Comparative Tests of Parasite Species Richness in Primates

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ABSTRACT: Some hosts harbor diverse parasite communities, whereas others are relatively parasite free. Many factors have been proposed to account for patterns of parasite species richness, but few studies have investigated competing hypotheses among multiple parasite communities in the same host clade. We used a comparative data set of 941 host-parasite combinations, representing 101 anthropoid primate species and 231 parasite taxa, to test the relative importance of four sets of variables that have been proposed as determinants of parasite community diversity in primates: host body mass and life history, social contact and population density, diet, and habitat diversity. We defined parasites broadly to include not only parasitic helminths and arthropods but also viruses, bacteria, fungi, and protozoa, and we controlled for effects of uneven sampling effort on per-host measures of parasite diversity. In nonphylogenetic tests, body mass was correlated with total parasite diversity and the diversity of helminths and viruses. When phylogeny was taken into account, however, body mass became nonsignificant. Host population density, a key determinant of parasite spread in many epidemiological models, was associated consistently with total parasite species richness and the diversity of helminths, protozoa, and viruses tested separately. Geographic range size and day range length explained significant variation in the diversity of viruses.

Keywords: host-parasite interactions, parasite diversity, comparative analysis, primates, population density.

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Infectious diseases and parasites are a common component of animal populations and produce major impacts on host abundance and evolution (e.g., Swinton et al. 1998; Begon et al. 1999; Hudson et al. 1999). Free-ranging mammals are typically exposed to a diverse array of parasites including microparasites, such as viruses and bacteria, and macroparasites, such as helminths and arthropods. An individual mammal may contain several hundred individual macroparasites, with the host population harboring a community of 40 or more different parasite species (Dobson et al. 1992). For example, feral Soay sheep on the island of St. Kilda, Scotland, harbor 20 different species of helminths alone (Gulland 1992), and more than 95 species of macroparasites have been reported in zebras in southern Africa (Roberts et al. 2002). Parasites represent an important component of natural communities, and understanding the factors that underlie patterns of parasite diversity is vital to identifying ecological principles governing biodiversity. Moreover, parasites have been linked increasingly with dramatic local and global declines of wildlife species, including lions, black-footed ferrets, Hawaiian forest birds, and many amphibian species (e.g., Dobson and Grenfell 1995; Packer et al. 1999; Daszak et al. 2000). Thus, identifying general principles governing parasite occurrence is critical for managing vulnerable wildlife populations and mitigating risks to human health.

Ecologists have made significant progress in understanding infectious disease dynamics operating within populations, but less is known about the factors that influence patterns of parasite community diversity. Questions about parasite biodiversity can be addressed at two levels (Morand 2000). First, patterns of species diversification within specific parasite lineages can be examined using information on parasite phylogeny and factors that may influence parasite speciation or extinction (Poulin and Morand 2000). A second approach investigates host characteristics that best explain variation in parasite species richness (PSR; Morand 2000). This approach requires information on host characteristics, host phylogeny, and parasite community diversity among multiple host species.

Numerous host characteristics have been shown to cor-

relate with PSR in individual analyses, but few studies have examined a broad range of hypotheses within a single host clade. Moreover, most studies have addressed only a subset of variables expected to influence parasite diversity using relatively narrow parasite groups (primarily intestinal helminths or ectoparasites infecting birds, fish, and mammals; reviewed in Morand 2000). A broader approach is needed because multiple host characteristics may independently or interactively influence patterns of parasitism, and different host characteristics may be important for understanding the community composition of different parasite groups.

In this study, we examined the correlates of PSR among primate hosts and asked what features of host biology are associated with interspecific variation in parasite diversity. We focused on primates because they represent a diverse mammalian order whose behavior, life history, phylogeny, and ecology have been relatively well studied. This information makes it possible to test multiple hypotheses for the host traits that influence parasite biodiversity. Because of their close evolutionary relationship to humans, much is known about primate infectious diseases including microparasites, such as viruses, protozoa, bacteria, and fungi, and macroparasites, such as helminths and arthropods. We collated data on these six types of parasites to investigate whether the following four sets of factors influenced PSR.

