

Host Breadth of Parasites in Ungulates and Carnivores

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Introduction

Most parasites infect multiple hosts. These include 60% of human parasites and 80% of domestic animal parasites and are thus a threat to both human health and wildlife conservation efforts (Pedersen et al. 2005). While many studies have focused on the parasite species richness of hosts, or the parasite species that share host populations (Poulin 1998), few studies have focused on characteristics of hosts and parasites that may cause differences in the host breadth. Here we investigate two facets of host breadth: variation in the number of host species different parasite species infect and the similarity of parasite communities among host species (i.e., overlap in the parasite species that infect different pairs of host species). We first test for the effects of parasite transmission mode and taxonomic identity on host breadth among parasites of ungulates and carnivores using a number of definitions of host breadth, and using several methods to try and correct for differences in sampling effort among parasite species. We next investigate the effect of phylogenetic distance, differences in mass, and the geographic overlap among ungulate host species on parasite community similarity between hosts. Finally, we explore the effect of trophic relationships among hosts on parasite overlap, testing to see whether carnivore species that prey on ungulates are infected by more parasite species of ungulates than carnivores that specialize on different prey items.

Materials and Methods: Host Breadth

- The Global Mammal Parasite Database (<http://www.mammalparasites.org/>) was updated to modern parasite taxonomy using the NCBI Taxonomy Database and the ICTV Viral Taxonomy Database. Data was also collected on the transmission modes of all parasites using various literature and web sources.
- Raw host breadth was recorded as the number of host species each parasite infects. Raw host breadth may underestimate the number of host species that a parasite can infect if the parasite has not been thoroughly studied, so the number of citations in the WOS Database were recorded for each parasite species. Residuals of a regression of raw host breadth on number of WOS citations were then calculated in R. The nonparametric Chao 2 and Jackknife estimators were also calculated for all parasites that infect two or more host species (Poulin 1998, Huang et al. 2014).
- Host phylogeny may play an important role in host breadth of parasites, since more closely related host species presumably have more similar ecological characteristics and immune responses. We therefore also explored variation in host breadth defined as the total phylogenetic diversity of hosts infected by a parasite species as well as the maximum phylogenetic distance between any two hosts. These measures were calculated using a published super-tree of all mammals (Bininda-Emonds et al. 2007) with the ape package in R.
- A Wilcoxon Rank Sum Test in R was used to evaluate correlations between parasite type, as well as transmission mode, and various estimates of host breadth.
- Parasite host breadth calculations were performed for 118 ungulate species and the 933 parasites that infect them (resulting in 2553 host-parasite pairs) as well as 156 carnivore species and the 827 parasites that infect them (resulting in 2940 host-parasite pairs).

Materials and Methods: Parasite Overlap Among Host Species

- We calculated parasite overlap for each pair of ungulate hosts species using Jaccard's index and the corrected Jaccard's index (Huang et al. 2014).
- We then used a GAM (Generalized Additive Model) model in R to test the correlation between parasite community similarity and mass differences, area overlap, and phylogenetic distance among host species.
- Preliminary results showed that viruses generally infect significantly more hosts than other types of parasites. We therefore repeated our analyses of community similarity using only viruses.
- We recorded whether or not each carnivore species in the GMPD preyed on ungulates based on several primary literature sources and determined how many parasites known to infect ungulates each of these carnivores species can be infected by based on GMPD records. We then tested the correlation between presence or absence of ungulate prey and the number of ungulate parasites that infect each carnivore species using a Wilcoxon Rank Sum Test in R.



Results and Discussion: Host Breadth

- When we considered all ungulate parasites, we found that viruses and sexually transmitted parasites infect significantly more hosts than other types of parasites regardless of the estimate of host breadth considered (Table 1).
- When we only considered ungulate parasites with at least two hosts, we found that viruses and vertically transmitted parasites infect significantly more hosts than other types of parasites regardless of the estimate of host breadth considered (Table 1).
- When we only considered carnivore parasites with two or more hosts, we found that parasites transmitted via feces infect significantly more hosts than other types of parasites regardless of the estimate of host breadth considered (Table 1).
- No other predictor variables showed consistent significant correlations with estimates of host breadth.

