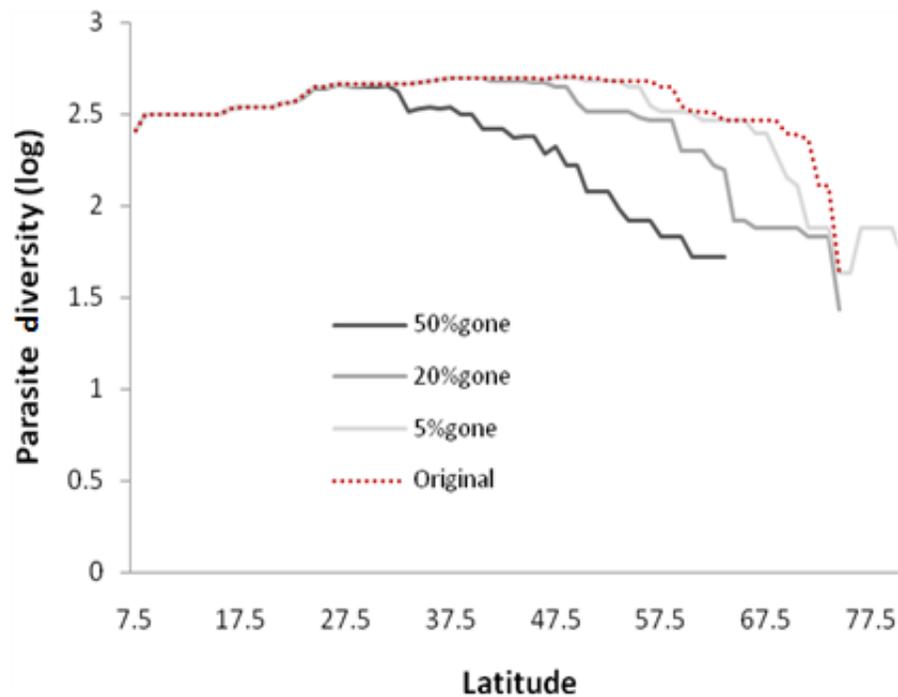


Figure S1.1. Because empirical estimates of how parasite diversity varies across the geographic range of hosts are lacking, we explored how using 5, 20, and 50% truncation amounts of parasite ranges would alter spatial patterns using the southern-bias scenario (where parasite distributions are limited from the northern-most regions). Enforcing these restrictions only affected the magnitude of deviation compared to the original model (with the assumption that all parasites occur throughout the range of the host) and further confirms the robustness of our model.

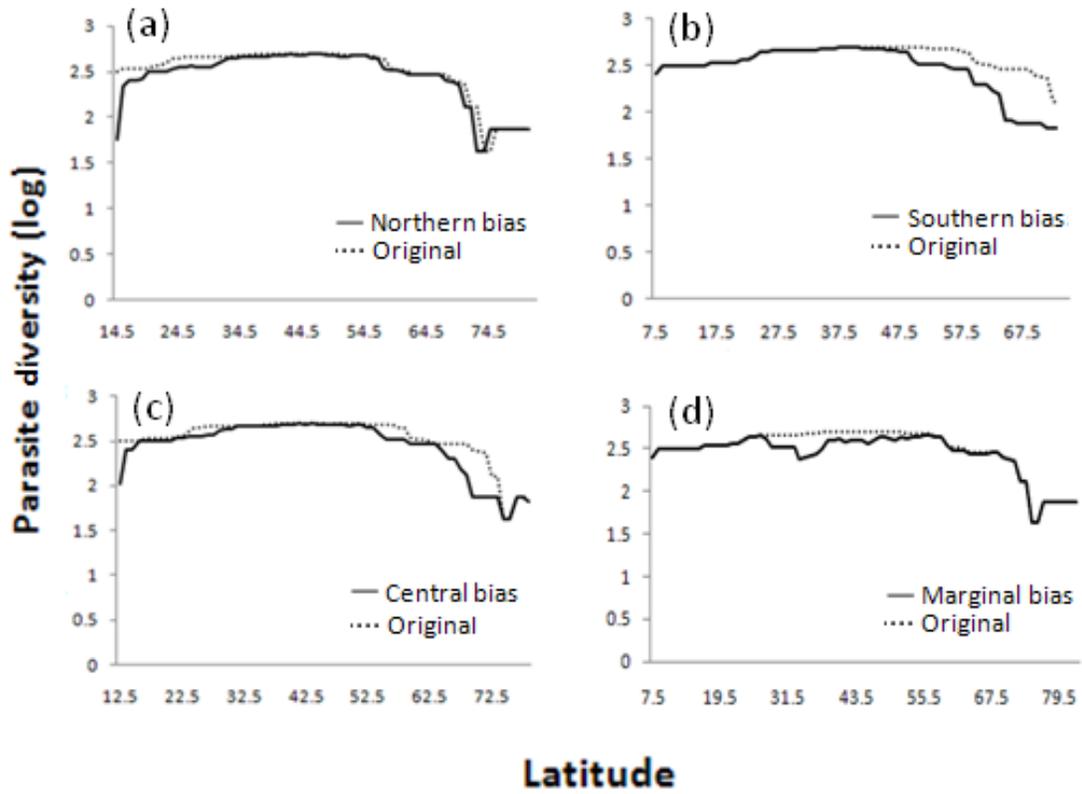


Figure S1.2. Latitudinal patterns in total parasite species richness with complete matching of host and parasite ranges for northern (a), southern (b), central (c) and marginal (d) biases relative to the distributions of their hosts. Solid lines, in each case, show parasite diversity after a bias is introduced, whereas dashed lines show the diversity pattern assuming perfect host-parasite range matching.

CHAPTER 2: THE INFLUENCE OF CARNIVORE EXTINCTION ON THE COMPOSITION AND GEOGRAPHY OF ZONOTIC PARASITES

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Abstract

The loss of species can have cascading effects, as is the case, when the loss of a host species results in the subsequent loss of affiliate parasite species. This phenomenon of co-extinction has potential consequences to human health, if shifts in parasite distributions alter levels of exposure across the landscape. We used presence-absence matrices of host-parasite associations for 29 North American carnivore species and simulated the corresponding changes in parasite community composition and diversity with the random extinction of hosts. We also explored the spatial distribution of zoonotic parasite diversity under three carnivore host composition scenarios and discussed implications for the corresponding levels of human exposure. We found that the composition of the parasite assemblage community changed independently across parasite groups with the proportion of zoonotic viruses markedly increasing with carnivore host extinctions. Co-extinction of carnivore parasites is unlikely, given that few specialist parasites exploit hosts of conservation concern. However, the loss of widespread carnivore hosts had the greatest impact by reducing overall zoonotic diversity and shifting the geographic distributions of parasite-rich areas. If high host diversity (and the resultant high zoonotic parasite diversity) dilutes disease prevalence in

humans, our findings demonstrate an added benefit of conserving widespread species for human health.

Introduction

Extinctions rarely occur in isolation. Instead, because of the connections among strongly interacting species, the loss of one species can lead to the loss of affiliate species, a phenomenon referred to as extinction cascades or co-extinction (Dunne et al. 2002; Koh et al. 2004; Stork & Lyal 1993). Parasites and pathogens, by virtue of their dependence on one or more hosts, are affected by changes in the abundance, diversity, and geography of their hosts (Ezenwa 2003; Hechinger & Lafferty 2005; Hughes & Page 2007; Krasnov et al. 2004b; Poulin 1997). As a consequence, these changes within the hosts will likely alter the relative commonness and distribution of zoonotic parasites able to colonize and infect humans (Krasnov et al. 2005; Woolhouse et al. 2001). Zoonotic parasites capable of infecting humans comprise nearly 60% of all human parasites (Taylor et al. 2001). It is evident that ecosystem processes can result in both changes in the composition and prevalence of zoonotic diseases (Daszak 2000; Jones et al. 2008; Wolfe et al. 2007; Woolhouse & Gaunt 2007). What remains unclear is the extent to which changes in host faunas might also affect zoonotic parasites, whether in terms of their diversity, composition, or geographic distribution.

The parasites of mammalian carnivores (Order Carnivora) comprise a diverse fauna that pose risks for human health and might simultaneously warrant conservation. On the one hand, carnivores have experienced some of the greatest threats to persistence of any

vertebrate taxon and many species are already extinguished (whether recently or during the Pleistocene). Extant carnivores include some of the most charismatic, vulnerable, and influential species on earth (Schipper et al. 2008). These animals generate millions of dollars annually for the tourism industry and often are the flagship species for campaigns aimed at securing donations for wildlife conservation. On the other hand, carnivores threaten other species including those of importance for human livelihood and harbor many harmful zoonoses such as rabies, plague, toxoplasmosis, and echinococcus (Murray et al. 1999). Therefore, carnivores not only succumb to the consequences of diseases themselves, but also serve as important reservoirs for the transmission of zoonotic diseases across broad landscapes. Over half of the 125 emerging zoonotic diseases are associated with carnivores (Cleaveland et al. 2001). While many carnivores are under threat and changes in carnivore populations will likely affect their community of parasites, no studies have considered the broad scale effects of carnivore extinctions on zoonotic parasites of importance for human health.

Ultimately, the fate of zoonotic parasites in light of host extinctions is dependent on the combination of attributes of both hosts and their parasites, namely parasite specificity and the threat status of hosts (Figure 1). A recent review suggested that the extinction of rare carnivores could lead to the extinction of specialist parasites and simultaneously cause generalist parasites such as some viruses to become proportionally more widespread (Dunn et al. 2009). We build on these findings to consider the implications of carnivore extinctions on the distribution of zoonotic parasites and associated human exposure. First, we quantified the diversity of zoonotic parasites in North American carnivores. Next, we evaluated the

proportional change in the composition of parasites as a function of host extinctions in North American fauna. Finally, we assessed how the loss of carnivores under different composition scenarios would affect the spatial distribution of zoonotic parasite diversity. Given the increased pressures on many carnivore populations and the continued emergence of zoonotic diseases, our study is both timely and pertinent to illuminate potential changes in the geographic patterns of parasite diversity and human health exposure in a changing environment.

Methods

Zoonotic parasite diversity in carnivores

We used a list of parasites recently compiled for North America carnivores to explore consequences of coextinction for human health and spatial patterns of zoonotic diversity (Harris & Dunn 2010). We applied a broad definition of parasite by including both microorganisms such as viruses, bacteria, and protozoa as well as macro-organisms such cestodes, nematodes, trematodes, and acanthocephale worms. We excluded arthropods (e.g., ticks, lice) from our analyses because though vectors of many problematic pathogens they themselves are infrequently the causative agent for diseases. We categorized each parasite as being zoonotic if it had been reported as a natural case in humans relying primarily on the host-parasite database from the Natural History Museum (www.nhm.ac.uk) and a review on human diseases (Taylor et al. 2001). With these data, we explored zoonotic diversity and patterns of specificity among parasite groups.

Co-extinction simulation and changes in parasite composition

We used presence-absence matrices of carnivore-host associations compiled from the literature and estimated parasite loss as a function of simulated random carnivore extinctions, following Koh et al. (2004) and Dunn et al. (2009). First, we partitioned the parasite data into zoonotic and non-zoonotic, and evaluated whether the consequences of carnivore loss were comparable. We expect that parasites with more hosts to be less vulnerable to extinction, which could consistently be the zoonotic parasites in our dataset. Then, we repeated the simulation for each parasite group individually (e.g., protozoa and then, separately, trematodes) to determine how parasite composition was altered by host extinctions. Parasites differ in their risks to humans and other animals based on their ability to transmit and exploit new hosts, so certain changes in parasite composition can be more problematic than others (Pedersen & Davies 2009; Woolhouse et al. 2005). Many viruses, in particular, are able to “jump” the species barrier to new hosts due to their high mutation and transmission rates (Jancovich et al. 2010; Pulliam 2008). Additionally, the vulnerability of parasites to host extinctions depends largely on their niche breadth and life-cycle requirements (Dobson et al. 2008; Koh et al. 2004; Lafferty & Kuris 2009). Therefore, we expected a differential response of parasites to carnivore host extinctions based on their taxonomic classification and pattern of host specificity.

Alterations spatial patterns in zoonotic diversity induced by host extinctions

We also examined how the loss of carnivores could affect the spatial distribution of zoonotic parasites. The paucity of surveillance data, even for the most ubiquitous zoonoses, makes depicting the individual distributions of parasites at a management-relevant scale across the

United States currently unattainable. Instead, we overlaid the distributions of hosts and assumed the entire parasite community occurs throughout the distribution of a given host. Though this approach is unlikely to reflect the actual distribution of parasites given additional abiotic and biotic requirements necessary for their presence, it is a reasonable first approximation. Harris and Dunn (2010) showed that spatial patterns of parasite diversity were consistent, even if the distributions of host and parasites were not completely congruent.

Because host extinctions are nonrandom and hosts pose varying levels of threat to humans based on their competency to be reservoirs, we evaluated changes in spatial patterns of zoonotic parasite diversity by comparing two host extinction scenarios to the original full model with all carnivores present. First, given widespread carnivores are often thought to be the most problematic in spreading zoonotic diseases, we removed widespread carnivore hosts that had distributions occurring in the highest quartile of species distributions in the entire dataset. These hosts included: red fox (*Vulpes vulpes*), ermine (*Mustela ermine*), coyote (*Canis latrans*), gray wolf (*Canis lupus*), American mink (*Mustela vison*), least weasel (*Mustela nivalis*), and wolverine (*Gulo gulo*). Second, we removed carnivore hosts that are of conservation concern, representing the most likely species threatened with extinction. We defined species of conservation concern as those species listed as threatened, endangered, or candidate on the U.S. Endangered Species Act. These threatened and endangered host species (TES) included: gray wolf (*Canis lupus*), red wolf (*Canis rufus*), island fox (*Urocyon littoralis*), Canada lynx (*Lynx canadensis*), fisher (*Martes pennanti*), black-footed ferret (*Mustela nigripes*), and brown bear (*Ursus arctos*).