Body size and life history. Hosts have been described as "island habitats" for their parasites, and larger-bodied hosts may represent larger habitat patches with more niches for colonization (Kuris et al. 1980; Poulin 1995; Gregory et al. 1996). More generally, body mass is associated with many variables that are thought to influence PSR. For example, larger-bodied hosts eat more food and may therefore ingest more endoparasites, and they provide a larger surface area for ectoparasites. In mammals, larger-bodied hosts exhibit slower life histories (Harvey and Clutton-Brock 1985; Ross and Jones 1999), which may further influence patterns of parasitism. Hosts that live longer should harbor greater parasite diversity because they encounter more parasite species and are exposed to more infectious stages throughout their lifetimes (Pacala and Dobson 1988). Mathematical models further predict that host life history should interact with key epidemiological processes because high host mortality is predicted to reduce parasite prevalence and limit parasite establishment (Anderson and May 1991; Thrall et al. 1993; De Leo and Dobson 1996; Altizer and Augustine 1997). We predict that associations between parasite diversity and host life history will remain when body mass is controlled for statistically.

Social contact and density. Social interactions generate a network of contacts through which many parasites spread within populations (Anderson and May 1979, 1991). A key measure of parasite success is the basic reproductive ratio, R_0, which reflects the ability of any directly transmitted parasite species to colonize and spread within a host population. Formally defined, R_0 is the average number of secondary infections produced by a single infected host in an otherwise susceptible population. Mathematical expressions for R_0 are typically a product of the transmission process, host abundance, and the duration of the infectious period (Anderson and May 1991). Parasite establishment requires that R_0 exceed unity, and host-parasite combinations that do not meet this criterion are in theory unlikely to persist. Factors influencing R_0, such as host population density, rates of among-host contact, and encounter rates with parasites in the external environment, should correlate positively with PSR (Morand 2000). Thus, hosts living at high density or with frequent intraspecific contacts are expected to accumulate more parasite species for which the criterion $R_0 > 1$ is satisfied (reviewed in Morand 2000; Roberts et al. 2002). Our primary measure of social contact is population density, but we also examined measures of contact involving mating promiscuity and social group size. In addition to effects of sociality on the transmission process, primate social groups may represent biological islands for parasites (Freeland 1979), again predicting greater PSR in larger social groups.

Diet. Intake of resources influences host exposure to parasites (e.g., Guegan and Kennedy 1993). In primates, invertebrates consumed as prey may serve as intermediate hosts for trophically transmitted parasites (especially trematodes, cestodes, and acanthocephalans), predicting increased diversity of complex-life-cycle parasites in insectivorous primates relative to folivores or frugivores. We also tested for an effect of folivory. Folivorous primates consume a higher volume of resources than do frugivores and may therefore ingest more parasites. Moreover, certain primate species have been reported to ingest leaves with antihelminthic properties as a form of self-medication (e.g., Huffman et al. 1997), although this might lead to predictions of a negative relationship between folivory and parasite diversity.

Habitat diversity. Hosts that occupy more diverse habitats are likely to encounter a larger number of parasites from other host taxa or environments, leading to increased PSR. Detailed data on habitat variation is not available for most species of primates, but habitat diversity is likely to increase with increasing geographic range size (Dritschilo et al. 1975; Price and Clancy 1983; Gregory 1990). In addition, animals that use a larger home range and travel a longer distance per day should encounter more parasite species. Finally, substrate use may influence PSR, with animals that use both terrestrial and arboreal substrates ex-

posed to more parasite species than animals that specialize in either of these substrates. Alternatively, terrestriality itself may increase PSR through greater exposure to soilborne parasites or those with fecal-oral transmission.