	Reported Host Breadth	Host Breadth Residuals	Chao 2	Jackknife	Phylogenetic Diversity	Maximum Phylogenetic Distance
Parasite Type						
Bacteria	>	⊗⊕>	⊕>	⊕>	⊕⊕	⊕⊕
Virus	⊗⊕⊕>	⊗⊕>	⊗⊕⊕>	⊗⊕⊕>	⊗⊕⊕	⊗⊕
Arthropod	NS	NS	NS	NS	⊗⊕	⊗⊕⊕>
Helminth	⊗	⊗	NS	NS	⊗⊕⊕>	⊗⊕⊕>
Protozoa	⊗⊕	⊗⊕	NS	NS	⊕>	⊕
Transmission Mode						
Close	⊗	⊗	NS	NS	NS	NS
Sexual	⊗⊕	⊗⊕	⊗⊕⊕	⊗⊕⊕	⊗	⊗
Vertical	⊕⊕	⊕⊕	⊕	⊕	⊕	⊕
Close Nonsexual	⊗	⊗	NS	NS	NS	NS
Nonclose	⊗	⊕	⊕	⊕	⊕	⊕
Environmental	⊗	⊗⊕	NS	NS	NS	⊕>
Soil	NS	⊗	NS	NS	NS	NS
Water	⊗	⊗	NS	NS	⊕	NS
Feces	⊗>	⊗>	>	>	⊕⊕>	⊕>
Vector	⊕>	>	>	>	⊗⊕	NS
Intermediate	⊗	⊗⊕	NS	NS	>	>

Table 1. Results of Wilcoxon Rank Sum Test on ungulate parasites. NS indicates a nonsignificant value, ⊗ indicates a p value of 0.05 or less when considering all ungulate parasites, ⊕ indicates a p value of 0.05 or less when considering ungulate parasites with two or more hosts. ⊕ indicates a p value of 0.05 or less when considering all carnivore parasites. > indicates a p value of 0.05 or less when considering carnivore parasites with two or more hosts.

