OIKOS 115: 526–536, 2006

Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla

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Ezenwa, V. O., Price, S. A., Altizer, S., Vitone, N. D. and Cook, K. C. 2006. Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. – Oikos 115: 526–536.

Host social, ecological and life history traits are predicted to influence both parasite establishment within host species and the distribution of parasites among host species. Yet only a few studies have investigated the role multiple host traits play in determining patterns of infection across diverse parasite groups. To explore the association between host traits and parasite species richness (PSR), we assembled a comprehensive database encompassing 601 parasites (including viruses, bacteria, protozoa, helminths and arthropods) reported to infect 96 species from two well-studied and diverse host clades: even- and odd-toed hoofed mammals (Artiodactyla and Perissodactyla). Comparative analyses were used to examine associations between three sets of host variables (life history and body mass, social and mating behavior, and ecological traits) and PSR for all parasites combined and for distinct parasite sub-groups. Results from a combination of phylogenetic and non-phylogenetic tests showed that PSR increased with host body size across all parasites groups. Counter to expectations, measures of parasite diversity decreased with host longevity and social group size, and associations between group size and PSR further depended on the underlying mating system of the host species. Our results suggest that body mass, longevity, and social organization influence the diversity and types of parasites reported to infect wild populations of hoofed mammals, and that multiple host and parasite traits can combine in unexpected ways to shape observed patterns.

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Identifying factors that determine parasite distributions in wild animal populations has basic and applied importance, in part because parasites can have pronounced impacts on the survival, fecundity and population dynamics of their hosts (Gulland 1992, Hudson et al. 1998, Swinton et al. 1998, Tompkins and Begon 1999, Albon et al. 2002). Widespread heterogeneities in parasite infection rates suggest that not all animals are vulnerable to the same number or types of parasites (Wilson et al. 2002), and observed differences in parasite diversity are likely a consequence of host characteristics, parasite characteristics, or both. Host traits that increase parasite establishment and spread within populations should also influence the types and diversity of parasite species that persist across host species (Morand 2000, Roberts et al. 2002). Yet the primary determinants of parasite diversity in natural host communities remain largely unknown, in large part because few studies have

Accepted 17 July 2006
Subject Editor: Michael Bonsall

ISSN 0030-1299

simultaneously considered the multitude of factors affecting parasite species richness (Gregory 1997, Morand 2000). Comprehensive approaches for examining large-scale patterns of parasite diversity in wild host populations typically require data on a diverse array of traits for multiple host species, knowledge of host phylogeny, and data on the occurrence of large numbers of parasite species. Because these data are generally not widely available or easily collated, most studies of parasite diversity have tended to focus on a relatively narrow range of hosts, parasites, or explanatory variables.

In this study, we examined the degree to which host traits were associated with patterns of parasite species richness (PSR) across 96 species of Artio- and Perissodactyla (also called even- and odd-toed hoofed mammals). These two well-studied and globally-distributed host orders capture a broad range of biological characteristics including variation in body size, social and mating systems, and life history traits. Furthermore, due to their close evolutionary relationships with domesticated livestock (e.g. cattle, swine, sheep, goats and camels), a large number of parasites and pathogens have been described from hosts in these two clades. As a consequence, we were able to collate an extensive dataset encompassing helminths, arthropods, bacteria, protozoa and viruses reported from free-living populations. By combining data on host biology with information on parasites, we tested a series of hypotheses focused on three sets of host traits that are widely predicted to influence parasite richness: body size and life history traits, traits determining rates of social contact, and traits associated with habitat use (Poulin and Rohde 1997, Morand 2000, Nunn et al. 2003, reviewed by Poulin 1997, Poulin and Morand 2000).

Island biogeography theory predicts that larger-bodied hosts represent larger habitat patches and provide a wider variety of niches to support more parasite species (Price 1980, Kuris et al. 1980). Indeed, PSR has been shown to increase with host body size across a range of birds, mammals and fish (Gregory et al. 1991, 1996, Sasal and Morand 1998, Nunn et al. 2003, Vitone et al. 2004), thus we expected a positive association between host body mass and PSR. In mammals, body mass is also correlated with host life history, leading to difficulties in testing the independent effects of these two sets of variables (Morand and Harvey 2000, Nunn et al. 2003). For example, larger-bodied hosts also tend to live longer and could encounter more parasites throughout their lifetimes (Pacala and Dobson 1988, Bell and Burt 1991). In addition, traits related to host reproduction that co-vary with body size, including age at first birth, gestation length and litter size, could further influence the numbers of susceptible hosts required for many parasites to establish and persist. We tested associations between three host life history traits and PSR: longevity, gestation length and litter size. We expected longer-lived hosts and hosts with higher reproductive rates (larger litter sizes and shorter gestation periods) to harbor more parasite species.