We evaluated the total and proportional change in zoonotic parasite diversity based on the various host composition scenarios: all hosts present, widespread hosts removed and TES hosts removed. Because the absence of certain species may alter spatial patterns of zoonotic diversity, changes in zoonotic risk for humans may also be observed. We defined risk based on exposure and assumed that risk was higher when more humans resided in parasite-rich areas (i.e., Mexico Brazil vs. Finland). We calculated the number of people inhabiting each grid cell in North America according to population abundance estimates. Human population size for 2010 was extracted from the Gridded Population of the World dataset at a 1° latitude/longitude resolution (<http://sedac.ciesin.columbia.edu/gpw/>).

Results

High specificity and diversity in zoonotic parasites of North American carnivores

The dataset comprised > 1300 host-parasite records. Of the 394 unique parasite species, about a third were classified as zoonotic (n=114) and thirty-two percent of those were nematodes. Half of all bacteria species known from North American carnivore hosts were zoonotic. Some of the most frequently reported (largest number of host species) zoonotic parasites included: *Yersinia pestis* (causative agent for Plague found in n=15 carnivore hosts), *Trichnella nativa* (n=16); *Toxoplasma gondii* (n=15), and *Leptospiro interrogans* (leading cause of foodborne illness in US found in n=10 hosts). Conversely, 35% of zoonotic species were found only in a single carnivore species (i.e., specialist parasites).

Carnivore hosts varied in the diversity of zoonotic parasites found in them (n=29, mean= 14, SE=2.5). The raccoon (*Procyon lotor*) and coyote (*Canis latrans*) had the greatest

diversity of zoonotic parasites with 42 and 45 species, respectively. At the opposite extreme, only one zoonotic parasite has been reported from the least weasel (*Mustela nivalis*), despite its broad geographic distribution. Zoonotic parasite diversity did not differ as a function of the conservation status of host species (Wilcoxon $W = 67$, $P\text{-value} = 0.627$) or their geographic range sizes (Wilcoxon $W = 70.5$, $P\text{-value} = 0.759$). But, host rarity influenced the diversity of specialist zoonotic parasites among hosts. In fact, the fisher (*Martes pennanti*) was the only threatened and endangered host species (TES) that had a zoonotic specialist parasite not reported on any other carnivore hosts. Generally, carnivore hosts of conservation concern were exploited by the most common zoonotic parasites.

Both the proportion and composition of zoonotic parasites were altered with carnivore host extinctions

Our models predict that the extinction of a single host could lead to multiple parasite extinctions. For example, we estimated that 35 total parasites would go extinct if 8 North American carnivores went extinct. The proportion of non-zoonotic parasite extinctions due to carnivore extinctions was higher than zoonotic parasites and the slope of the curve as more linear, indicating high parasite specificity in this group (Figure 2). The change in the proportion of parasites that were zoonotic was not consistent across parasite taxa. Carnivore extinctions led to increases in the proportions of parasite species that were zoonotic parasites for viruses and Acanthocephale worms, but not for other parasites in our simulations (Figure 3).

Importance of carnivore host composition on zoonotic parasite dynamics

Carnivore hosts varied in their contribution to patterns of zoonotic parasite diversity, which results in alterations to spatial patterns. Removing carnivore hosts of conservation concern resulted in similar estimates of zoonotic diversity per grid cell (range = 2 - 108) as compared to the scenario when all hosts were present (range = 2 - 109). Furthermore, there was almost complete spatial congruence in where more and less zoonotic parasites occurred between the TES removed and all hosts present scenarios. Conversely, removing widespread hosts reduced zoonotic parasite diversity (range = 2 – 89, Figure 4) and led to the extinction of 13 parasite species from carnivores including *Giardia duodenalis*, Canine rotavirus, and *Dirofilaria repens*. Losing widespread carnivore hosts (as opposed to TES hosts) also altered the geographic pattern of zoonotic diversity; shifting the geographic locations of high zoonotic diversity of species to more mid-longitudes and creating a more homogeneous pattern across southern latitudes of North America (Figure S1).

Contrary to *a priori* predictions, host extinctions did not consistently reduce the diversity of zoonotic species to which human population centers were exposed. For widespread host extinctions (the only host extinctions to substantially alter parasite faunas), nearly all 1° latitude/longitude grid cells (98%) experienced some change in carnivore diversity and hence zoonotic parasite diversity. The proportional decrease in zoonotic diversity across space varied from 0.0 – 0.77 when widespread hosts were removed. The greatest change in zoonotic diversity occurred in northern latitudes where the human population is lower (Figure 5). Nevertheless, over 900,000 people reside in the 57,860 km²

area that would experience a 75% or greater reduction in zoonotic parasite diversity with the extinction of widespread carnivores.

Discussion

Despite growing efforts to explore consequences of species loss, no studies have examined how the loss of species alters patterns of diversity for affiliated parasite species. Nor have many studies considered the implications of changing patterns in biological diversity for human health. Here we show that the extinction of carnivore hosts can substantially affect zoonotic parasite composition, the relative diversity of zoonotic and non-zoonotic species, and spatial patterns of zoonotic diversity. Often higher diversity at one trophic level increases diversity at others (e.g., Jetz et al. 2009; Nieberding & Olivieri 2007; Ricklefs 2007). Conversely, although it has received far less attention, the loss of diversity in one group of organisms can also cause the loss of diversity in another. Predictably, the extinction of carnivore hosts led to the extinction of parasites. However, parasite extinctions were not random with respect to the type of parasite or whether or not a parasite was zoonotic. Some types of zoonotic parasites were more likely than non-zoonotic parasites to go extinct such as nematodes (Figure 2), which might actually be beneficial to humans. Conversely, other types of zoonotic parasites are likely to be proportionally more common as more carnivores become extinct. Zoonotic viruses, in particular, tend to be generalist and so, are robust to individual host extinctions. They persist, in other words, even when host extinctions are common. This is potentially troublesome since many emerging diseases in humans and wildlife are zoonotic viruses including West Nile, avian influenza, and monkeypox (Pedersen et al. 2007; Pulliam 2008).

We also found that the extinction or extirpation of carnivores has the potential to alter geographical patterns of zoonotic exposure (Figures 5). The precise spatial patterns of zoonotic diversity and exposure to humans that resulted, however, depended greatly on which hosts were removed. When we simulated the extinction of carnivore hosts of conservation concern such as the black-footed ferret or Canada lynx, the effects on zoonotic diversity were minimal because rare hosts tended to have few unique zoonotic parasites, as they occupied narrow geographic distributions. In contrast, losing widespread hosts such as the red fox or American mink not only reduced the diversity of zoonotic parasites, but also altered the geographic distribution of areas with high zoonotic diversity. Losing widespread hosts resulted in the extinction of 13 zoonotic parasites from North America. Some of these species will persist in other non-carnivore hosts, while other parasite species that require a mammalian carnivore to complete their life cycle such as *Echinococcus granulosus* would be completely extinguished from wild animal populations within the geographic boundaries of our study.

We assumed initially that, as carnivores go extinct, specialist parasites will succumb to the same fate as their hosts. Surprisingly, given the number of documented or predicted animal and plant extinctions, few empirical examples of parasite co-extinctions have been recorded (Dunn et al. 2009). One reason for the rarity of observed co-extinction events may be that rare hosts tend to have relatively fewer specialist parasites (Altizer et al. 2007). However, if carnivores now considered common were to come under threat, the impact on zoonotic parasites would be very different. While the extinction of widespread carnivores may seem unlikely, the reality is that to-date most of the vertebrates that have gone extinct in

North America were, at one time, widespread (e.g., passenger pigeon, *Ectopistes migratorius*). Many carnivore species that are currently common also harbor many specialist parasites. Because of this diversity and their relatively large geographic ranges contribute significantly to patterns of parasite diversity.

Even, however, if hosts with specialist parasites go extinct, it is not necessarily a foregone conclusion that their parasites will also go extinct. Other possible scenarios exist. For example, when host populations dwindle, parasites may switch to more abundant hosts even if the abundant hosts are less preferred, as has been argued to have been the case with the transition of bedbugs from bats to humans (Reinhardt & Siva-Jothy 2007). In the modern context, abundant, alternate hosts onto which parasites might switch are most likely to be our domesticated species or ourselves. It is possible that many of the non-zoonotic species in our database might, when faced with a rare host, switch on to humans. Such events where parasites have “jumped” onto humans—whether or not they were triggered by host rarity—include HIV-1, SARS, Ebola and Hendra virus (Jones et al. 2008; Pulliam 2008; Wolfe et al. 2007; Woolhouse et al. 2005). Clearly not all rare parasites are equally likely to switch onto human. Pedersen and Davies (2009) postulated the reasonable hypothesis that geographic proximity was, for example, a prerequisite for cross-species transmission of parasites between primates and humans. In this context, it is useful to consider not just the locations of zoonotic hotspots or rare zoonotic species, but also how those regions overlap with human populations. The distributions of carnivores overlap some of the most densely populated regions, which provoke concern about zoonotic parasites converting to solely human exploiters in portions of North America or at minimum switching to domesticated animals.

Our results highlight the sensitivity of parasite communities to changes in host composition; where there are more widespread hosts there are generally more parasites. But, the connection between whether more parasites equates to more risk for humans still remains unanswered. In a global analysis of human diseases, Dunn et al. (2009) found a significant positive relationship between pathogen diversity and prevalence. Likewise, we might expect geographic variation in prevalence for certain zoonotic parasites to be associated with overall zoonotic diversity in North America. However, at least at fine spatial scales, biodiversity has been shown to buffer or “dilute” the impacts of zoonotic diseases for humans (Ezenwa et al. 2006; Keesing et al. 2010; Keesing et al. 2006; Ruedas et al. 2004). For example, the prevalence of *Bartonella* spp. was inversely correlated to the diversity of small mammals (Ostfeld & Keesing 2000). If the dilution hypothesis were to apply at the spatial scale of our study, it would suggest that reductions in host diversity might increase the risk to humans from those parasites that persist, because the hosts that went extinct no longer dilute the impacts of such parasites. If the dilution hypothesis held, maintaining a diverse assemblage of carnivores could reduce risks from zoonotic diseases to humans. However, the opposite is also possible. At broad spatial scales, host diversity may amplify rather than dilute effects of parasites on humans. In either case what remains conspicuous in our results is that hosts vary in their contribution to human health risk and anticipating changes in host composition can help inform both parasite conservation and disease mitigation efforts.

The consequences of species loss for human health have not been well studied, whether in conservation, biogeography, or other fields. Parasites that lose their hosts could have one of three fates (extinction, increased prevalence, or host switching), which pose

varying levels of threat to humans. Conceptually, this fate depends on both host and parasite characteristics (Figure 1). Here, we have identified the host species whose extinction seems likely to have the largest impact on parasite communities and human health – namely widespread species. Our study highlights the need for a broader inclusion of abundant species in future conservation efforts. It also provides another example, in a growing list of cases, in which rare host species are relatively inconsequential in the story of co-extinction and now also, human disease risks. Furthermore, if host diversity (and the resultant zoonotic diversity) dilutes disease risk in humans, conserving widespread species could be the single most important “ecosystem services” our environment provides for human welfare.

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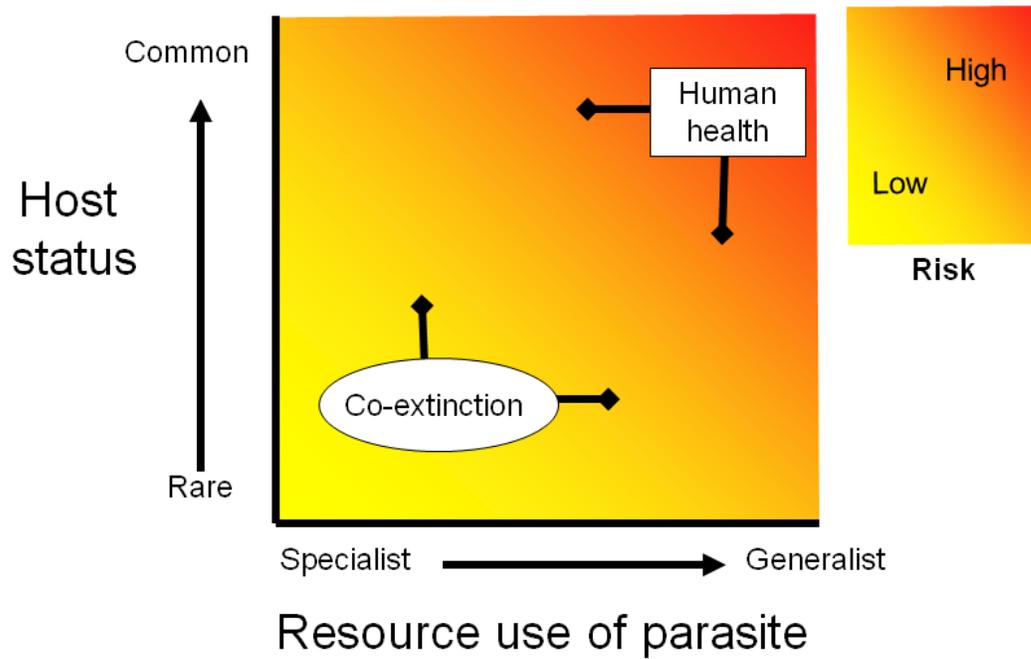


Figure 2.1. Conceptual framework of understanding risk to human health (red) and threat of co-extinction for zoonotic parasites (yellow) based on host and parasite characteristics.

