

## Introduction

Parasite species richness (PSR) and the impact of parasites is of great importance in ungulates, as it can affect ungulate survival and fecundity, as well as population dynamics (Enzenwa et al, 2006). Previous studies have considered 7 host traits and their impact on PSR in ungulates, and included analyses for distinct groups of parasites (Enzenwa et al, 2006). This project takes the analysis a step further and considers 20 additional host traits as well as geographic information from the host ranges (e.g., longitudinal and latitudinal midpoints of host ranges). We also investigate whether the correlates of PSR differ among parasites with different transmission modes. Finally, this work includes three new estimators of PSR that were used in addition to residuals of regression for the 22 best-studied host species, and uses a more fully resolved ungulate tree for phylogenetic analysis than was available for previous analyses.



## Materials and methods

### Updating the Phylogeny of Ungulates

In order to study the influence of phylogeny on parasite species richness, the phylogenetic tree of the ungulates from the Bininda–Emmonds et al (2007) supertree was updated using data from two sources. Most of the Cervid relationships were resolved by Pitra et al (2004), and Mesquite was used to alter the ungulate tree by hand to reflect their results. Petra et al included only a single species of *Muntiacus* in their analysis. Additional genetic analysis was required to understand the *Muntiacus* genus and the placement of its species in the tree.

Genetic analysis of the *Muntiacus* genus used the ND4L, 16S, and Cyt B gene sequences available for all but one species of *Muntiacus* in Genbank. The sequences were aligned in Se-AL, and RaxML was used to conduct a maximum likelihood analysis of the sequences using one model partition per gene. The resulting, fully resolved, *Muntiacus* phylogeny was used in Mesquite to further detail the Cervidae tree, which in turn was used to update the ungulate supertree.

### PSR Estimators

To correct for differences in sampling effort among the host species, the residuals of PSR on sampling effort were calculated in R and used for analysis of variation in PSR in all 115 species. Three non-parametric PSR estimators were also used for the 22 best-studied species, in addition to residuals of regression. These estimators were the Chao 2 estimator - PSR<sub>C</sub> (Poulin 1998, Chao 2005), the Jackknife estimator - PSR<sub>J</sub> (Poulin 1998), and the Bootstrap estimator - PSR<sub>B</sub> (Poulin 1998).

### Parasite Details

A database was updated to include recently discovered parasites and their transmission modes. These details, from numerous literature and internet sources, were used to determine if correlates of PSR are influenced by parasite type or the mode of transmission. Parasite types used in analysis included Arthropods, Bacteria, Helminths, Protozoa, and Viruses. In studying transmission mode, vector-born parasites and parasites transmitted through close contact or nonclose (environmental) contact were considered.

### Details of Host Traits

Data on a large variety of host traits were obtained primarily from a published species-level database of mammalian traits (PanTHERIA)

### Data Analysis

Preliminary bivariate analysis on host traits' effect on PSR was conducted using residuals of regression for all 115 species in the study. Residuals of regression and the three other non-parametric PSR estimators were used for the 22 best-studied species in the study.

## Materials and methods, cont'd

This analysis was performed in R using Pearson's product-moment correlation for normally-distributed data and Spearman's rank correlation for non-normal data. For the effects on parasite type and transmission mode, preliminary bivariate analysis was conducted using residuals of regression for all species that recorded that parasite type or that mode of parasite transmission. For these analyses, Spearman's rank correlation method was used in R.

Traits found to be significant in these analyses were used in the final, multivariate analysis. Multivariate analysis utilized the R package Caper to perform two sets of phylogenetically informed multivariate analyses of the predictor variables that showed significant correlations in bivariate analyses.

Preliminary analyses showed that latitude and longitude were consistently correlated with PSR estimates. We therefore used geographic midrange longitude and latitude of host species, to create a map in ArcGIS. Residuals of regression were used to graduate colored points to visualize the location and estimated PSR of each host.



Figure 1: ArcGIS map showing host midrange. Colored points range from light pink and low PSR to purple and high PSR.