The rate of contact between hosts is considered to be one of the most important epidemiological parameters influencing parasite spread (Anderson and May 1979, 1991), and traits that increase host proximity and contact rates should positively influence parasite species richness (reviewed by Altizer et al. 2003). Specifically, local population density and social group size can increase rates of between-host contact, therefore we expected a positive correlation between PSR and host group size and population density. Although several studies have reported significant positive associations between host population density or group size and PSR (Morand et al. 2000, Nunn et al. 2003, Vitone et al. 2004), analyses failing to find any links between one or both of these traits and PSR are also common (Gregory 1990, Nunn et al. 2003). In addition, negative associations between group-living and parasite diversity have been reported in some cases (Ranta 1992, Watve and Sukumar 1995), suggesting that rates of inter-group contact and correlations between group size and other aspects of host social or mating systems are important determinants of parasite occurrence. For this reason, we also examined potential interactions between host social group size, mating system and PSR.

Finally, host traits associated with habitat use can also influence the diversity of parasites that hosts encounter in their environments. For example, hosts that occupy larger home ranges and use a wider diversity of habitats may encounter more parasites than relatively sedentary hosts (Price and Clancy 1983, Gregory 1990, Nunn et al. 2003). As such, we tested associations between host home range size and PSR, predicting higher parasite species richness among hosts using larger home ranges.

To test the predictions outlined above, we used both non-phylogenetic and phylogenetically-controlled comparative analyses to examine patterns of parasite richness in relation to seven distinct host traits: body mass, longevity, gestation length, litter size, population density, social group size, home range size. We used a multivariate statistical approach to explore the independent effects of each of the host traits on PSR while controlling for confounding and inter-correlated factors. In addition, we ran analyses across the entire range of parasites as well as within distinct parasite taxonomic groups to further understand how interactions between host and parasite characteristics shape parasite distributions in free-living populations.

Material and methods

Parasite data

We compiled a comprehensive database of the parasites and pathogens of free-living artio- and perissodactyl species using reports from the published literature. Parasites were broadly defined to include microbial pathogens such as viruses and bacteria, and metazoan parasites such as nematodes and arthropods. To locate published references documenting host–parasite records, we used the Latin binomials for 230 host species representing 13 families (as reported in Wilson and Reeder 1993) combined with a string of parasite-related terms (parasite, pathogen, disease, infection, arthropod, bacteria, helminth, fungi, protozoa, vector or virus) as search keywords in two major online reference databases (Biosis and Web of Science). We also searched by host genus name and common synonyms or taxonomic variants of host species names based on Wilson and Reeder (1993) and Nowak (1999). Parasite data were generally available from three main sources of published information: surveys that documented multiple parasite species from wild populations, epidemiological studies focusing on one or a few specific parasites, and museum reports documenting new parasite species or revised parasite taxonomies. In total, data were drawn from 584 papers published between 1981 and 2002 to compile the host–parasite dataset. A version of this data set is available online at www.mammalparasites.org.

For each parasite reported from a wild host population, we recorded the host Latin binomial, the type of parasite (arthropod, bacteria, fungi, helminth, protozoa, prion, virus), the parasite genus and species names, the number of hosts sampled, location and year of sampling, whether the host population was managed or unmanaged, and the bibliographic reference. For parasitic arthropods, we included only species reported to live on or in the host for at least part of the life cycle (e.g. botflies, ticks, mites, lice) and excluded micropredators (e.g. mosquitoes, biting flies). Prior to analysis, data were screened to include only parasites reported from unmanaged populations of non-domesticated host species sampled from within their native range (following Wilson and Reeder 1993). Thus, we excluded host–parasite records from all captive populations, and records from 11 major domesticated lineages including *Ovis aries*, *Bos taurus*, *Capra hircus*, *Sus scrofa*, *Equus caballus*, *Equus asinus*, *Bubalis bubalis*, *Camelus dromedarius*, *Camelus bactrianus*, *Llama glama* and *Llama pacos* (Clutton-Brock 1999). For semi-domesticated lineages such as *Bos grunniens*, *Bos frontalis* and *Rangifer tarandus*, we only included host–parasite records for unmanaged populations. We combined data from perissodactyls and artiodactyls for the purposes of analysis based on the assumption of a sister-taxon relationship between the two orders (Bininda-Emonds et al., unpubl., Madsen et al. 2001, Murphy et al. 2001).