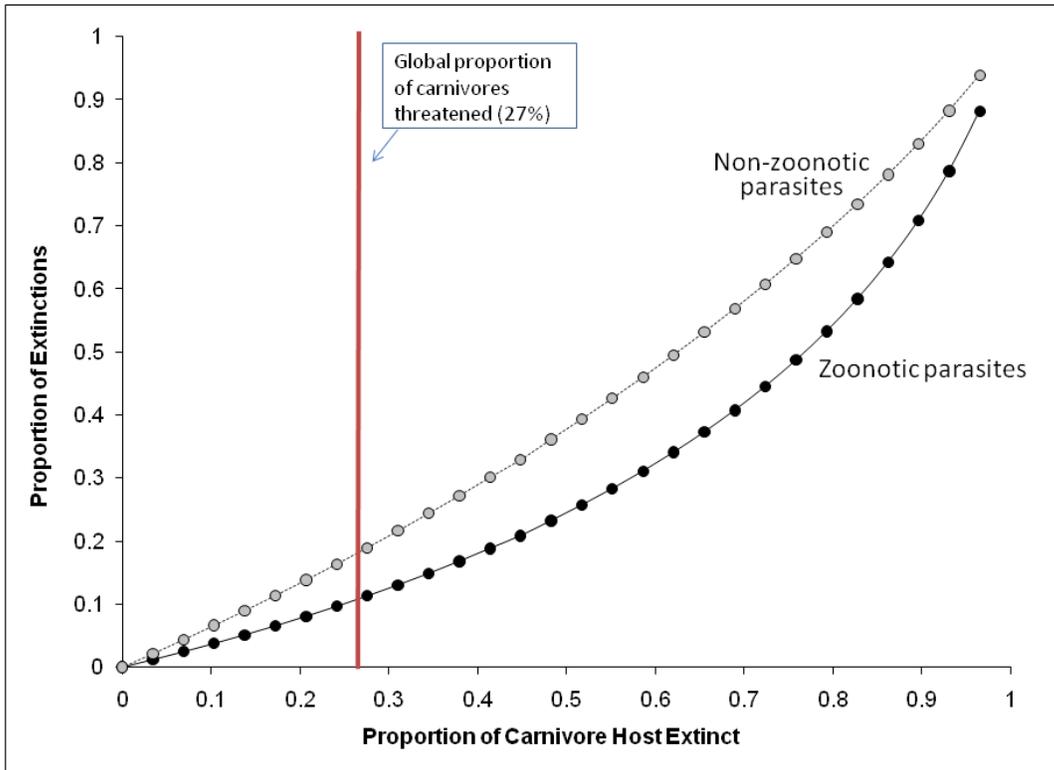


Figure 2.2 Estimated coextinction of zoonotic and nonzoonotic parasites induced by the simulated loss of North American carnivores.

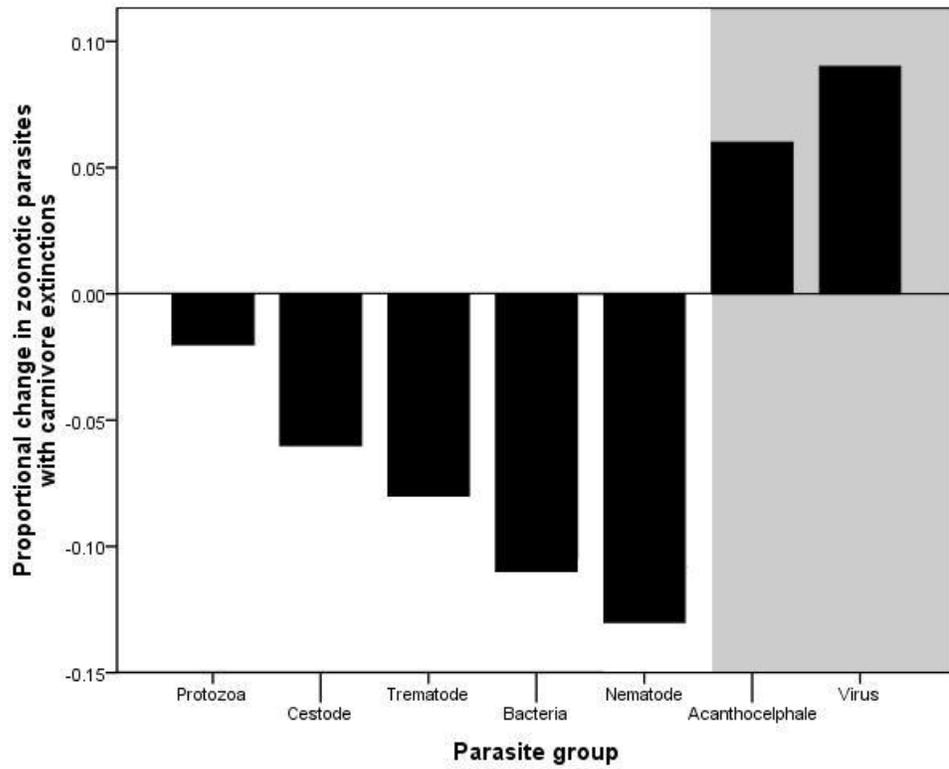


Figure 2.3 Proportional change in zoonotic parasite composition resulting in simulated carnivore host extinctions. Shaded region highlights the only parasite groups that proportionally increased.

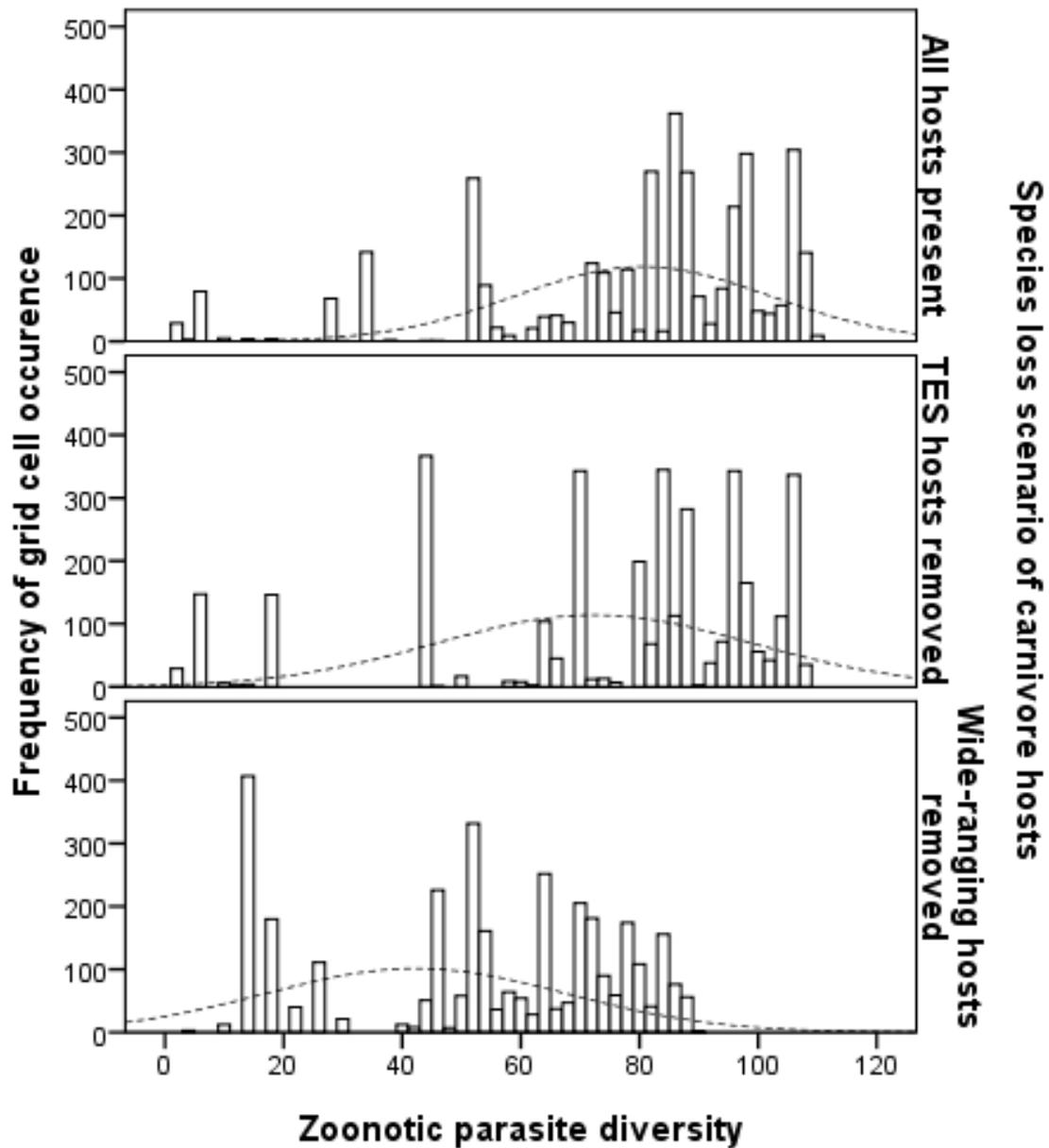


Figure 2.4 Frequency distribution of zoonotic parasite diversity across 1° latitude-longitude grid cells of North America according to various carnivore host community compositions.

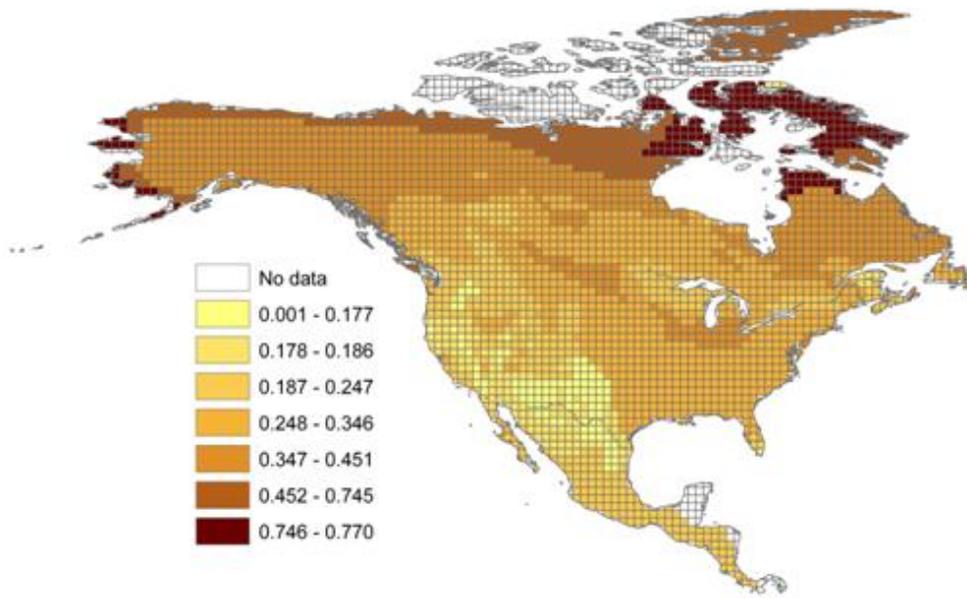


Figure 2.5 Proportional decrease in zoonotic parasite diversity after the removal of widespread carnivore hosts

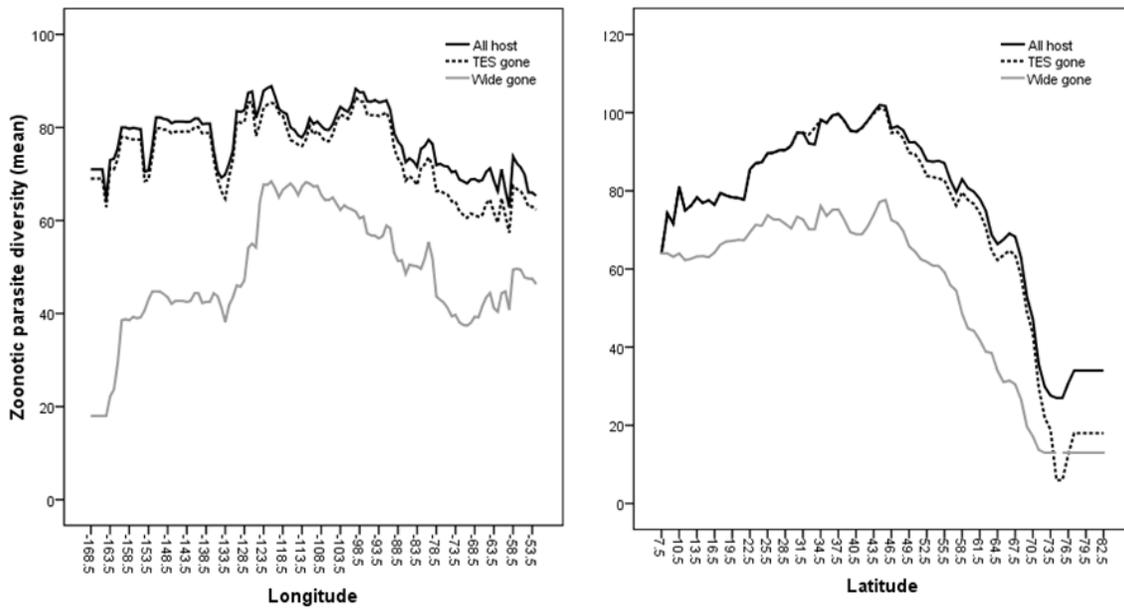


Figure S2.1 Patterns of zoonotic parasite diversity resulting from three carnivore host composition scenario: all host present, species of conservation concern removed (TES), and widespread hosts removed.

CHAPTER 3: REVISITING PARASITE CONSERVATION IN ENDANGERED SPECIES

A paper submitted to *Conservation Biology*

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Abstract

Iconic examples of species extinctions and recovery efforts such as those associated with the passenger pigeon, California condor – and the focus of this paper- the black-footed ferret (*Mustela nigripes*) brought particular attention to the consequences of host rarity for affiliate species such as parasites. Gompper and Williams (1998) speculated on the loss of an endemic louse due to captive breeding, but over ten years later no one has bothered to confirm. Here, we explored the composition and diversity of ectoparasites in the black-footed ferret (*Mustela nigripes*). Because black-footed ferrets have experienced precipitous declines, extinction in the wild and more recently, marked recovery success, the assemblage of their parasite community is of great conservation interests. Furthermore, it is thought that an endemic louse went extinct when black-footed ferrets were brought into captivity for breeding. We found that species richness of ectoparasites on black-footed ferrets was relatively low, when compared to sympatric, more abundant carnivore hosts. The extant parasite community found on black-footed ferrets comprised species that are not host-specific, have low probabilities of extinction, and are found commonly in association with prey species. We did not find the infamous louse on the over 800 individuals sampled from 2006-2010 in the largest, reintroduced population in South Dakota. However, the most abundant ectoparasite found on black-footed ferrets, the flea - *Oropsylla hirsuta*, is an

important vector of plague. Black-footed ferrets may have once harbored endangered or specialist parasites, but now only generalist parasites remain. Black-footed ferrets like other endangered species undergo repeated parasite removal and vaccination efforts to facilitate population recovery, which may have unintentionally contributed to their depauperate ectoparasite community.