These outlined predictions are not mutually exclusive, and, within hypotheses, independent variables may covary. By focusing on a well-studied host clade and including multiple predictor variables, we distinguished among confounding or correlated factors. Moreover, the wide taxonomic diversity of parasites represented by our survey enabled statistical tests to reveal patterns among the broader parasite community in addition to patterns specific to three major parasite groups (helminths, protozoa, and viruses) that are well documented in primates. We also incorporated phylogenetic information by using independent contrasts. Thus, we deal with the possibility that parasite communities, like host morphology or behavior, are shared through common descent, an assumption that we test and find is supported.

Methods

> The parasitology literature contains a wealth of information on the diverse taxa of parasites and on their relationship with their hosts. There are tens of thousands of pages devoted to descriptive studies, laboratory experiments and field surveys on parasites. The next step is to examine this information in a broad evolutionary context; this is where we are now. (Poulin 1998, p. 179)

Parasite Data and Controlling for Sampling Effort

We compiled parasite data as individual records of micro- or macroparasites reported in free-living primate species by using primate Latin binomials as search keywords in the major online reference databases (Biological Abstracts, AGRICOLA, Medline, Web of Science). We also searched by primate genus name, following the taxonomic scheme of Corbet and Hill (1991), as well as by common taxonomic variants (on the basis of Rowe 1996; Groves 2001). We used the Corbet and Hill (1991) taxonomy rather than a newer one with more than 100 taxonomic additions (Groves 2001) because most references on parasites preceded publication of the more recent taxonomies. For example, 64% of 258 references in our database were published before 1995. Moreover, the phylogeny used to conduct the comparative tests (Purvis 1995) follows the Corbet and Hill (1991) taxonomy (see "Comparative Methods"). In addition to using electronic databases, we also examined edited volumes (e.g., Fiennes 1972), reviews (e.g., Garnham 1966; Brack 1987), and studies that were cited by publications that we located in our first round of searches.

We found that parasite data on wild primates were available from four main sources: surveys that documented the parasite fauna of wild primate populations, detailed epidemiological studies focusing on one or a few specific parasites, museum reports documenting new parasite species or revised parasite taxonomies, and surveys of wild primates to assess zoonotic risks to humans or domesticated animals. For each parasite or infectious disease reported from a wild primate population, we recorded the type of parasite (virus, protozoan, fungi, arthropod, helminth, bacteria), parasite genus and species names, the number of hosts sampled, and location and year of sampling. When possible, we also included the primary mode of parasite transmission, symptoms and effects on host mortality or morbidity, and the prevalence and intensity of infection. We initially included data from wild-captured and semifree-ranging primates but later screened the data set to include only parasites reported from wild populations. We also included nine host species that were screened for one or more parasite species but found to have none, but we excluded 59 anthropoid primates for which we could find no information on parasites in the published literature. Thus, our data set included 63% of the anthropoid primate species.

A parasite may be missing from a host species because it does not occur or because the host has been sampled insufficiently (Gregory 1990; Walther et al. 1995). To control for uneven sampling effort in estimating PSR, we followed previous researchers (Gregory 1990; Poulin 1995; Walther et al. 1995; Poulin and Rohde 1997; Morand and Harvey 2000; Arneberg 2002) by incorporating information on sampling effort in the analyses. Sampling effort was estimated in three ways. First, we collated data on the number of references for each host species using the Web of Science (WOS) citation index. Second, we repeated this process using an anthropological database from Research Libraries Group (RLG), which includes major journals that report studies of primate behavior and ecology in the wild. For both databases, we used the maximum range of years covered (1975–2001 for WOS, 1984–2001 for RLG) to maximize overlap with dates of studies in the parasite data set. For our final measure of sampling effort, we totaled the number of individuals that had been sampled for each host species (animals sampled). For sources that did not report the number of animals sampled, we assigned a default value of 6.4 individuals on the basis of the lower tenth percentile of mean number of individuals per study, thus assuming that studies failing to report sample size probably sampled fewer individuals.