Parasite species richness was calculated as the $\log_{10}(x+1)$ transformed value of the number of parasite species reported from each individual host species. This measure was calculated for all parasite groups combined (total PSR), and was also repeated to obtain measures for helminth PSR, arthropod PSR, and for bacteria, viruses and protozoa combined (microparasite PSR). Before computing PSR, we matched and corrected host latin binomials from each published reference to a current taxonomy (Wilson and Reeder 1993). We also verified parasite nomenclature using the International Committee on the Taxonomy of Viruses (ICTV) Database (http://www.ncbi.nlm.nih.gov/ICTVdb/Ictv/) for viruses, and guidelines published by the National Center for Biotechnology Information (NCBI) and various taxonomic authorities for other parasites. Parasites and hosts with clear synonyms were collapsed into a single species. Parasites identified to genus level were included in the analysis only if they represented a unique record for that genus within a given host species.

Controlling for sampling effort

Because uneven sampling effort across host species can influence estimates of PSR (Gregory 1990, Walther et al. 1995), we incorporated information on the degree to which each host species has been studied into all statistical analyses to control for these effects (Poulin 1995, Gregory et al. 1996, Morand and Poulin 1998, Nunn et al. 2003). First, we collated data on the number of published references (on any topic) for each host species by searching for Latin binomials on three major online citation indices, using the full range of years covered to maximize overlap with dates of studies in the parasite dataset: Web of Science (1975 to 2004), Biosis (1985 to 2004) and Zoological Record (1978 to 2004). Since the log-transformed values of these three citation counts were highly correlated (e.g. Pearson's $R_{WOS\text{-}Biosis}=0.979$; Pearson's $R_{WOS\text{-}ZooRecord}=0.967$; $n=96$) we used factor analysis to obtain a composite measure of citation-based sampling effort. The first principal component (hereafter called 'citation-PC') explained 98% of the variance and was positively associated with all three measures (0.994 Biosis, 0.990 WOS, 0.980 ZooRecord). A second estimate of sampling effort was obtained by summing the number of animals across all parasite studies referenced in the database for each host species. For sources that did not report the number of animals sampled, we assigned a default value of five individuals based on the lower 10th percentile mean number of individuals per study, assuming that studies failing to report sample size probably sampled fewer animals. This measure of sampling effort was

significantly correlated with citation-PC (Pearson's $r = 0.714$, $n = 96$, $p < 0.001$), and we repeated all initial analyses using both citation-PC and the number of animals sampled.

Each measure of sampling effort has its strengths and shortcomings. Citation indices control for how well a species has been studied overall, but not necessarily for parasites. Counts of animals sampled summed across multiple studies might over-represent sampling effort in cases where hundreds or thousands of animals were sampled but only for a single parasite species. Nevertheless, when included as covariates in multi-regression models both indices generally produced congruent results. We report detailed statistical results only for analyses using citation-PC, in part because the number of animals sampled generated inconsistent results for a small number of tests during model selection, possibly due to a higher degree of collinearity with other host traits.

Host trait data

We obtained data on host body mass, life history and behavioral traits from a previously compiled comparative database (Cardillo et al. 2005, Jones et al., unpubl.) and supplemented this information using additional references from the primary literature. We examined seven distinct continuous traits: 1) adult body mass; 2) longevity; 3) gestation length; 4) litter size; 5) population density; 6) social group size; and 7) home range size; and also compiled categorical data on host mating system. Information on host trait variables covered between 64–96 species depending on the variable in question (Table 1). All continuous host trait variables were log $(x+1)$ transformed prior to analysis.

Table 1. Sample sizes for host traits used in PSR analyses. For all variables except mating system, data were provided by the PanTHERIA project (Cardillo et al. 2005, Jones et al., unpubl.). Mating system categories were collated by S. Price (unpubl.). Host traits represented by continuous measures or count data were log-transformed prior to analysis.

Host trait	Description	Sample size
Adult body mass	Median of adult males and females in g	96
Longevity	Maximum adult age in months	86
Gestation length	Median length in days	92
Litter size	Median number per litter per female	91
Population density	Median number per km^2	79
Social group size	Median number per group	64
Home range size	Median size of area inhabited by individuals or groups	66
Mating system	Monogamous or polygynous	80

Statistical analysis

Testing for phylogenetic patterns

Closely related host species may share parasite species (Poulin 1995) or show similarities in life history and ecology, leading to phylogenetic patterns in host traits. If so, individual host species might not represent independent sampling units for comparative analysis; and hypothesis testing across species may require phylogenetic comparative methods to reduce the risk of type I errors (Harvey and Pagel 1991). We assessed whether phylogenetic correction was needed for our dataset by calculating Pagel's λ statistic for each measure of PSR and the seven host traits using the software program Continuous (http://www.rubic.rdg.ac.uk/meade/Mark/) (Pagel 1997, 1999). The lambda statistic tests whether a trait is evolving among species as if the species were independent ($\lambda = 0$) by determining if phylogeny correctly predicts patterns of covariance among species. We used a likelihood ratio test to compare the maximum likelihood estimate of lambda for each host trait to a lambda estimate of zero, and assumed phylogenetic patterning when the lambda estimate for a trait was significantly different from zero.