Introduction

Parasites offer an interesting and challenging dichotomy in conservation biology. Typically, parasites are viewed as a threat to biodiversity because of diseases they can induce within rare species (Pedersen et al. 2007; Smith et al. 2006). Chytrid fungus, white-nosed syndrome, canine distemper, and West Nile virus, for example, have led to both local extirpations and global extinctions (Frick et al. 2010; Lips et al. 2006; Marra et al. 2004; Murray et al. 1999). Conversely, parasites represent much, if not most, of biological diversity; and thus, warrant conservation in their own right (Durden & Keirans 1996; Whiteman & Parker 2005; Windsor 1995). The ratio of the number of parasite species to the number of free living hosts has been estimated to be as high as 4:1 (May 1992), with estimates of the total number of animal parasites alone in the hundreds of thousands (Dobson et al. 2008). Reductions in parasite diversity can have ramifying consequences for animal populations and ecosystem health (Hudson et al. 2006; Marcogliese 2005). While parasites have been implicated as a cause of many conservation problems, their vulnerability highlights the importance of maintaining species interactions and brings greater attention to invertebrate conservation.

Parasites are, almost by definition, sensitive to changes in their hosts' densities and distributions (Krasnov et al. 2004b; Lafferty & Kuris 2009; Poulin 1997). As hosts become rare and increase in their probability of extinction, so may their parasites (Stork & Lyal 1993). Cases in which endangered host species have endangered parasites include the pygmy hog (*Porcula salvania*) and the pygmy hog louse (*Haematopinus oliveri*), and the tuatara (*Sphenodon punctatus*) and the tuatara tick (*Amblyomma sphenodeonti*); two endangered host species with highly host-specific ectoparasites (Godfrey et al. 2008; Whiteman & Parker 2005). One might expect there to be many more examples of parasites co-endangered due to the rarity of their hosts. For example, nearly 1500 species in the Order Carnivora are threatened with extinction and one might expect carnivores, with their diverse parasite assemblages, to harbor many equally threatened parasites (Lindenfors et al. 2007; Schipper et al. 2008). Yet, we are aware of only one carnivore species for which the presence of a threatened parasite has been suggested, the black-footed ferret (*Mustela nigripes*, (Gompper & Williams 1998).

The black-footed ferret remains one of the most threatened carnivores in North America, even after receiving over 40 years of legal protection under the Endangered Species Preservation Act (precursor to the Endangered Species Act) (Clark 1987). Black-footed ferrets were once found from the Great Plains of Canada to northern Texas (Figure 1). The species experienced precipitous declines throughout the 20th century due to the conversion of grasslands for agricultural practices, epidemics from canine distemper and plague, and local extermination efforts of the prairie dogs (*Cynomys spp.*) their primary prey (Lockhart et al. 2006). Black-footed ferrets now persist in reintroduced populations (Figure 1). Even with

this modest success, black-footed ferrets represent one of the most successful conservation stories globally and are included in the 5% of threatened vertebrate species that show improved persistence attributed to conservation efforts (Schipper et al. 2008). Despite the recovery successes in black-footed ferret populations across their historical range, it remains unclear if their parasite community has been maintained. Gompper and Williams (1998) speculated that the parasite *Neotrichodectes minutus*, a specialist louse that may have been endemic to black-footed ferrets (Emerson 1964), went extinct when black-footed ferrets were extirpated from the wild. Their evidence, though anecdotal, brought attention to the parasite assemblages of endangered species. However, it remains unclear whether this or other specialist species persist on the black-footed ferret throughout its restored geographical range.

At the heart of the apparently divergent views concerning parasites and conservation is the empirical reality that we know very little about determinants of parasite communities in general and more specifically, the consequences to parasites of host rarity. Here, we evaluate whether parasites affiliated with an endangered species are at risk of extinction. We explored ectoparasite diversity and composition in one of the largest and most successful reintroduction sites for black-footed ferrets for the first time. In this massive effort, we sampled over 800 individual black-footed ferrets during a 5-year period and sought partially to rediscover the endemic louse thought to have gone extinct. We then quantified the dissimilarity in parasite community composition between our samples from black-footed ferrets and those reported from other carnivore species within the geographic range of the black-footed ferret. Finally, we estimated an index of extinction risk for black-footed ferret

parasites according to the number and conservation threat status of known alternative host associations. We expect black-footed ferrets to have no endemic parasites and a relatively depauperate assemblage, given its tumultuous journey to recovery. Our findings will illuminate the current state of extinction risk for affiliated parasites in a still endangered host.

Methods

Study area

Black-footed ferrets were extirpated from South Dakota by 1974 and absent until reintroductions from captive breeding efforts began in 1994 within Badlands National Park and Conata Basin (Lockhart et al. 2006). Conata Basin, located in western South Dakota is a portion of the Buffalo Gap National Grassland, and is directly adjacent to the Badlands National Park. We considered Conata Basin and Badlands functionally one site and refer to them as such hereafter. Reintroduction into this area has been the most successful to-date with exponential increases in black-footed ferret population sizes (Lockhart et al. 2006). In part, this success may stem from the high densities of prairie dogs and relatively low occurrence of disease epidemics in the Conata Basin compared to other reintroduction areas. Approximately 15,000 ha of black-tailed prairie dog (*Cynomys ludovicianus*) colonies existed in Conata Basin/Badlands in 2007 on mixed-grass prairie dominated by western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*).

Ectoparasite Collection

We captured black-footed ferrets in Conata Basin/Badlands during annual population monitoring surveys from August-December in 2006-2010. Black-footed ferrets were anesthetized using isoflurane and systematically sampled for ectoparasites. Unconscious animals were held by the scruff of their neck and combed from the shoulders to the tail on both dorsal and ventral surfaces for a total of 20 seconds to sample fleas. Ticks, typically concentrated on the head and neck areas, were removed with fine tweezers for 30 seconds total. In 2009-2010, we opportunistically collected other invertebrates (e.g., mites, larval ticks) that fell off of black-footed ferrets during the flea sampling process and collected a hair sample to search for more ectoparasites. Ectoparasites were then either frozen or immediately stored in 95% ethanol for subsequent identification. Only specimens confidently identified with pictorial keys to species were included in our analyses. Voucher specimens were deposited in the Insect Collection at North Carolina State University and the U.S. National Tick Collection at Georgia Southern University.

We estimated total ectoparasite species richness using Chao1 richness estimators and derived a species accumulation curve to evaluate the importance of sampling effort on observed richness (Colwell 2006). We calculated prevalence and the 95% confidence intervals for each parasite as the number of individuals infested divided by the total number of individuals examined (Quantitative Parasitology 3.0, Rozsa et al. 2000). Insecticide to kill fleas was applied to portions of Conata Basin/Badlands since 2005 to protect black-footed ferrets from sylvatic plague. Because these actions are known to be effective in reducing flea

populations, we present prevalence data only from black-footed ferrets that occupied areas without insecticide application (Biggins et al. 2010).

Ectoparasite compositional similarity

Black-footed ferrets are sympatric with at least thirteen different carnivore species and co-occur throughout most of their geographic distribution with the coyote (*Canis latrans*), badger (*Taxidea taxus*) and swift fox (*Vulpes velox*) (Harris & Dunn 2010). Thus, black-footed ferrets may be vulnerable to additional parasitism due to their close proximity to alternative hosts, resulting in an unexpectedly diverse parasite community. We test this hypothesis by employing the presense-absense version of the Bray-Curtis dissimilarity index to compare ectoparasite composition between those found on black-footed ferrets during this study to those reported in the literature on sympatric carnivores. We only included parasites that are known to occur in South Dakota and surrounding states opposed to throughout their entire geographic range of sympatric carnivores. This approach helps to minimize potential biases associated with uneven sampling effort among species. We depict pair-wise similarity indices on a series of axes scaled from 0.0 – 1.0 for each of the sympatric carnivore species co-occurring with black-footed ferrets. Species with a similarity index of 0.30, for example, had 30% of their ectoparasites in common with black-footed ferrets.

Index of parasite extinction risk

The risk of co-extinction induced by the loss of black-footed ferrets is most pertinent for specialist parasites (Koh et al. 2004). For affiliates with one host, their probability of extinction is equal or greater than that of their host (Fonseca 2009). We employed two approaches to evaluate co-extinction dynamics of carnivore parasites. First, we used a

compiled list of host-parasite associations from North American carnivores to construct presence/absence matrices (Harris and Dunn 2010). Following Koh *et al.* (2004), we then used the diversity module in the software program EstimateS 8.0.0 to estimate extinction in parasites induced by the simulated loss of carnivore hosts (Colwell 2006). We partitioned the parasite data according to their number of reported hosts, ranging from only one to greater than or equal to 10 hosts, and ran 1000 simulations sampling without replacement. We generated lines that depict parasite and host extinctions for each specificity level and expect more curvilinear relationships for less specialized parasites (Koh et al. 2004)

Second, we determined patterns of specificity of all ectoparasites found on black-footed ferrets during our study by searching published reports and museum records to compile a list of alternative hosts for these parasites. Though the probability of extinction for a parasite is conditional upon all of its hosts going extinct, hosts pose varying levels of relative risk for affiliated parasites. This risk corresponds to their conservation threat status and also levels of infestation on each hosts. Presumably, losing a common host that is heavily exploited and has a low probability of extinction should conceptually have a more pronounced effect on the probability of parasite extinction than the loss of a threatened host. Based on this assumption, we estimated extinction risk for affiliate parasites (ext risk):

$$Ext\ risk = \frac{\sum P(host\ ext)}{N}$$

where host ext was the extinction probability associated with the conservation threat status and N is the number of alternative hosts including the black-footed ferret. We used the extinction probabilities associated with the IUCN threat categories as follows: Least Concern

= 0.0005; Near Threatened = 0.004; Vulnerable = 0.05; Endangered = 0.42; Critically Endangered = 0.97 (Mooers et al. 2008).

Results

Ectoparasite diversity

We captured 587 black-footed ferrets throughout our study areas in South Dakota from 2006-2010. Specimens only identified to the genus level and larval ticks as well as mites that were indistinguishable were excluded from our analyses. In the remaining samples, we found 10 flea and tick species (mites were not included). We did not find the host-specific louse, *Neotrichodectes minutus*, presumed to be extinct, or any lice for that matter. Our sampled appeared sufficient to detect species, given the shape of the species accumulation curve (Figure S1). We recorded several new parasite associations for black-footed ferrets. The following flea species are noted on black-footed ferrets for the first time here: *Amaradix euphorbia*, *Aetheca wagneri*, *Epitedia wenmanni*, *Peromyscopsylla hesperomys*, and *Stenoponia americana*. We confirmed *Ixodes kingi* and *Oropsylla hirsuta* from black-footed ferrets as reported by Boddiiker (1968). The number of ectoparasite species found on a given individual ranged 1 - 4 species with 28% (n=41) of infected ferrets having at least one ectoparasite species.

Prevalence of specific ectoparasites found in association with black-footed ferrets showed marked variation ranging from 0% - 45% (Table 1). The most specialist parasites may be the most prevalent on a rare host because they possess adaptations that best allow them to reach high abundances on their host. However, in the absence of specialists, the

most generalist species might be best able to colonize rare hosts and reach high abundances. Here, we did not find any specialist parasites but, found a strong positive relationship between the parasite abundance and diversity on a given black-footed ferret individual. *Oropsylla hirsuta*, a flea implicated in the transmission of plague, was among the most abundant ectoparasite found in black-footed ferrets, accounting for 56% of all parasites encountered.

Dissimilarity with sympatric carnivores

Although the composition of parasites were similar in coyotes, badgers, and swift foxes compared to black-footed ferrets, no sympatric carnivore (n = 13) had the entire ectoparasite assemblage belonging to that of the black-footed ferret (Figure 2). Black-footed ferrets harbor only half as many ectoparasite species as their more abundant, sympatric counterparts. Parasite composition dissimilarity ranged 0.56 - 1.0. Several ectoparasites commonly found on other carnivores and reported in South Dakota were not detected on black-footed ferrets, despite our extensive sampling. These undetected species included the fleas: *Foxella ignota*, *Euhoplosyllis affinis* and *Ctenocephalides felis*. Conversely, at least four ectoparasite species that exploit black-footed ferrets have never before been detected on any other mammalian carnivore. The uniqueness of the black-footed ectoparasite fauna means that changes in ferret abundance or distribution could alter parasite communities, even if, no specialist parasite species are present.

Index of Parasite extinction risk

None of the parasites we detected were specialists on the black-footed ferret and so no parasites were, strictly speaking, co-endangered because of the endangered status of their

host. Of the species present, not surprisingly, the proportion of parasites that go extinct following the loss of a carnivore hosts was predicted to be most pronounced for the more specialized parasites (Figure 3). Ectoparasites that exploit more carnivore hosts (e.g., ticks- *Ixodes kingi*, *I. sculptus*) appear buffered against consequences associated with the loss of individual hosts. Most of the ectoparasites we found on black-footed ferrets have a diverse and abundant alternative host community (Table 1). Over 100 alternative hosts have been reported in association with the parasites found on black-footed ferrets. The estimated risk of extinction was therefore, relatively low across all black-footed ferret parasites because these parasites exploit other alternative hosts that have a relatively lower risk of extinction. However, the effect of host removal on parasite extinction is sensitive to which hosts are removed. The extinction of host species classified as of least concern resulted mostly in no change in parasite extinction risk, and 94% of the alternative hosts for black-footed ferret parasites are of least concern. In contrast, removing host species with a high threat status (e.g., with an IUCN classification of endangered or critically endangered) such as black-footed ferrets resulted in a decrease in the probability of extinction for parasites.

Discussion

Why no specialist parasites on black-footed ferrets?

The challenges of studying endangered species have long been realized and much effort has focused on strategies to mitigate error when sampling such proportionately rare occurrences (e.g., MacKenzie et al. 2005; Venette et al. 2002). Missing the presence of a species (i.e., false negative) is particularly problematic when one considers parasitic organisms, due to the

risks of future disease outbreaks. In other words, even if only a single infected individual remains in a population, the chance for disease spread still exists, though low. Here, we studied ectoparasite diversity and composition in a host species that had been previously gone extinct in the wild and in the midst of active recovery, the black-footed ferret. We also sought to detect specialist parasites in affiliation with this rare species, namely a louse suspected to have gone extinct with the demise of the black-footed ferret (Gompper & Williams 1998).