Acknowledgements

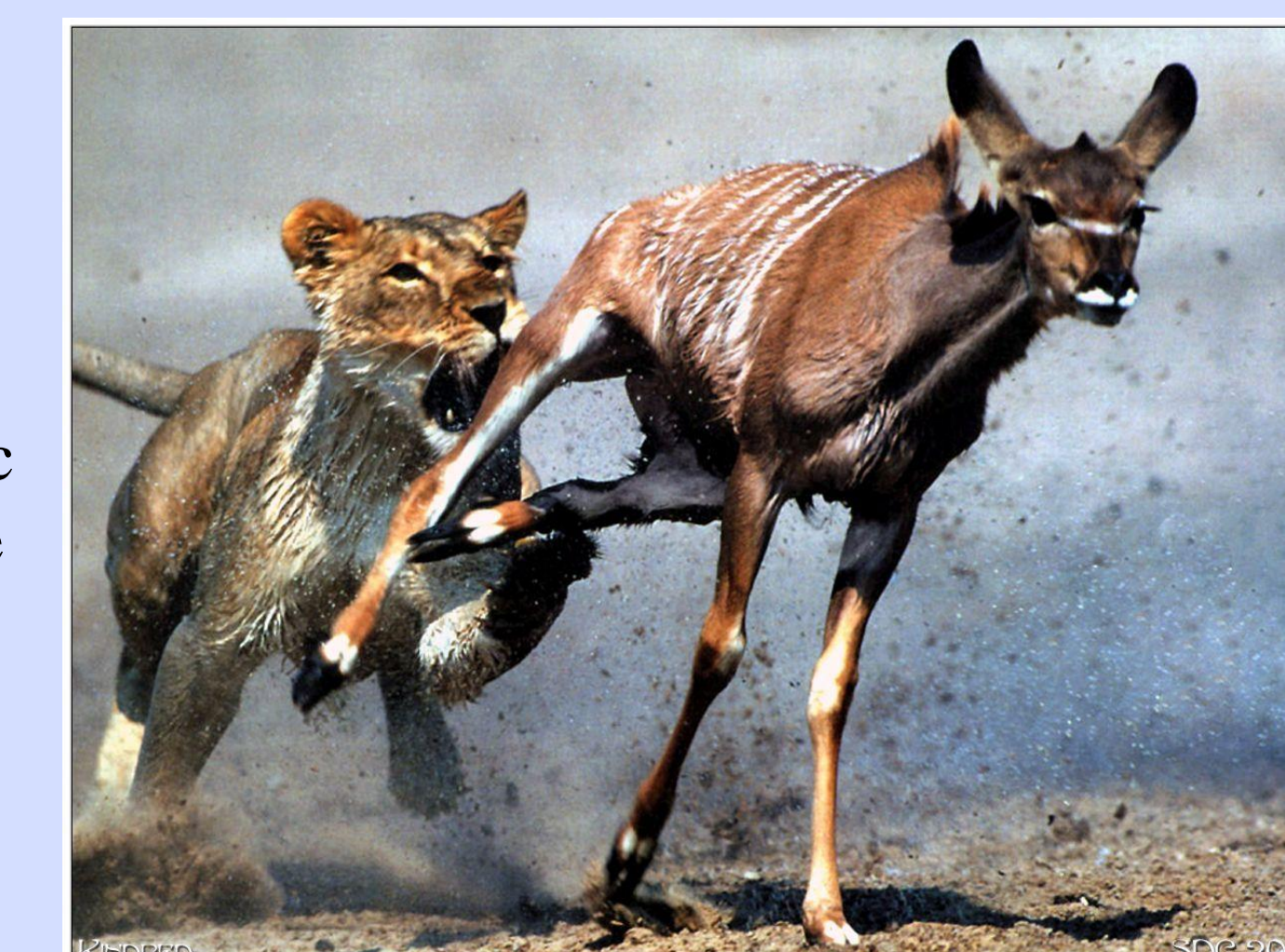
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Results and Discussion: Parasite Overlap Among Host Species

- When considering all ungulate parasites, we found a significant association between community overlap and mass, phylogenetic distance, and range area overlap. However, we found that phylogenetic distance and range area overlap were much stronger predictors of overlap than mass (Table 2). Our results were almost identical for viruses, save that mass was an even weaker predictor of overlap.
- We found that the relationship between phylogenetic distance and parasite community overlap is negative and the relationship between range area overlap and parasite community overlap is positive (Fig. 1).
- We found that carnivore species that prey upon ungulates were infected by significantly more ungulate parasites than carnivore species that specialize on other prey. Carnivores that prey upon ungulates were infected by on average twice as many ungulate parasites than non-ungulate carnivores.



	Overlap		Relationship	Corrected Overlap		Relationship
	F	p		F	p	
Mass (log)	12.32	0.000452	positive	11.48	0.000709	positive
Distance	31.74	2.00E-16	negative	40.88	2.00E-16	negative
Area (Percent)	120.83	2.00E-16	positive	101.15	2.00E-16	positive

Table 2. Results of GAM model analysis of Overlap and Corrected Overlap using Jaccard's index versus mass of ungulate, phylogenetic distance between species, and percent of shared geographic area.