Multivariate analyses of host traits and PSR

We examined associations among host traits, sampling effort and PSR using both phylogenetically controlled tests and non-phylogenetic tests of transformed species values. Independent contrasts to control for host phylogeny (Felsenstein 1985) were calculated using the Ape package (Paradis) of the software program R (http://www.R-project.org) and the topologies of Price et al. (2005) for artiodactyls and Price and Bininda-Emonds (unpubl.) for perissodactyls. Polytomies in the phylogeny were treated as soft (following Purvis and Garland 1993) and the programs for analyzing the data in this way were provided by Andy Purvis and Dave Orme. Branch length information was unavailable and therefore not used.

For all analyses, we used multiple regression (through the origin when using independent contrasts following Garland et al. 1992) with model simplification (Crawley 2002) to test the effects of host traits on measures of PSR. We evaluated the degree of collinearity among predictor variables by checking variance inflation factors (VIF) (Petraitis et al. 1996). Since $VIF < 10$ for all variables ($VIF_{max} = 5.4$), we included all seven continuous predictors and a measure of sampling effort (citation-PC) in all initial regression models. We then reduced these full models to find minimum adequate models following a procedure modified from Crawley (2002). Predictor variables with p-values greater than 0.10 were sequentially deleted from the full model

starting with the variable with the highest p-value, and then model fit was evaluated at each step using the adjusted r^2. For this study, r^2 was preferred over AIC because missing data for some host traits led to changes in sample sizes for different combinations of predictors. If a factor with $p > 0.10$ affected the significance ($\alpha = 0.05$) of another variable it was retained in the final model, and the model with the highest r^2 was considered to be the minimum adequate model. In cases where the r^2 for competing models deviated by $\leq 5\%$, the model with the fewest non-significant terms was selected. Citation-PC was retained in all models to control for the effects of uneven sampling effort across host species.

For additional analyses focusing specifically on social contact and PSR, we used a general linear model (GLM) to test the effects of interactions between host social group size and mating system on parasite species richness. We included citation-PC, group size, mating system, and group size × mating system as factors in each model and used model simplification to find the minimum adequate model that best explained variation in PSR. Only non-phylogenetic analyses were run in this case because the modified version of independent contrasts (as implemented in the program CAIC, Purvis and Rambaut 1995) that we used to analyze discrete traits was not readily combined with the model simplification procedure.

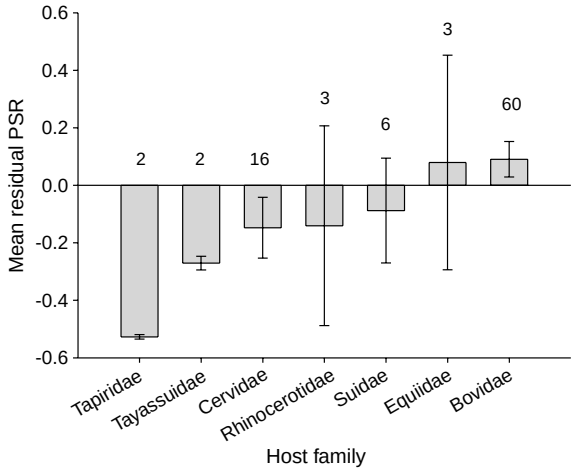

Fig. 1. Corrected measures of PSR (residuals from a regression of PSR on citation-PC as one measure of sampling effort) for the seven host families best represented in the dataset, including Artiodactyla (e.g. Bovidae, Cervidae, Suidae, Tayassuidae) and Perissodactyla (Equidae, Rhinocerotidae, Tapiridae). Numbers above each bar represent the number of host species assigned to each family. Not shown are four host families with only a single species represented, including the Antilocapridae, Camelidae, Giraffidae, and Hippopotomidae. Error bars represent standard errors.

Results

General results

The final host–parasite dataset included 1791 records of parasites infecting 96 host species (8 Perrisodactyla and 88 Artiodactyla) from 11 different families. Among host species, the best represented families included the Bovidae (e.g. small antelope, bison, impala), Cervidae (e.g. moose, elk, caribou, deer) and Suidae (e.g. bushpigs, warthogs; Fig. 1). Additional host families represented in the data set included the Tapiridae (tapirs), Tayassuidae (peccaries), Rhinocerotidae (rhinoceroses), and Equidae (asses and zebras). Among the 601 parasites in the dataset, helminths (primarily roundworms, with a smaller number of tapeworms and flukes) were the best-represented group in terms of both taxonomic diversity and number of records comprising 46% of all parasites reported. These were followed in order by arthropods (primarily ticks, warble flies, lice and mites (25%)), viruses (12%), bacteria (10%) and protozoa (7%).