In revisiting the question of whether endangered species have endangered parasites, we did not find any ectoparasites unique to black-footed ferrets in our study. Many studies have investigated the assertion of declaring a species is gone or missing in the context of disease screening, invasive species management, and inferring extinction (Collen et al. 2010; Fenichel et al. 2008; Regan et al. 2006). In our case, the absence of specialist parasites on black-footed ferrets could result from one of three scenarios relevant to co-endangerment and further parasite conservation attention. First, specialist parasites may simply have not been detected because we did not sample for ectoparasites on enough ferrets or throughout their entire extant geographic range. Although, there were several specimens damaged and excluded from the analyses, none of these included lice. The Conata Basin/Badland population sampled not only represents the largest and most successful recovery effort for black-footed ferrets, but also serves as the source population to augment or establish other populations. The likelihood of missing ectoparasites in the over 800 individuals sampled and finding new species in another population is low. Also, the species accumulation curve

confirms that our sampling efforts were sufficient enough to detect rare occurrences of ectoparasites (Figure S1). It is just these rare species are not specialists.

A second plausible scenario is that ferrets never had any specialist ectoparasites. Museum records of ticks found on black-footed ferrets dating back nearly 70 years when the ferret was widespread and abundant, report only *Ixodes kingi* and *Ixodes sculptus*; which are the same species we found in extant populations (personal communication, L. Beati, NC National Tick Collection, Institute of Arthropodology and Parasitology, Georgia Southern University). However, most species are thought to have at least one specialist parasite and since, the black-footed ferret is the only native ferret to North America, they are probably no exception (May 1988).

The third and most likely scenario is that specialist parasites were lost when black-footed ferret populations were reduced or when the remaining individuals were deloused in captivity (Windsor 1995). Both theoretical and empirical evidence demonstrate a critical community size is necessary to sustain disease in a population, which results in specialists on rare species being atypical (Altizer et al. 2007; Lloyd-Smith et al. 2005). Therefore, it is perhaps not surprising, that despite our extensive sampling efforts, we were unable to detect a single occurrence of *Neotrichodectes minutus*. This louse species is thought to persist on the closely-related long-tailed weasel, *Mustela frenata* (Price et al. 2003). But, whether the louse once known from the black-footed ferret was really unique or not remains undeterminable because comparisons with historic specimens are impossible.

Overall, the ectoparasite community on black-footed ferrets was depauperate and comprised only generalist parasites found mostly on prey species such as prairie dogs and

Peromyscus mice. Black-footed ferrets have ample opportunity to be exploited by many other ectoparasites, given their co-occurrence with over 10 different carnivore species. Sympatry is thought to be a prerequisite for shared parasite communities among hosts (Davies & Pedersen 2008), which may not be the case for the parasites of endangered species. The dissimilarity in parasite composition between ferrets and sympatric carnivores may be attributed to the low densities of black-footed ferrets throughout a geographically restricted range. In most cases, when specialist parasites are present in communities, they are most prevalent on hosts that are abundant and widespread (Hughes & Page 2007).

Parasite conservation and monitoring

Once, black-footed ferrets represented a conservation conundrum due to the challenges posed in conserving both rare hosts and rare parasites. Tension magnified because of management actions such as parasite removal or dusting prairie dogs colonies with insecticide aimed to lessen ectoparasite loads. Black-footed ferrets, in some respects, were the “flagship” host for parasite conservation (Gompper & Williams 1998). Results from our study indicate that not a single ectoparasite species in association with black-footed ferrets is in danger of extinction, regardless of the management action employed. For example, *Oropsylla hirsuta* will persist even if strategies aimed at extirpating this plague vector throughout the geographic range of ferrets are successful because of it exploits numerous alternative hosts (Lewis 2002). At present, conserving black-footed ferrets for the benefit of ectoparasites is not warranted because the parasites of ferrets have low probabilities of extinction.

Apparently, the answer of whether endangered hosts have endangered parasites is not answered so simply. Our ability to detect those endangered affiliates and enforce a successful

conservation strategy is time-dependent. We may have been too late to identify parasites in need of protection in the case for black-footed ferrets; a scenario that may apply to numerous other endangered vertebrate species. Because parasites are sensitive to host density, they may go extinct or switch to new resources as their hosts become rare and approach extinction. Monitoring the parasite community of hosts through time, especially in populations that are declining, will inform when parasites may switch to alternative hosts or become species of conservation concern. Few or no parasite records exist in associations with many host species now extinct, justifying longitudinal collection of host-parasite data for abundant and rare species alike (Muniz-Pereira et al. 2009). As good practice, we recommend that parasite samples be collected and preserved in every study that involves handling animals or collecting scat. At first glance, making parasites a priority for conservation may seem unrealistic, but may become increasingly important as the consequences of losing species become realized.

In some instances, new parasitic organisms have actually been discovered on species of conservation concern. A new *Felicola* louse and *Babesia* protozoan species were found on the Iberian lynx (*lynx pardinus*) and cheetah (*Acinonyx jubatus*), respectively; two of the most endangered felids in the world (Bosman et al. 2010; Perez & Palma 2001).

Additionally, a new species of tick was discovered on the endangered Ploughshare tortoise (*Geochelone yniphora*) in Madagascar, an area high in species richness and endemism (Durden et al. 2002). Most recently, a new species of coccidia parasite were discovered in an endemic boa constrictor on the Mauritius Island (Daszak et al. 2011). These discoveries may suggest that parasites can be relatively resilient and adaptable, though clearly that is not

always the case. Furthermore, because of these tight associations, our conservation efforts targeted at a single species can unintentionally, yet gratifyingly ensure the persistence of affiliated species. However, the story is remarkably different for the black-footed ferrets. Their low parasite diversity implies that, indeed specialists and other parasites were lost throughout their road to recovery, and despite the continued conservation success of the host, parasites associated with black-footed ferrets have not reaped the same benefits of conservation efforts.

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Table 3.1. Ectoparasite species collected from black-footed ferrets (*Mustela nigripes*) in South Dakota, 2006-2010. Prevalence calculated as the proportion of infected individuals out of the total number of individuals examined across sites throughout the duration of the study (n=227)¹. Number in parentheses represents the 95% confidence interval. N represents the total number of specimens collected of each ectoparasite Alternative host is the number of North American mammals in association for each parasite reported in the literature. Extinction risk was calculated as the sum of host extinction probability according to their IUCN threat status divided by the number of host.

Ectoparasite species	N	Prevalence (95% CI)	Alternative hosts	Extinction risk
TICKS				
<i>Ixodes sculptus</i>	189	0.37 (0.30 - 0.43)	57	0.022
<i>Ixodes kingi</i>	271	0.45 (0.38 - 0.51)	60	0.015
FLEAS				
<i>Oropsylla hirsuta</i>	612	0.43 (0.37 - 0.50)	14	0.030
<i>Pulex irritans</i>	4	0.02 (0.01 - 0.05)	13	0.182
<i>Epitedia wenmanni</i>	3	0.01 (0.00 - 0.03)	8	0.053
<i>Oropsylla tuberculata</i>	2	0.01 (0.00 - 0.03)	4	0.105
<i>Stenoponia americana</i>	3	0.00 (0.00 - 0.02)	17	0.025
<i>Peromyscopsylla hesperomys</i>	2	0.01 (0.00 - 0.03)	16	0.026
<i>Aetheca wagneri</i>	2	0.00 (0.00 - 0.01)	33	0.013
<i>Amaradix euphorbi</i>	1	0.00 (0.00 - 0.02)	4	0.105

¹Prevalence calculated only from undusted locations where black-footed ferret were captured

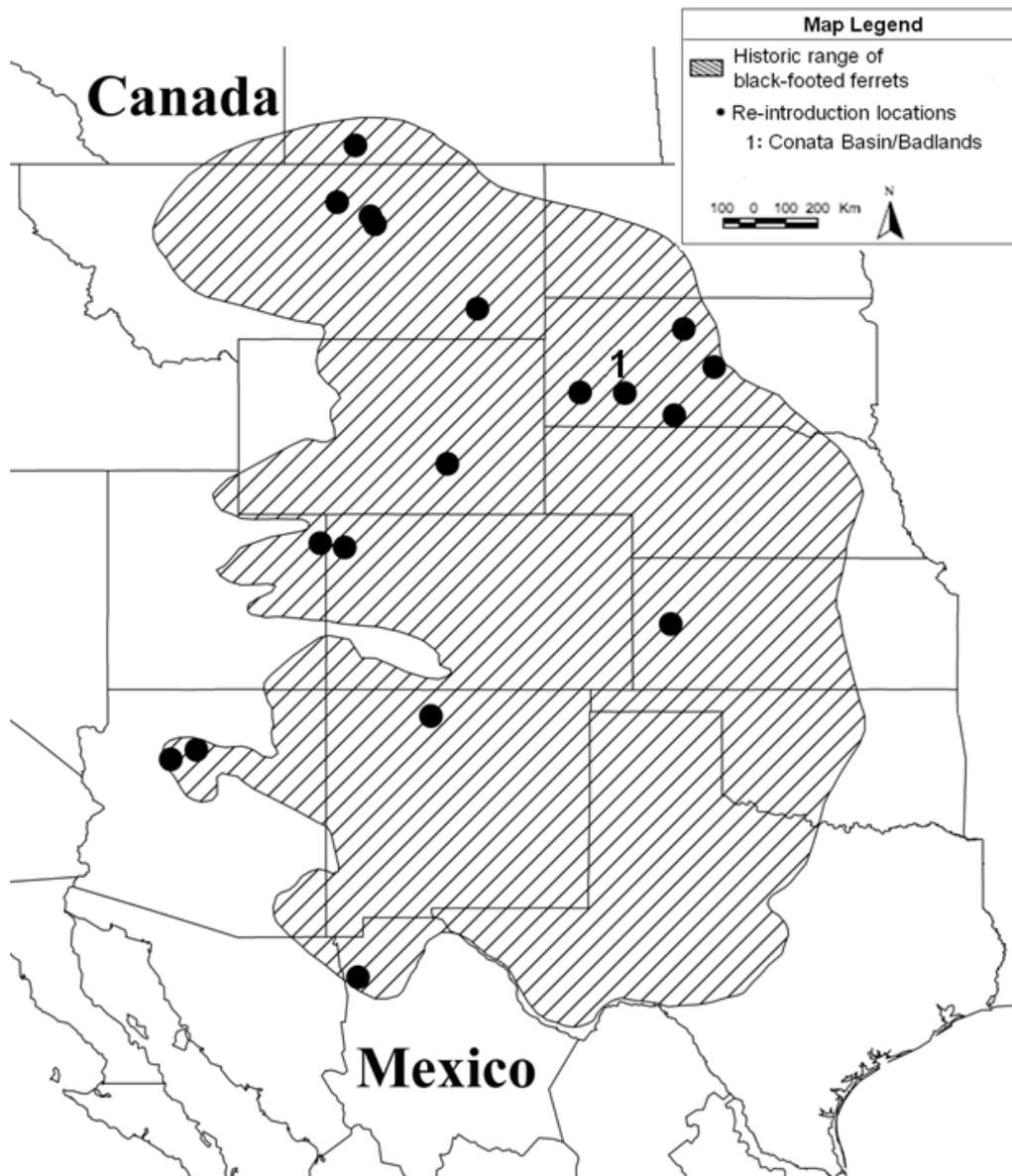


Figure 3.1 Geographic distribution of black-footed ferrets (*Mustela nigripes*). Our study occurred within the Conata Basin/Badlands National Park relocation site.

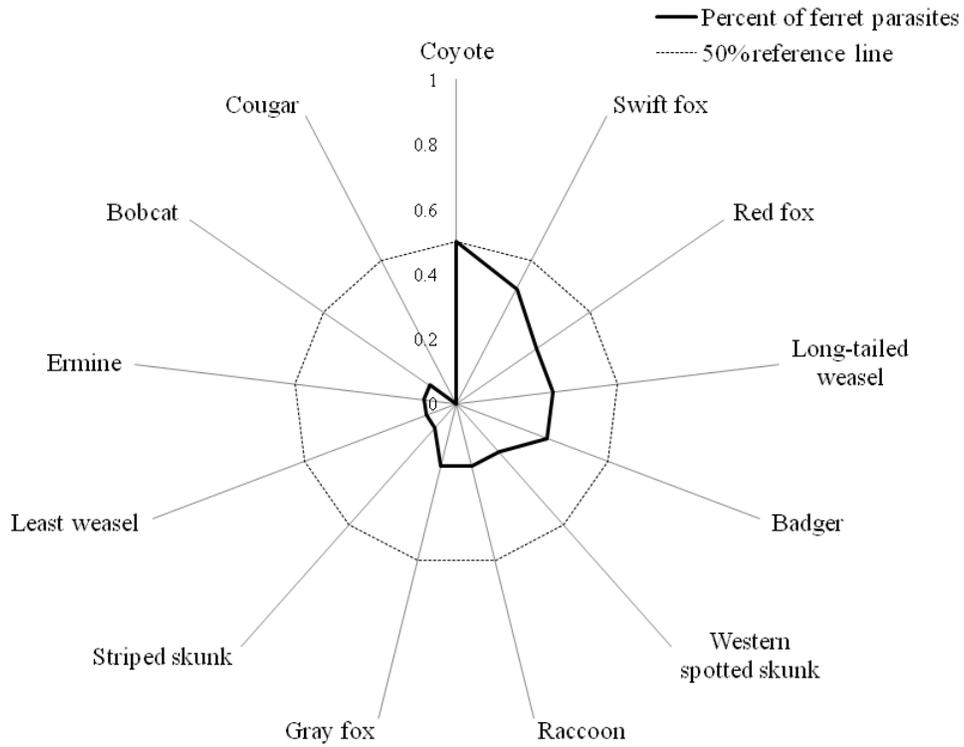


Figure 3.2 Pair-wise comparisons in ectoparasite community composition between black-footed ferrets and their 13 sympatric carnivores with a different hosts depicted on each axis. The swift fox, badger, and coyote shared the most parasites with the black footed ferret.