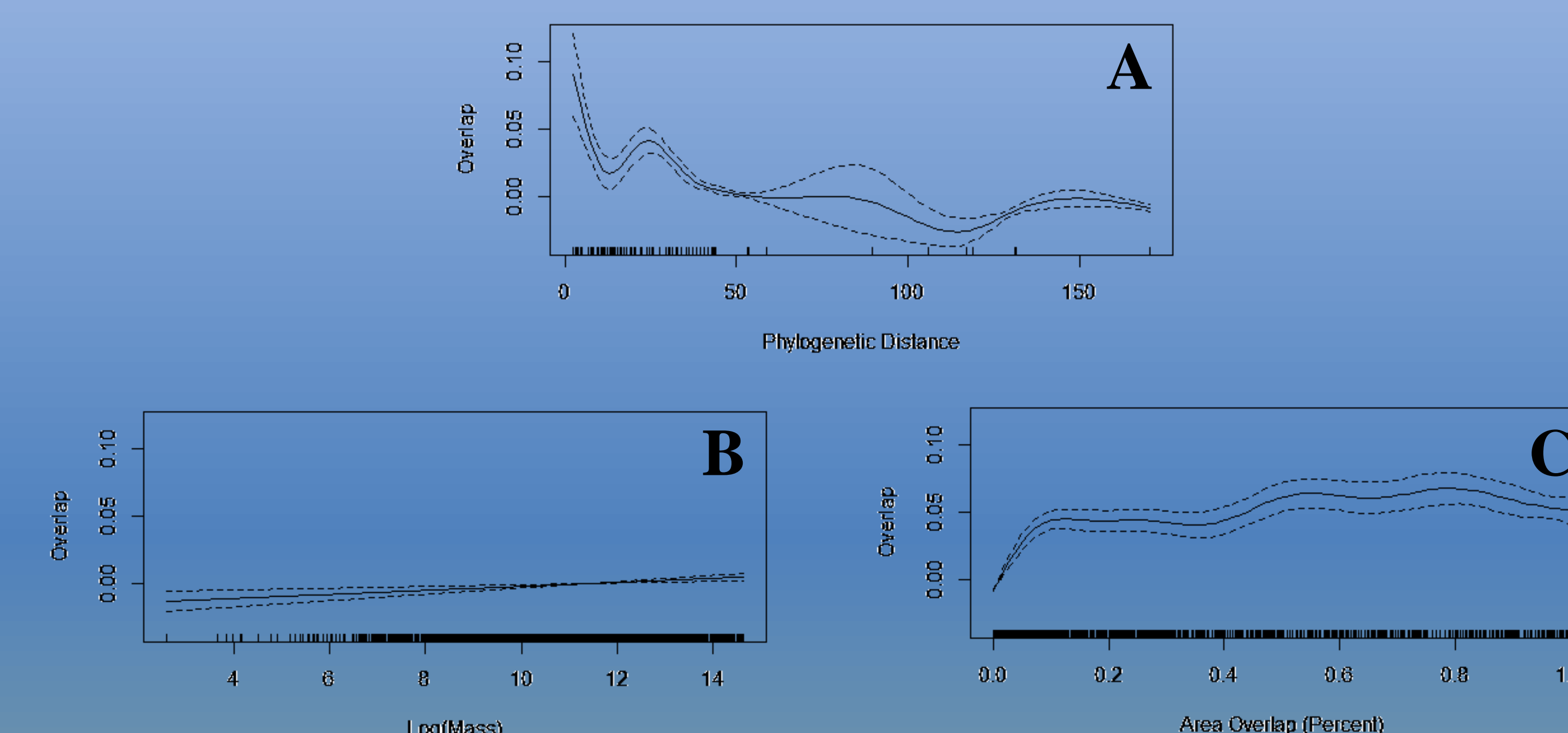


Figure 1. Results of GAM test on Parasite Community Similarity. (A) compares phylogenetic distance of hosts with parasite community similarity, (B) compares the log difference between masses of hosts and parasite community similarity, (C) compares geographic overlap between hosts as a percent of total host area with parasite community similarity. Similar graphs were found using corrected parasite community overlap and only using viruses.