Before controlling for sampling effort, the distribution of parasites across host species was highly skewed, with most hosts having fewer than 10 parasites, and a few hosts having over 90 parasite species (mean = 19, median = 9 parasite species per host). As expected, we found highly significant associations between the degree to which a host has been studied and the number of parasites reported in the database. Thus, our primary measure of sampling effort, citation-PC, was significantly correlated with all four measures of PSR (total PSR: $r^2 = 0.28$, $t_{1,94} = 5.98$, $p < 0.001$; helminth PSR: $r^2 = 0.15$, $t_{1,94} = 4.05$, $p = 0.001$; arthropod PSR: $r^2 = 0.08$, $t_{1,94} = 2.95$, $p < 0.004$; microparasite PSR: $r^2 = 0.51$, $t_{1,94} = 9.95$, $p < 0.001$). The number of animals sampled was also significantly correlated with all four measures of PSR ($r^2 = 0.51$ to 0.99, $p = 0.01$ to 0.001) and with citation-PC (Pearson's $r = 0.768$, $n = 96$, $p < 0.0001$).

Tests of the correlation between parasite diversity and host phylogeny (λ test) did not provide strong support for measures of PSR being associated among closely related host taxa. Prior to performing this test we controlled for host sampling effort by regressing PSR measures on citation-PC; residuals from this analysis were then used as adjusted measures of PSR. Of the four measures of parasite richness examined (total PSR, helminth PSR, arthropod PSR and microparasite PSR), only microparasite richness was phylogenetically patterned (maximum likelihood estimate of $\lambda = 0.795$, $p = 0.001$). For all other measures of PSR there was no evidence of phylogenetic patterning (maximum likelihood estimate of $\lambda = 0$, $p = 1$). In contrast, tests for the seven host traits indicated that these variables did not evolve independently among species, with all showing some degree of phylogenetic patterning ($\lambda > 0$). Given this variation in the amount of phylogenetic patterning

observed across traits, we reported results from both the non-phylogenetic and independent contrasts analyses.

Host traits and total PSR

When we examined associations between host traits and the richness of all parasite species combined (total PSR), three out of seven traits emerged as significant predictors of parasite species richness in the non-phylogenetic minimum adequate model. Body mass was positively correlated with PSR, and longevity and social group size were significantly negatively correlated with PSR (Table 2). In addition, population density was weakly positively associated with PSR ($p < 0.1$; Table 2). Results of the phylogenetic analysis using independent contrasts were similar to those of the non-phylogenetic analysis. Both body mass and social group size remained significantly correlated with PSR, and longevity was marginally correlated with PSR (Table 2). Gestation length, litter size and home range size did not enter into the final models for phylogenetic or non-phylogenetic tests (Table 2).

Helminth, arthropod and microparasite PSR

In non-phylogenetic tests, four variables entered the final model for PSR for all or most of the three parasite sub-groups: body mass, longevity, social group size and population density. Body mass entered the minimum adequate models for all three parasite types and was significantly positively correlated with PSR in all tests (Table 2). Longevity entered the final models for helminth and microparasite PSR; in both cases longevity was significantly negatively correlated with PSR (Table 2). Social group size entered the final models for all three parasite types and was marginally and negatively correlated with both helminth and arthropod PSR (Table 2). Population density entered the final models for arthropod, helminth and microparasite PSR, but was only significantly positively correlated with PSR for arthropods (Table 2). Finally, of the three remaining host traits, gestation length entered the final model for arthropods and was weakly negatively correlated with PSR for this parasite type ($p < 0.1$; Table 2). Home range size entered the final arthropod model, but was not significantly correlated with PSR (Table 2), and litter size did not enter the final model for any parasite group.

No host traits entered the minimum adequate phylogenetic model for helminth or arthropod PSR, and both models included only the measure of sampling effort (Table 2). For microparasite PSR, body mass and social group size entered the final phylogenetic model. Body mass was significantly positively correlated with microparasite PSR and social group size was

Table 2. Minimum adequate model results for non-phylogenetic (species values) and phylogenetic (independent contrasts) multiple regression analyses. Seven host traits and a measure of sampling effort (Citation-PC) were included in all full models. Adjusted r^2 is shown for the final reduced models.