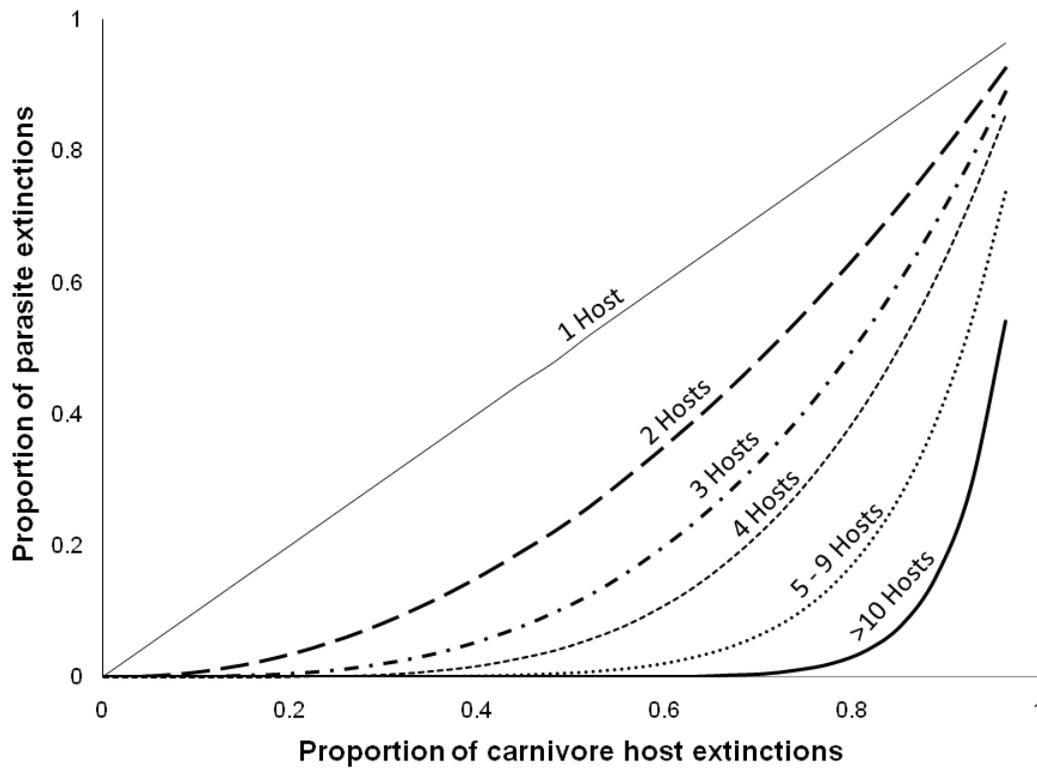


Figure 3.3 Simulated extinctions of ectoparasites due to the extinction of 29 North American carnivore hosts across a gradient of host specificity patterns. A parasite species with one host would have exactly a 100% probability of extinction with the loss of its host. In the context of our study, no such parasite species found on black-footed ferrets where restricted to a single host. On average, ectoparasites had 23 alternative hosts.

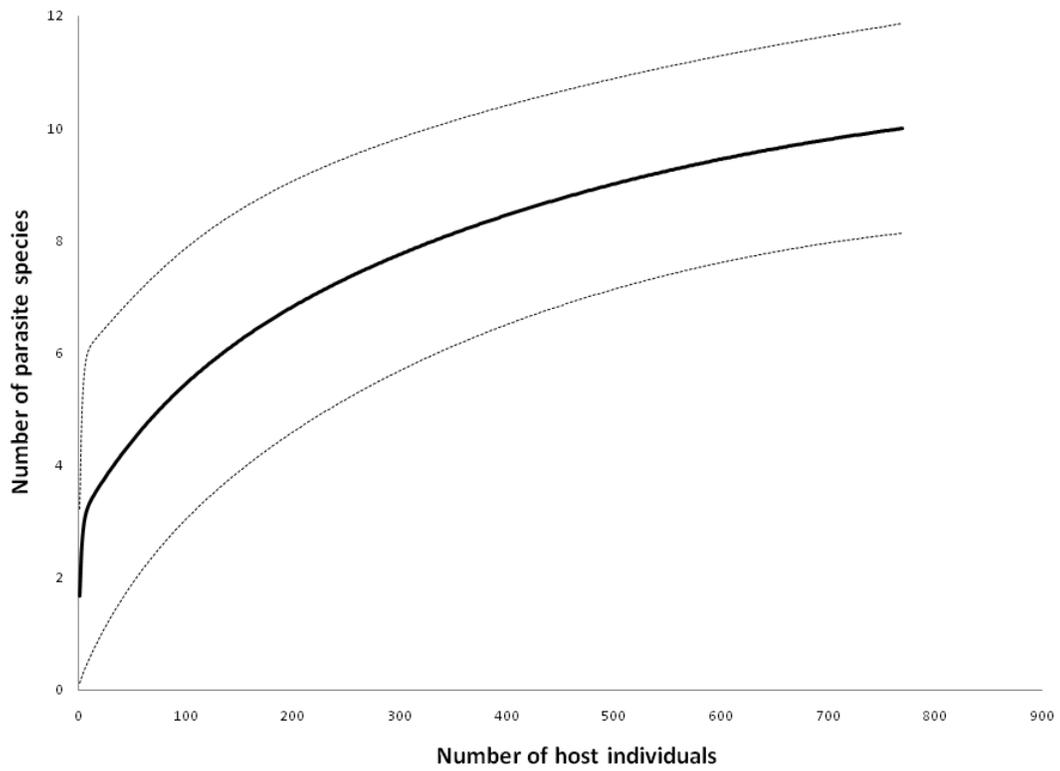


Figure S3.1 Species accumulation curve to evaluate the importance of increased sampling effort of ectoparasite species richness in black-footed ferrets

CHAPTER 4: CONSERVING ENDEMIC HOST-PARASITE INTERACTIONS IN RARE SPECIES

A paper submitted to *Diversity and Distributions*

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Abstract

The ecology of a species may differ throughout its geographic distribution due to a plethora of extrinsic and intrinsic factors. We evaluated whether the role of an endangered species to supply habitat for ectoparasites varied across the range of the host. We captured 234 island foxes (*Urocyon littoralis*), an endemic carnivore of the Channel Islands, from three populations: Santa Catalina (n=72), Santa Rosa (n=79), and San Miguel (n=83). We identified 8 ectoparasites species in total, but ectoparasite diversity varied among populations. Furthermore, we found there to be unique host-parasite associations in each island fox population. Given this information, we would be able to assign a fox of unknown origin to its respective population 70% of the time. Our findings highlight the importance of conserving populations to maintain endemic interactions and emphasize always considering the role of a species in a local-specific context.

INTRODUCTION

“The history of evolution and biodiversity is fundamentally a history of the evolution of species interactions” (Thompson 1999).

A growing body of work argues that conservation should target not only genotypes, populations, species and habitats, but also interactions (Forup et al. 2008; Kearns et al. 1998; Thompson 1996; Tylianakis et al. 2010). Implicit in conserving interactions is the idea that species behave differently throughout their geographic distribution because they differ in the extent and overlap of their ranges; thus, promoting unique associations throughout space (Schemske *et al.* 2009; Sexton *et al.* 2009). This also means that populations of a given species are not necessarily functionally equivalent. As such, efforts that consider not just the unique genes or traits of species within populations, but also their unique interactions, are needed to ensure that management actions aimed at preserving species also conserve processes that promote species evolution, population viability, and ecosystem health. However, a key barrier to conserving interaction diversity is actually documenting whether distinct interactions among populations exist, as we do in this study.

Parasites by virtue of their diversity and dependence on other species are embedded in every ecological network or food web (Lafferty *et al.* 2008) and therefore, the most common species interaction in nature. Parasites account for most species on Earth (May 1988), can exert strong selection pressures on their hosts (e.g., Wegner *et al.* 2003), and can vary in their diversity independent of the diversity of their host (e.g., Krasnov *et al.* 2004b). On the one hand, the parasite assemblages of a host may exhibit marked differences

population to population due to climate variables altering life-history traits, the composition of alternative hosts, and transmission efficiency. This highlights the importance of considering host and parasite interactions in the context of local and regional environments (Brooks & Hoberg 2007; Lafferty 2009; Wolinska & King 2009). This variation among populations is perhaps most realized when one considers the parasite assemblage of a species in its native versus introduced range (Torchin & Mitchell 2004). Parasites may be absent from or limited in host populations because competitive interactions and parasite-induced immune responses in the host exclude parasite species from co-occurring (Jolles et al. 2008; Lello et al. 2004; Pedersen & Fenton 2007).

On the other hand, one might expect that in at least some host populations, the interaction diversity between host and parasite is geographically invariant. Similar parasite communities and hence interactions may plague host populations throughout the range of species because of strong co-evolutionary histories or due to the persistence of common threats, for example (Thompson 1999). Arguably, the most fundamental resource delimiting distributions for parasites is the presence of hosts. However, which hosts and how many hosts are present do affect the spatial patterns of parasite diversity. Numerous studies have demonstrated that where there are more hosts there are proportionately more parasites (Vaughn & Taylor 2000; Ezenwa 2003; Krasnov *et al.* 2004b; Hechinger & Lafferty 2005; Novotny *et al.* 2006; Harris & Dunn 2010). This variation in parasite diversity across space also likely leads to variations in host-parasite interactions among host populations. Yet, while it has been emphasized that interactions should be conserved, the extent to whether these interactions vary among different populations of species in a predictably unique manner

necessary to anticipate selective pressures and inform conservation prioritization in less understood.

Empirical studies depicting if and how host-parasite associations vary across host populations are limited, but exist in other systems. For example, ruby-throated hummingbirds (*Archilochus colubris*) vary spatially and temporally in their contribution to pollination in a ubiquitous North American plant (Fenster & Dudash 2001). Considering predators and their prey, Canada lynx (*Lynx canadensis*) have a diet restricted to snowshoe hares (*Lepus americanus*) throughout most of its range, but populations in areas with high prey diversity exploit alternative species (Roth *et al.* 2007). Here, we focus on the endangered Island fox (*Urocyon littoralis*), which resides only on Channel Islands off the coast of California, to evaluate differences in host-parasite interactions across three populations. If populations differ in attributes, then the unit of interest for conservation should be the population, not simply the species. Hosts already represent figurative “islands” of suitable habitat with individuals acting as hierarchical replicates for parasites. Studying parasites on geographic islands further strengthens these among population comparisons because islands literally are discrete locations with generally limited mammalian species turnover and allow various mechanisms influencing distributions to be isolated. Additionally, our study illuminates whether species of conservation concern exhibit expected associations with their remaining parasites, since often rare or geographically restricted species have fewer specialist (Altizer *et al.* 2007; Harris & Dunn 2010).

Specifically, we assessed whether individual island foxes differed in the composition, diversity, and intensity of the ectoparasite species they harbored. If foxes generally have the same parasite assemblage, conservation of a single population maintains all necessary species interactions. Then, we assessed how parasite intensity (i.e., load) was distributed among host individuals and determined whether this aggregation is a species-specific trait. Finally, we compared the extent to which this variation was due to differences among individuals or populations. As a measure of the latter, we determined whether individuals from the same population “cluster” together when comparing patterns of intensity in various ectoparasites. If so, this would indicate the presence of unique host-parasite interactions that warrant additional conservation attention.

METHODS

Ectoparasite collection

Island foxes are a small endemic fox of the Channel Islands in California, closely related to the gray fox (*Urocyon cinereoargenteus*) on the mainland that have a larger body size and geographic distribution (Moore & Collins 1995). Island foxes inhabit the six largest Channel Islands, each with a different subspecies, and diverged from the mainland species 10,000-15,000 years ago (Wayne et al. 1991). Island foxes are listed as endangered by the US Fish & Wildlife Service in four of those populations due to disease and the colonization of a novel predator, and have remained the focus of much conservation effort (Roemer *et al.* 2002). We captured and sampled individuals from three endangered populations in August – October 2009: Santa Catalina Island (33°24’N, 118°24’W), Santa Rosa Island (33°57’N, 120°06’W), and San Miguel Island (33°02’N, 120°18’W).

Island foxes were captured during annual trapping efforts to monitor population recovery. Once an individual was restrained, we systematically combed (~ 20 strokes) the entire body of the individual to collect ectoparasites using a flea comb. Ticks that are attached or engorged are unlikely to be removed through combing and instead, were individually removed using fine-tip tweezers. This sampling method took less than two minutes and ectoparasites were preserved in 95% ethanol for subsequent identification using pictorial keys and direct comparison to reference entomological specimens.

Ectoparasite summary statistics

We estimated prevalence and intensity of infection for each ectoparasite found during the sampling of island foxes. We calculated prevalence and the 95% confidence intervals as the number of individuals infected divided by the total number of individuals examined (Rozsa *et al.* 2000). We used chi-square and 2-sample t-tests to explore differences in prevalence among Island fox populations. We also calculated ectoparasite intensity as the number of ectoparasite individuals recorded from infected hosts; mean values with 95% confidence intervals are provided. We used Multivariate analysis of variance (MANOVA) to evaluate whether the variation in intensity and diversity was due mainly to differences among individuals or among populations for each ectoparasite species. Significant results indicated that among population variation is larger than the variation among individuals within a population.

Structure in ectoparasite communities

Key to understanding how parasites are distributed both within and among populations is an understanding of their relative abundance on different hosts. Disease theory and previous empirical studies demonstrated a skewed, over-dispersed pattern in parasite intensity among individuals within a population; in that, most individuals have few parasites and that only a small fraction of the population are heavily parasitized (Poulin 2004; Shaw & Dobson 1995). But, if the population of interest has a greater proportion of susceptible individuals, deviations from the negative binomial distribution may exist (e.g., Wirsing et al. 2007). In addition, aggregation could either be consistent among populations (if it is an attribute of parasite species) or vary from island to island (if it is a function of local conditions). We evaluated the skewness of parasite distributions for each parasite species among populations using three common indices: variance-to-mean ratio, exponent k of the negative binomial, and index of discrepancy (D). The ratio of the variance to the mean of number of parasites per hosts is greater than unity and k approaches zero, while D tends towards a maximum of 1 in aggregated populations (Poulin 1993).