	Activity Cycle	Mass spec Prod	Gestation Length	Litter Size	Max Longevity	Neonate Body Mass	Teat Number	Weaning Body Mass	Geographic Area	Brain Residuals	PGLS	Crunch
Bacteria	NS	NS	NS	❖❖	NS	NS	❖	NS	❖❖	NS	0.30 ❖	0.32 ❖
Arthropod	NS	NS	NS	❖❖	NS	NS	NS	NS	NS	NS	0.04 NS	0 NS
Protozoa	NS	❖	NS	NS	NS	NS	NS	❖	❖	❖	0.32 ❖	0.14 NS
Helminth	❖❖	NS	NS	❖❖	❖❖	NS	NS	NS	❖	❖	0.32 ❖❖	0.24 ❖
Virus	NS	NS	❖	❖	NS	❖	NS	NS	NS	NS	0.28 ❖❖	0.1 NS
Vector	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NA	NA
Close	NS	NS	NS	❖	NS	NS	NS	NS	NS	NS	0.13 ❖❖	0.13 ❖❖
Nonclose	❖❖	NS	NS	❖❖	❖	NS	NS	NS	NS	NS	0.23 ❖❖	0.26 ❖❖

Table 2: Correlates of PSR for parasites of differing types and transmission modes, as well as results from phylogenetically-informed multivariate analyses. NS legend indicates a non-significant value, while ❖❖ indicates a P-value less than 0.01 and ❖ indicates a P-value of less than 0.05.

## Results and Conclusion

In analyses of host traits, litter size was found to generally influence PSR regardless of the PSR estimator used, type of parasite, or parasite transmission mode. In analyses of all other species traits, results varied depending on PSR measures and parasite type considered (Table 1, Table 2). Phylogenetically informed multivariate analyses in general explained roughly 20% of the variation in PSR for parasites of a particular type or transmission mode, and roughly 50% of variation in PSR overall. Geographic data, such as longitude and latitude, temperature, rainfall, and human population density also influenced PSR (Table 1, Fig. 1). Future work will focus on using spatially explicit models to determine whether these results simply reflect spatial autocorrelation or the direct influence of environmental variables and anthropogenic factors on PSR.

	Residuals	Residuals Best Studied	PSR <sub>B</sub>	PSR <sub>J</sub>	Chao <sub>2</sub>
Activity Cycle	NS	❖❖	NS	NS	NS
BMR/BMRM	❖	NS	NS	NS	NS
Litter Size	❖❖	❖❖	NS	NS	NS
Max Longevity	NS	NS	NS	NS	NS
Neonate Head Body Length	❖	NS	NS	NS	NS
Sexual Maturity Age	NS	NS	❖	❖	NS
Weaning Age	NS	NS	❖	NS	NS
Geographic Range Area	NS	❖❖	NS	NS	❖
Max Latitude	❖❖	❖❖	NS	NS	NS
Min Latitude	❖❖	❖	NS	NS	NS
Mid-Range Latitude	❖❖	❖❖	NS	NS	NS
Min Longitude	NS	❖❖	NS	❖	NS
Human Pop. Density Mean	NS	NS	❖	❖❖	❖❖
Human Pop. Density Change	❖❖	❖	NS	NS	NS
Temp. Mean	NS	❖	NS	NS	NS
AET Mean	NS	NS	NS	NS	NS
PET Mean	NS	❖❖	NS	NS	NS
PGLS	0.21 ❖❖	0.89 NS	0.58 ❖❖	0.60 ❖❖	0.31 ❖
Crunch	0.10 NS	0.93 ❖	0.40 NS	0.39 ❖	0.28 NS

Table 1: Correlates of PSR in ungulates, and results of phylogenetically-informed multivariate analyses. NS legend indicates a non-significant value, while ❖❖ indicates a P-value less than 0.01 and ❖ indicates a P-value of less than 0.05.

Species	Threat status	Reported	Potentially Endemic	Residuals
Axis porcinus	E	2	0	76.322
Equus caballus	E	35	7	577.337
Equus grevyi	E	13	4	-46.672
Gazella spekei	E	3	0	58.686
Tapirus indicus	E	1	0	113.958
Addax nasomaculatus	CE	2	0	93.322
Diceros bicornis	CE	71	17	-491.555
Equus asinus	CE	34	2	-40.026
Saiga tatarica	CE	15	4	-47.944

Table 3: Threat status (Endangered – E, Critically Endangered – CE) of 9 host species and reported parasite species. Potentially endemic parasites within endangered hosts are also in danger of extinction.



## Acknowledgements

This project was done thanks to the Population Biology of Infectious Diseases, Research Experience for Undergraduates, program. Special thanks to the administrators, research mentors, and other participants of this REU program.

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