Predictor	Total PSR		Helminth PSR		Arthropod PSR		Microparasite PSR	
	Species values (DF = 5, 45)	Independent contrasts (DF = 4,40)	Species values (DF = 5,45)	Independent contrasts (DF = 1,72)	Species values (DF = 6,34)	Independent contrasts (DF = 1,72)	Species values (DF = 5,45)	Independent contrasts (DF = 3,45)
Citation-PC	r = 0.35***	r = 0.32***	r = 0.32***	r = 0.26***	r = 0.14^{+}	r = 0.15*	r = 0.37***	r = 0.32***
Log body mass	r = 0.79***	r = 0.52*	r = 0.58**	–	r = 0.63**	–	r = 0.60***	r = 0.37**
Log longevity	r = −3.1***	r = −1.37^{+}	r = −2.99**	–	–	–	r = −1.73***	–
Log gestation length	–	–	–	–	r = −1.44^{+}	–	–	–
Log litter size	–	–	–	–	–	–	–	–
Log population density	r = 0.28^{+}	–	r = 0.25	–	r = 0.34*	–	r = 0.07	–
Log social group size	r = −0.32*	r = −0.43*	r = −0.33^{+}	–	r = −0.32^{+}	–	r = −0.08	r = −0.27*
Log home range size	–	–	–	–	r = −0.02	–	–	–
Adj. R^2	0.47***	0.40***	0.29***	0.11***	0.29**	0.06*	0.73***	0.61***

$^{+}p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

significantly negatively correlated with microparasite PSR (Table 2).

Group size, mating system and PSR

To explore the processes underlying group size patterns, we ran a more detailed analysis focusing on interactions between social group size and mating system, since mating behavior may combine with group size to influence contact rates between hosts. In these analyses, social group size, mating system and the interaction between the two variables were significant predictors of total PSR (Table 3), with the slope of the relationship between social group size and total PSR varying as a function of mating system. Group size was significantly negatively correlated with PSR among monogamous species but not among polygynous species (Fig. 2). We found no significant main or interaction effects for helminth, arthropod or microparasite PSR (Table 3).

Discussion

Patterns of parasite diversity in Artio- and Perissodactyla suggest that components of host socioecology and life history play an important role in driving parasite occurrence in wild populations. Results based on a combination of non-phylogenetic and phylogenetically-controlled tests highlight three key host traits as significant predictors of parasite species richness in these two host groups. Body mass, longevity and social group size had strong effects on total parasite richness, and also entered the final models for individual parasite types. Of the remaining traits examined, population density had more limited effects, appearing as a weak predictor of total PSR and a significant predictor of arthropod richness. Gestation length emerged as a weak predictor for arthropod PSR only, and litter size and home range size were not significant predictors of any measure of parasite richness.

Unlike recent comparative studies of parasite species richness in wild primates (Nunn et al. 2003, 2004, 2005), our results showed an overall weak or non-existent phylogenetic signal for parasite richness in hoofed mammals, which may explain the very different outcomes for phylogenetic and non-phylogenetic tests for some measures of PSR. Although the role of host phylogeny has been recognized in many previous studies of parasite species richness (Poulin 1995, Morand and Poulin 1998, Nunn et al. 2003), our tests for evolutionary inheritance of parasite richness scores among Artio- and Perissodactyla showed that microparasite PSR was the only measure with significant phylogenetic patterning. Although phylogenetically-controlled analyses are necessary when the distribution of the traits of interest are phylogenetically patterned, these tests should not be used when the trait is unpatterned (Gittleman et al. 1996, Abouheif 1999), possibly explaining why no host traits entered into our phylogenetic models for helminth and arthropod richness. However, because phylogenetic patterning was demonstrated for the majority of host traits used as independent variables in our analyses, we ran phylogenetic and non-phylogenetic analyses for all parasite types, and placed the most confidence in results that remained consistent across both tests.

Of the seven host traits we examined, body mass showed the most broad and consistent associations with parasite richness. Among artio- and perissodactyls, larger body size was associated with higher parasite species richness similar to patterns reported across a broad range of vertebrates (Gregory et al. 1996), as well as within specific host groups such as fish (Guégan et al. 1992, Sasal and Morand 1998, Poulin 1995), birds (Gregory 1990, Gregory et al. 1991, Poulin 1995) and primates (Nunn et al. 2003, Vitone et al. 2004). For hoofed mammals, this pattern applied to all parasites combined (total PSR) and to each distinct parasite subgroup (helminth, arthropod and microparasite PSR) we examined. Associations between body size and parasite richness could arise from several different processes. Larger hosts may support more parasites because they provide more habitat (serving as larger 'biological islands' or providing a greater variety of niches); they may acquire more parasites because they eat more food; or the increased parasite diversity among large hosts could stem from other host traits correlated with body size (Kuris et al. 1980, Pacala and Dobson 1988, Poulin 1995). Finally, some studies have shown that body size patterns often emerge in non-phylogenetic tests, but disappear when the effects of phylogeny are controlled (Poulin 1995, Morand and Poulin 1998, Nunn et al.