Host population designation by ectoparasite assemblage

Individual hosts may differ because of differences in their genotypes, behavior, health, sex or other local traits (Altizer et al. 2011; Jolles et al. 2008; Pedersen & Fenton 2007; Wirsing et al. 2007). Or, hosts may differ not due to individual traits but instead due to regional contexts. We used discriminate function analysis to classify individuals from three island fox populations based on their parasite assemblages and used the leave-one-out cross validation approach. This approach is robust to violations of normality and equal covariance

assumptions. Discriminate function analysis uses a priori information on group designation to minimize within group variance and maximize between group variance. We recognize that it is not simply which parasites that are present on an individual, but also which parasites are absent from populations that is necessary in defining conservation priorities. Using this rationale, one might in the future be able to determine the source population of a host individual of unknown origin solely by determining what parasites they harbor.

RESULTS

We captured 234 island foxes across three island fox populations (Figure 1): Santa Catalina (n=72), Santa Rosa (n=79), and San Miguel (n=83). The proportion of individuals infected with at least one ectoparasite species was high and the same (94% of individuals) on both Santa Rosa and Santa Catalina Islands. In contrast, only about a third (24/83) of island foxes were infected with any ectoparasites on San Miguel Island, the smallest island on which only one other native mammal resides (the deer mouse, *Peromyscus maniculatus*). Ectoparasite diversity also varied among populations ($F = 14.26$, $df = 2$, $P < 0.001$) ranging from only 2 species on San Miguel Island to 7 species on Santa Rosa (Table 1). Five of the nine ectoparasite species were restricted to a single island, resulting in unique species interactions between parasites and host in each Island fox population (Figure 2). The fleas, *Oropsylla montana* and *Opisodasys nesiotus* were only observed in association with foxes on Santa Catalina and San Miguel Islands, respectively. Differences among islands were not due simply to distances. For example, ectoparasite assemblages appear most dissimilar between Santa Rosa and San Miguel, despite their close geographic proximity (~5 km).

When combining all ectoparasite species, overall prevalence ($X^2 = 77.65$, $df = 2$, $P < 0.001$) and mean intensity of infection ($F = 3.79$, $df = 2$, $P = 0.025$) differed among island fox populations, with the greatest prevalence and intensity of infection on Santa Rosa Island both overall and for half of all parasite species individually (Table 1). Nevertheless, in all populations, there was only one ectoparasite species that had prevalence levels that exceeded 50%. Differences in intensity among populations were observed for 5 of the 9 ectoparasite species reported from island foxes: *Pulex sp.* (MANOVA: Wilk's λ : $F_{2,152} = 33.17$, $P < 0.001$), *Ixodes pacificus* ($F_{2,152} = 7.69$, $P = 0.001$), *Echidnophaga gallinacea* ($F_{2,152} = 5.42$, $P = 0.005$), *Opisodasys nesiotus* ($F_{2,152} = 5.54$, $P = 0.005$), and *Neotrichodectes mephitidis* ($F_{2,152} = 2.74$, $P = 0.068$). Though one might expect the intensity of parasite infection to be higher when fewer individual hosts are infected; overall, we found no association between prevalence and mean intensity ($R^2 = 0.057$, $P = 0.649$). *Ixodes pacificus* was the only species for which a species with low prevalence had a high mean intensity of infection when it was present (the case on Santa Catalina Island, but not on Santa Rosa Island). The prevalence and infection intensity of *I. pacificus* has great significance because this species vectors numerous zoonotic pathogens including *Borrelia burgdorferi* and *Anaplasma phagocytophilum*. For all ectoparasite species that occurred in more than one population, the intensity of infection varied differently among individuals within a host population (Figure 3). In other words, the distribution of ectoparasite infection was not consistent among populations, indicating that intensity is likely not an intrinsic, biological attribute of the parasite, but instead a manifestation of extrinsic conditions. Most notably, *Ixodes pacificus* was not detected on San Miguel Island, aggregated on Santa Catalina, and more segregated in

infected foxes on Santa Rosa. Similar patterns in the lack of repeatability of aggregation metrics were observed when considering different ectoparasites. When we considered the mean intensity of all ectoparasites combined, all populations were structured (Discrepancy index: San Miguel = 0.83, Santa Rosa = 0.55, Santa Catalina = 0.80).

A discriminate function analysis was done to test whether the population of origin for island fox individuals can be discerned based on the intensity and composition of their ectoparasite infection. The five ectoparasites that demonstrated greater among, than within, population variation were used in discerning population designations in the discriminate function analysis (Table 1). The cross-validated classification showed that 70% of fox individuals were correctly classified to their actual population of origin (Figure 4). The false assignments were highest from individuals occurring on San Miguel Island; 92% of these foxes were incorrectly classified as residing on Santa Catalina Island. Individuals from this population that were correctly classified host only one ectoparasite affiliate, but represented a unique association.

DISCUSSION

Parasites are interesting and important in their own right but have also become an increasingly visible tool for understanding hosts. Parasites have proven useful in understanding the evolutionary and biogeographic history of hosts, be they humans or hawks, across a range temporal and spatial scales (Blakeslee & Byers 2008; Reed et al. 2007; Whiteman & Parker 2005). Studies have also shown that parasites can inform whether a particular host species is present, when a parasite that requires multiple hosts to complete its

life-cycle is present (e.g., Byers *et al.* 2011). We add to this growing list of examples of the ways in which parasites inform host's ecology by showing for the first time that knowing the parasite composition of a host individual can aid in identifying its population of origin because of unique host-parasite interactions.

We demonstrated that host-parasite associations exhibited spatial variation among populations of an endangered host. Specifically, we found that island foxes on Santa Rosa had the highest ectoparasite diversity, but only shared one (of their 8) species in common with foxes on the neighboring San Miguel, located just 5 km away (Figure 1). In our present study, this among population variation in parasite assemblages could be attributed to many factors including differences in fox densities, recovery efforts, alternative host diversity and species invasions. Foxes on both San Miguel and Santa Rosa Islands went extinct in the wild in the late 1990s due to substantial predation from a novel, exotic aerial predator, the golden eagle (Roemer *et al.* 2002). Nevertheless, our findings highlight that host populations can be predictably unique in their species interactions, a result with at least two important implications for conservation.

First, when interactions of a host species differ throughout its geographic range; in effect, they are expressing different ecological phenotypes (Stone *et al.* 2011). Whether these different phenotypes deserve independent conservation is a topic for discussion, but clearly a population that maintains 2 ectoparasite species (San Miguel) and one that maintains 7 species (Santa Rosa) have very different roles in their communities and their loss would yield different consequences. Here, we clearly demonstrate that these differences in interaction diversity exist, even though both environmental and genetic differences among island fox

populations are minimal. And because the persistence of species is dependent on maintaining multiple populations, identifying these unique associations can aid in identifying conservation priorities and mitigating future threats.

Second, host populations with different parasites are likely to experience divergent selection pressures (Altizer et al. 2003; Rigaud et al. 2010; Thompson 1996). Clear examples exist in which regional differences in parasite faunas yield regional differences in selection. For example, stickleback populations in northern Germany exposed to a wider array of internal parasites including cestodes and microsporidia were more diverse in their major histocompatibility complex (MHC) class genes – a suite of genes influencing parasite resistance through an adaptive immune response (Wegner *et al.* 2003). We suspect that regional differences in parasite faunas and the selective pressures they impose may be common, particularly in isolated populations such as these island foxes. The resultant variations in host-parasite interactions could then generate novel evolutionary trajectories in hosts, population to population (Thompson 1999). It is interesting to note, in this regard, that high levels of diversity in MHC were observed in San Nicholas island foxes, a population that has experienced high levels of mortality from canine distemper and other canine parasites (Aguilar *et al.* 2004).

In addition to the variation among island fox populations in the species composition of parasites, we also observed variation among populations in the attributes of the parasites. We found different levels of aggregation, prevalence, and intensity in each ectoparasite considered among island fox populations. Similar (and more extreme) levels of spatial variations in parasite attributes have also been reported in many other systems (e.g., Gomez-

Diaz et al. 2008; Krasnov et al. 2004a; Salkeld et al. 2008). The mean number of *Colpocephalum turbinatum* lice (i.e. intensity) found in Galapagos birds ranged 24- 206 individuals across island populations (Santiago-Alarcon et al. 2008). However, whether specific populations of Island foxes endure comparable rates of infestation for other parasites is unlikely. Foxes on San Miguel had a seemingly low prevalence values for ectoparasites. But for other parasites, San Miguel had some of the highest prevalence values of canine heartworm and moderate values for a *Bartonella* bacterium compared to other Channel Islands (Namekata et al. 2009; Roemer et al. 2000). This variation in parasite attributes further emphasizes the need for conservation at the population level, not only at the species level. A key next step is to consider more islands in order to begin to understand why both the species and attributes of parasites differ among populations.

One might imagine the progressive transformation of the field of conservation biology from a species-centric view to a more process-based model, where maintaining interactions is the metric of recovery or restoration success (Forup et al. 2008; Thompson 1996; Tylianakis et al. 2010). In practice, this transition has been slow if it has occurred at all. One straightforward step closer to considering not just species, but interactions would be to consider the conservation value of species based both on their number of connections with other species (i.e., ecological value). Theoretical work suggests that losing species on which many species depend is more likely to compromise the architecture, stability, and function of ecological networks; and potentially lead to co-extinctions (Dunne *et al.* 2002; Koh *et al.* 2004; Tylianakis *et al.* 2010). But more simply, hosts with different parasite interactions are, because of those interactions, different from each other in their consequences. If the goal of

conservation is, in large part, to conserve the roles of species, then conserving populations that differ in their interaction phenotype seems important. Recognizing the value of such interactions would require a broader acceptance of the value of parasites, which has yet to be accomplished, despite the acknowledged reality that most species on Earth are parasites and that parasites appear to have consequences (in their presence or absence) on genetic, population and even ecosystem levels in many, perhaps all, ecosystems (Dobson et al. 2008; Dunn et al. 2009; Hudson et al. 2006; Windsor 1995) .

However, the story is apparently more complicated because species not only can vary in the diversity of their interactions, but also vary in terms of the number of endemic or rare species with which they interact. So to go a step further, one might prioritize populations of species according to the number of interactions with endemic or rare species. Traditionally, the term endemic refers to a species geographically restricted to a single locale and remains a common strategy for conservation practices. Here, we expand this concept to include unique host-parasite associations found within the distribution of an endangered species. For example, a host-specific tick was present on only 8 of the 28 islands in the range of its tuatara host (*Amblyomma sphenodonti*), an endangered reptile endemic to the New Zealand (Miller et al. 2007). Similarly, we found endemic associations between island fox and their ectoparasites, even after considering data from a fourth island fox population (Crooks et al. 2001). Island foxes on Santa Cruz did not have any unique associations, but the Santa Cruz Island skunk (*Spilogale gracilis amphiala*) harbored an endemic flea not found the island foxes in our study. Other examples exist of endemic interactions between hosts and parasites

include: Acacias and plant louse, (Taylor & Moir 2009), tick and tortoises (Durden *et al.* 2002), and fish and helminthes (Perez-Ponce de Leon & Choudhury 2005).

As our results make clear, the presence of suitable hosts is required, but does not guarantee the occurrence of affiliated parasites. But where host and parasite are both present, unique associations may emerge. Much research has focused on mapping the distribution of endangered and endemic species (Grenyer *et al.* 2006; Orme *et al.* 2005). As the number of research projects studying the geographic distribution of some species of interest increases, implicitly our understanding about other species also improves because those species are likely either promoting or mimicking the same patterns. It is now necessary to explicitly determine the geographic distributions of rare and significant ecological interactions; see Real *et al.* (2009) for such an example. In the case of the island fox, the species is both endangered and endemic, but harbors no specialist ectoparasites to our knowledge. In other words, losing the island fox does not obviously result in a subsequent extinction of an affiliated ectoparasite (i.e., co-extinction, Koh *et al.* 2004). However, we argue that unique species interactions may be lost with the extirpation of endemic hosts and this consequence warrants more attention from the conservation community. It is naïve to assume no consequence of losing such interactions. One plausible outcome that may result from the loss of a host is that additional risks are accrued by the remaining hosts. Furthermore, the growing evidence suggests that maintaining species interactions is necessary for the health of ecosystems (Hudson *et al.* 2006; Lyons *et al.* 2005). As the disciplines of conservation biology and biogeography continue to merge (Whittaker *et al.* 2005) and we expand our traditional single species concepts to encompass species interactions (Araujo & Luoto 2007),

it is perhaps also necessary to redefine metrics of conservation success. In revisiting Thompson's (1999) plea calling for greater conservation of interaction diversity, we too, advocate efforts that maintain ecological relationships to ensure that promoting processes in our environment remain.

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Table 4.1 Summary statistics for ectoparasite species detected on three endangered island fox populations. Prevalence is the proportion of individuals infected of the total number of individuals sampled. Mean intensity is the average number of parasite individuals sampled on infected hosts. Shaded boxes indicate no ectoparasite of that species was detected and na indicates insufficient sample sizes to calculate population attributes. Asterisk indicates significant differences among island fox populations (P value = 0.000) in prevalence and mean intensity using chi-square test and multivariate analysis of variance, respectively.

Parasite species	San Miguel Island		Santa Rosa Island		Santa Catalina Island	
	Prevalence (95% CI)	Mean load (95% CI)	Prevalence (95% CI)	Mean load (95% CI)	Prevalence (95% CI)	Mean load (95% CI)
Louse						
<i>Neotrichodectes mephitidis</i> *	0.27 (0.18-0.37)	6.32 (4.55-8.50)	0.01 (0.01-0.07)	na	0.31 (0.21-0.43)	18.82 (5.64-64.82)
Flea						
<i>Opisodasys nesiotus</i> *	0.02 (0.00-0.08)	na				
<i>Pulex sp.</i> *			0.92 (0.84-0.97)	16.92 (13.49-21.38)	0.01 (0.00-0.07)	na
<i>Malareus telchinum</i>			0.05 (0.02-0.12)	na	0.01 (0.00-0.07)	na
<i>Echidnophaga gallinacea</i> *			0.15 (0.09-0.25)	3.83 (2.67-5.25)		
<i>Oropsylla montana</i>					0.01 (0.00-0.07)	na
Tick						
<i>Ixodes pacificus</i> *			0.43 (0.32-0.54)	5.79 (4.59-7.21)	0.74 (0.63-0.83)	2.32 (1.91-2.81)
<i>Ixodes kingi</i>			0.01 (0.00-0.07)	na		
<i>Ixodes rugosus</i>			0.05 (0.02-0.13)	na		
Overall*	0.29 (0.20-0.40)	5.88 (4.21-8.00)	0.92 (0.84-0.97)	20.38 (16.14-25.56)	0.76 (0.65-0.85)	9.82 (4.42-28.15)

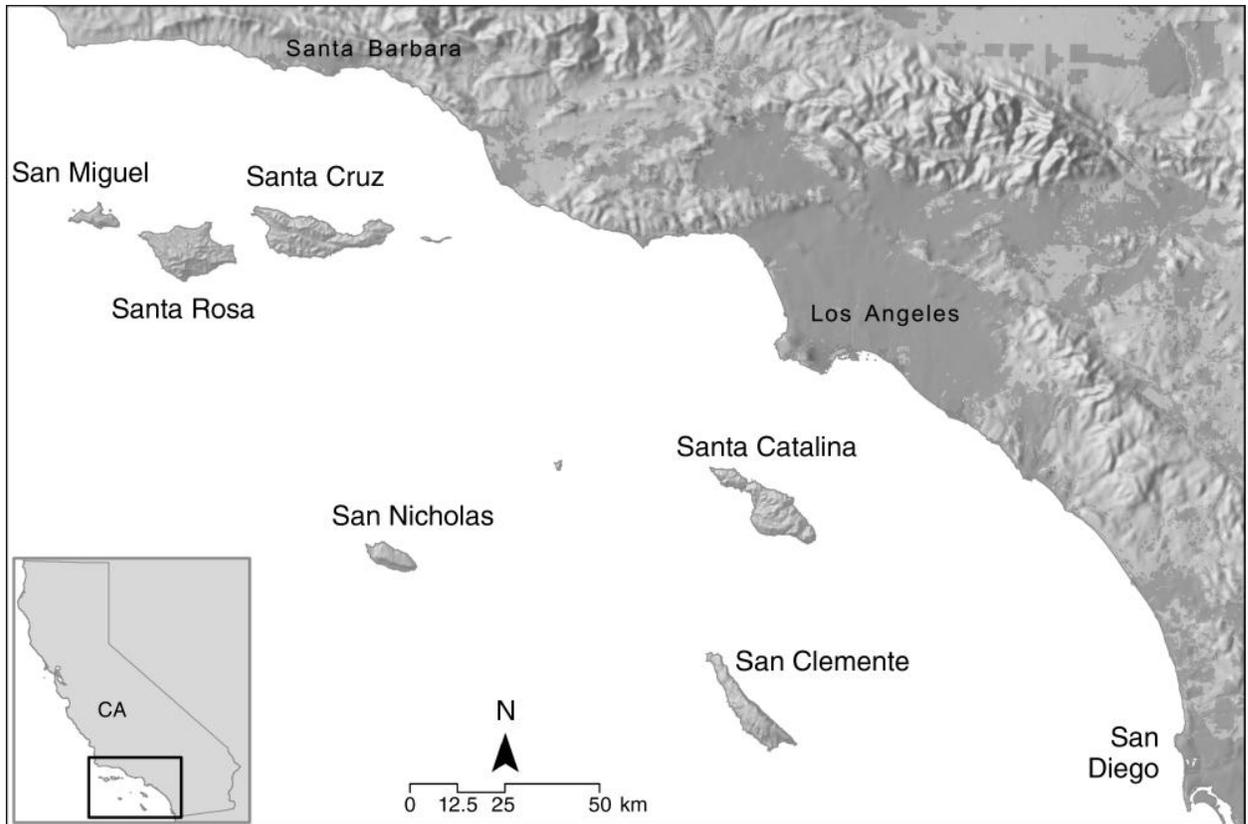


Figure 4.1 Channel Islands. Populations from which island foxes were sampled for ectoparasites during this study, July-September 2009 included San Miguel, Santa Rosa, and Santa Catalina. From Bakker and Doak (2009).

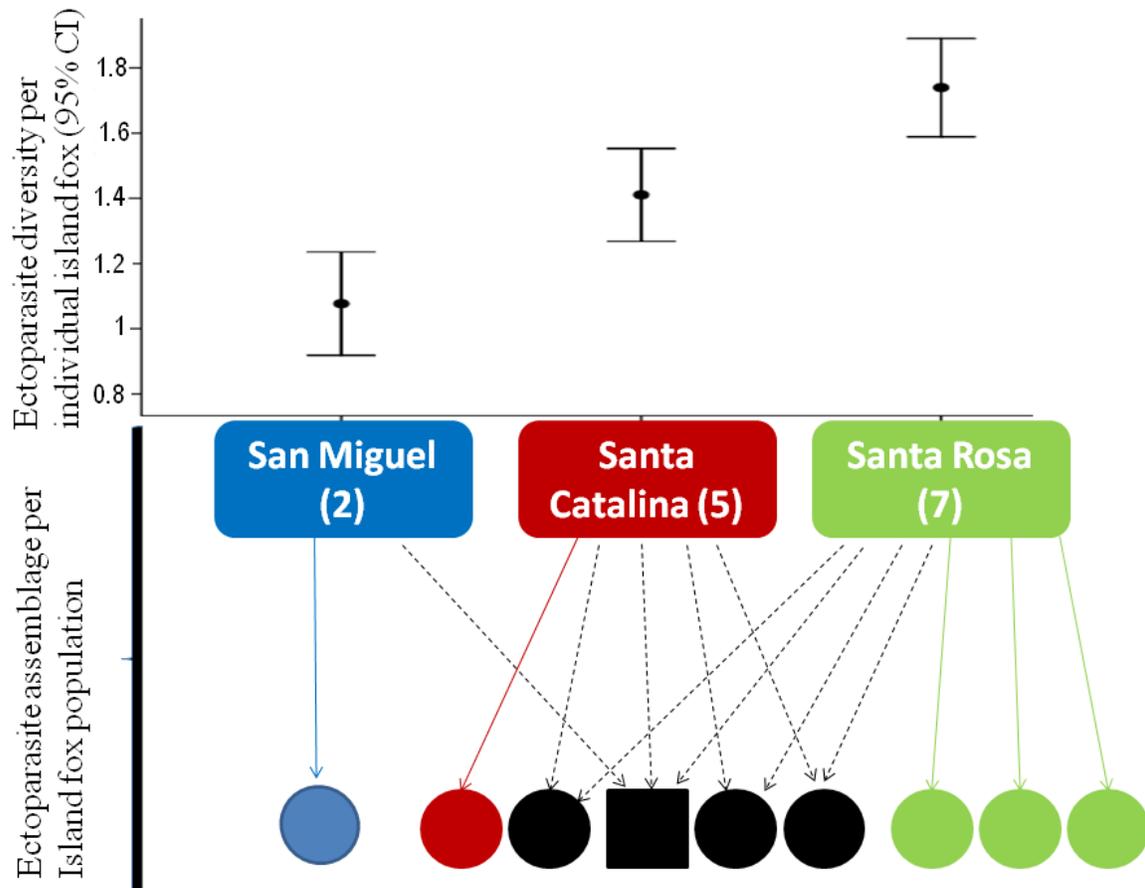


Figure 4.2 Variation in ectoparasite diversity and assemblage among island fox populations. Number in parenthesis is the total number of ectoparasite species reported. Black circles represent species present on more than one population. Color circles indicate unique host-parasite interactions corresponding to the respective colored island fox populations. The black square represents the only ectoparasite species found in all three island fox populations, the louse *Neotrichodectes mephitidis*.

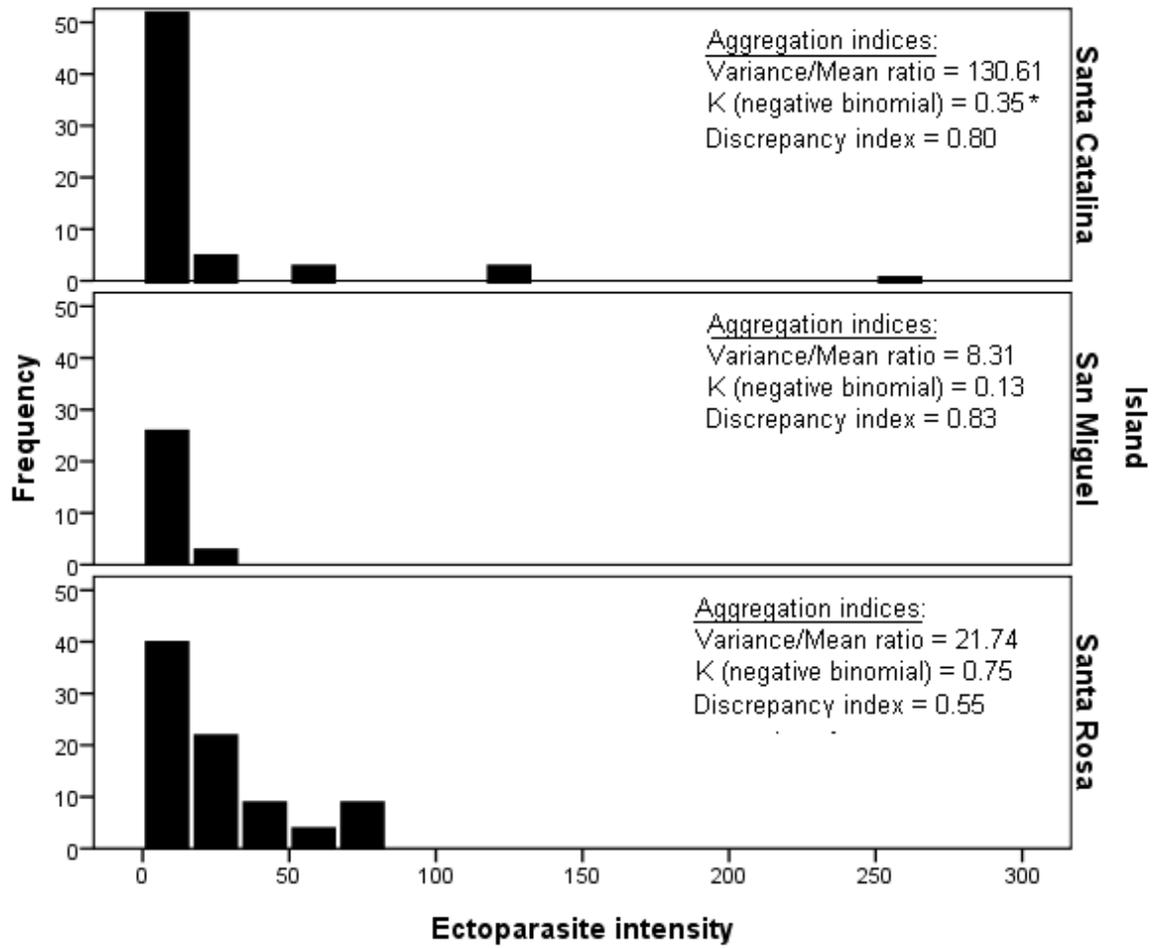


Figure 4.3 Distributions of ectoparasite intensity measured as the total number of ectoparasites per infected host individuals among Island fox populations. Three aggregation indices were calculated. High variance/mean ratios, k values close to 0, and D values close to 1 indicated aggregation.

Canonical Discriminant Functions

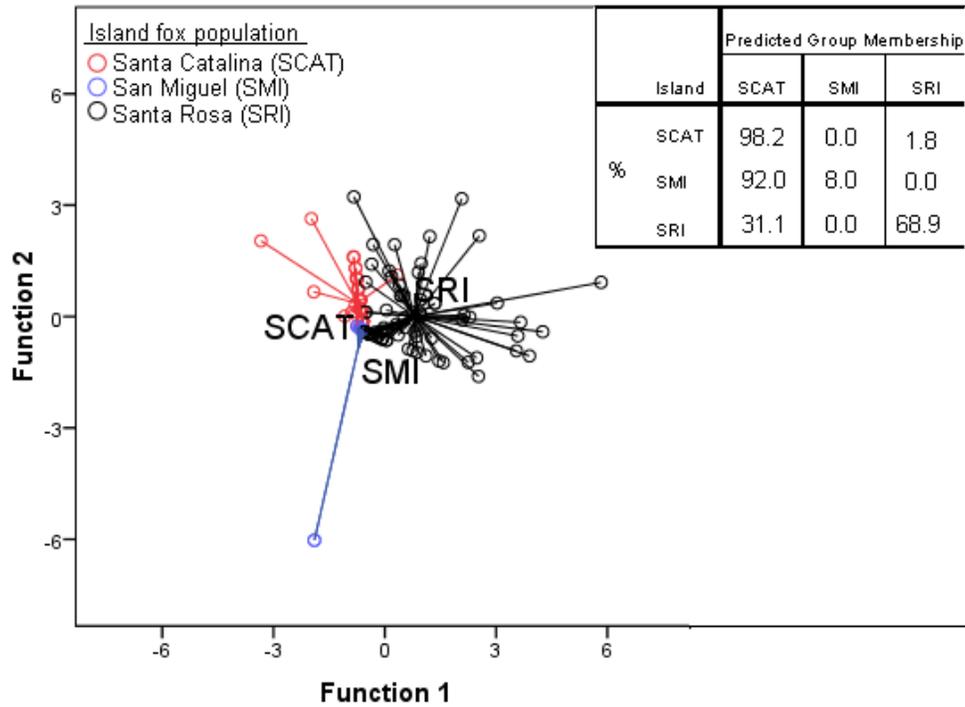


Figure 4.4 Discriminate function analysis assigning Island fox individuals to discrete populations based on intensity estimates of ectoparasite species present. 70% of individuals were correctly classified with most of the error occurring in San Miguel individuals where only 2 ectoparasite species were reported.