Table 3. Results of non-phylogenetic general linear models showing the effect of social group size, mating system and their interaction on parasite species richness (PSR).

	Total PSR (DF = 4,52)	Helminth PSR (DF = 4, 52)	Arthropod PSR (DF = 4, 52)	Microparasite PSR (DF = 4, 52)
Citation-PC	$F = 20.8^{***}$	$F = 11.7^{**}$	$F = 3.44^{+}$	$F = 45.2^{***}$
Log social group size	$F = 5.97^{*}$	$F = 2.76$	$F = 2.08$	$F = 0.22$
Mating system	$F = 4.14^{*}$	$F = 0.81$	$F = 2.08$	$F = 1.3$
Log group size × mating system	$F = 4.45^{*}$	$F = 2.1$	$F = 1.32$	$F = 0.09$

$^{+}p < 0.1$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

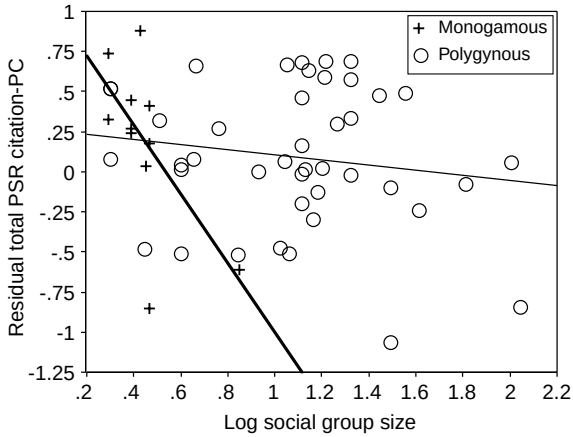

Fig. 2. Relationship between social group size and total PSR for monogamous species (dark line, $r = -0.63$, $p = 0.04$) and polygynous species (fine line, $r = -0.15$, $p = 0.33$). The residuals of total PSR and citation-PC were used as corrected estimates of PSR.

2003). However, our results showed more robust associations between body mass and parasite species richness that were relatively consistent across both non-phylogenetic and phylogenetic tests.

Host life history is considered to be a key element affecting rates of parasite colonization and extinction (reviewed by Poulin 1997), but associations between life history traits and parasite species richness that are independent of body size are rarely observed (Gregory et al. 1991, Nunn et al. 2003, Vitone et al. 2004). Host longevity is one of the few life history traits that has been previously linked to parasite species richness in mammals (Morand and Harvey 2000, Nunn et al. 2003). Our study showed a negative association between longevity and richness of all parasites, helminths and microparasites, contradicting prevailing hypotheses that longer-lived animals should accumulate more parasites compared to animals with shorter life spans (Bell and Burt 1991, reviewed by Poulin and Morand 2000). One explanation for the negative association between host longevity and PSR is that rather than host longevity driving parasite species richness, the parasites themselves could reduce host longevity (Morand and Harvey 2000, Moore and Wilson 2002). Another possible explanation is that longer-lived host species invest more in 'maintenance functions', including immunological and behavioral anti-parasite defenses (Hart 1990, Moore 2002, Nunn and Altizer 2006), and are thus more effective at reducing parasite infections.

Traits that increase contact between hosts should promote parasite spread and may facilitate the establishment of larger numbers of parasite species. Host population density and social group size are two commonly used indices of between-host contact rates (Coté and Poulin 1995, Arneberg et al. 1998, Altizer et al. 2003) and these were the primary measures we used to quantify levels of social contact in artio- and perissodactyls. Hosts living at higher population densities had significantly more arthropod parasites and marginally more total parasites (Table 2; $p = 0.052$ for total PSR). Although not significant, population density also entered the non-phylogenetic models for both helminth and microparasite PSR. Evidence from other studies indicates that population density is indeed a primary factor explaining variation in parasite species richness in certain host taxa (Morand et al. 2000, Nunn et al. 2003). Because the transmission of vector-borne and complex life-cycle parasites will be influenced to some degree by vector and intermediate host ecology, host population density is more likely to affect the transmission of directly transmitted parasites than indirectly transmitted parasites (Arneberg 2001). Therefore, future analyses examining parasites according to their transmission strategy might provide additional insights on the role host population density plays in determining patterns of parasite richness in artio- and perissodactyls.

Counter to initial expectations, a second index of social contact, host group size, was negatively correlated with parasite richness. This relationship was significant for both phylogentic and non-phylogenetic tests of total PSR and was apparent in the non-phylogenetic tests for helminths and arthropods and in the phylogenetic test for microparasites. Positive effects of grouping behavior on PSR are expected if host contact rates and parasite transmission increase in larger groups (Møller et al. 1993, Altizer et al. 2003), yet some authors have argued that sociality should lower the risk of parasite transmission if increased clustering of individuals into relatively permanent groups (and limited among-group dispersal) effectively quarantines parasites into discrete host patches (Hess 1996, Watve and Jog 1997, Wilson et al. 2003). Results from previous studies testing associations between group size or group-living and parasite richness have varied considerably, with some studies showing positive relationships, some showing negative relationships, and others showing no relationship at all (Gregory et al. 1991, Poulin 1991a,1991b, Ranta 1992, Watve and Sukumar 1995, Nunn et al. 2003, Vitone et al. 2004). Given the complexities of host social behavior, it is likely that the degree and directionality of the effect of host group size on PSR depends on the specific social system of the hosts under consideration and on other elements of host behavior that also influence contact rates (Wilson et al. 2003).

To explore the processes accounting for the negative relationship between parasite species richness and group size in hoofed mammals, we tested interactions between group size, mating system and PSR, since mating behavior is another key factor that can influence rates of contact between hosts (Freeland 1979, Møller et al. 1993, Loehle 1995). Among

polygynous species, there was no association between group size and PSR, suggesting that within these hosts, group size either has no effect on parasite transmission or increases the risk of some infectious organisms while lowering the risk of others, with the net effect leading to no apparent pattern. In contrast, our finding that total PSR decreased with group size in monogamous species suggests that contact rates may actually decline with increasing group size among hosts in this category.

Approaches such as those described in this paper, which encompass large numbers of hosts, a broad range of parasites, and incorporate multiple explanatory variables are needed to develop a deeper understanding of host behavior and other factors governing the distribution of parasites in free-living populations. As a case in point, the observed interaction between group size and mating system highlights the fact that processes underlying host trait-PSR patterns can be complex and multifaceted, potentially varying across different host and parasite groups. Furthermore, our broader set of analyses suggest that multiple host traits are likely to interact in determining patterns of PSR in the Artio- and Perissodactyla. Minimum adequate models included a combination of significant factors, as well as some traits which, although not significantly correlated with any measure of PSR, improved model fit. For example, home range size entered the final arthropod model but had no detectable effect on PSR (Table 2), suggesting that the predicted effect of host habitat use on parasite richness may operate via complex interactions with other host traits. Interestingly, we found that host geographic range size, a measure of species-level range use, also had no independent effect on PSR (Ezenwa and Altizer, unpubl.), further suggesting that either host range use has little influence on parasite distributions in hoofed mammals or that the effects of geographic range size also depend on other host traits.

Finally, it is worth noting that the strongest patterns we report in this paper emerged for those host traits that are probably the least subject to measurement biases: body size and longevity. In contrast, patterns were weaker for variables that are inherently more difficult to measure such as host social group size and population density. More standardized techniques for measuring relevant host social and ecological traits, and more precise estimates of these variables should greatly improve our ability to detect associations between host characteristics and parasite diversity. The inclusion of more detailed information on parasite characteristics in future analyses will also allow for a more nuanced view of the processes underlying parasite persistence and establishment in natural populations. In this study, we focused on parasite taxonomic categories, but studies that incorporate information on parasite transmission mode, host specificity and the duration of the infectious period (a function of parasite life history, virulence, and host recovery) will provide a more integrative framework for understanding global patterns of parasitism and the links between host and parasite characteristics.

Acknowledgements – We thank Elizabeth Harp, Nerlyne Jimenez and Laura Gold for assistance with compiling the host-parasite dataset. Kate Jones provided assistance in obtaining much of the host trait data, and we thank other members of the PanTHERIA project for providing access to these data (Georgina Mace, John Gittleman, Andy Purvis, Marcel Cardillo, Jon Bielby and Olaf Bininda-Emmonds). This research was supported by funding from the NSF (DEB 0212096 to C. Nunn and S. Altizer), the Center for Applied Biodiversity Science at Conservation International, and PanTHERIA project grants from NSF (DEB 0129009), NERC Canada (NER/A/S/2001/00581), Bundesministerium für Bilungund Forschung (031U212E), and the Earth Institute. This work was initiated as part of the "Infectious disease and host behavior" working group supported by the National Center for Ecological Analysis and Synthesis (NCEAS), funded by the National Science Foundation, the University of California, and the Santa Barbara campus.

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