Measures of sampling effort are not independent of one another (see "Results"), and each measure has strengths and weaknesses. Citation indices control for how well a species has been studied but not specifically with regard

to parasites. The number of animals sampled is based on data from the studies comprising our data set, but it fails to capture the number or types of parasite species that were screened in each study. Thus, large studies (e.g., hundreds or thousands of individuals sampled) that measured the prevalence of a single parasite may overrepresent the sampling effort given to a host species (e.g., Hayami et al. 1984; Milton 1996). For testing the main hypotheses, we included sampling effort as an independent variable in a multiple regression model and repeated the analysis for each measure of sampling effort. For bivariate plots and some phylogenetic tests, we calculated residual PSR by regressing the size of the observed parasite community on measures of sampling effort. We conducted analyses using all measures of sampling effort. For some secondary tests, however, we give detailed statistical results only for analyses using WOS citation counts.

Data on Host Characteristics

We augmented previously compiled comparative databases that included information on primate life history and ecological traits. Information on data, sources of data, and sample sizes (number of species) is available from appendix A and appendix B in the online edition of the *American Naturalist* and at http://www.phylodiversity.net/cnunn. Body size was estimated as mean female body mass (Smith and Jungers 1997). Among host life-history traits, longevity is the key factor that should influence the size and diversity of the parasite community and was measured as maximum recorded longevity (years; Ross and Jones 1999). Because longevity is measured with error in long-lived species such as primates, we also examined age at first reproduction (age at first birth in years; Ross and Jones 1999). Using the published literature on free-ranging primate behavior and ecology (see Nunn and van Schaik 2001), we obtained estimates of group size (mean number of adult and immature individuals), population density (on the basis of field studies of local population density, measured as the number of animals per square kilometer), day journey length (kilometer), home range size (hectare), and diet (percentage of leaves and insects in the diet). As our measure of mating promiscuity, we used testes mass after correcting for male body mass (Harcourt et al. 1981, 1995) because this morphological trait correlates with female mating behavior (see also Nunn et al. 2000). Geographic range size was compiled using published secondary and primary literature to establish an extent of occurrence map for each species. Each source was digitized into a geographic information system, and an equal-area projection was used to calculate range size. Substrate use (e.g., terrestriality) was measured as a continuous variable as the percentage of time spent in terrestrial locomotion. We also examined the effect of substrate use when it was treated as a categorical trait, with ordinal character states as follows: arboreal, terrestrial in a wooded environment, and terrestrial in an open environment (Nunn and van Schaik 2001). In testing the effect of habitat diversity, we assumed that terrestrial species in wooded habitats (classifications from Nunn and van Schaik 2001) come into contact with more parasites through their use of both terrestrial and arboreal substrates.

Comparative Methods

Traits shared through common descent lead to nonindependence of data points in comparative analyses and cause higher Type I error rates in studies that ignore phylogeny (Martins and Garland 1991; Purvis et al. 1994; Harvey and Rambaut 1998). An important assumption of comparative methods that control for host phylogeny is that the traits in question are shared through common descent. Although parasite community diversity and our measures of sampling effort are not necessarily heritable or evolving traits in primates, they may be associated with other traits that are shared through common descent.

We investigated the correlation between traits and phylogeny by using the test for serial independence (TFSI; Abouheif 1999). The TFSI measures the degree of nonrandomness in a series of continuous values, such as traits along the tips of a phylogeny. A randomization procedure addresses the arbitrariness of the species' order in a binary tree (Abouheif 1999). To implement the TFSI, we used the program Phylogenetic Independence (version 1.1, Reeve and Abouheif 1999), with phylogenetic information from Purvis (1995). Statistical significance was assessed using simulations to generate a null distribution ($n = 1{,}000$ simulations), as described in Abouheif (1999). Because this version of the program requires a fully bifurcating tree, four polytomies were resolved randomly in MacClade (Maddison and Maddison 1992) before running the test. Results revealed a significant association among all measures of PSR and primate phylogeny for most of the variables tested (table 1), indicating that parasite diversity is more similar among closely related host taxa.

On the basis of the TFSI results, we investigated the association between host traits and PSR by using least squares regression (through the origin) of phylogenetically independent contrasts (Felsenstein 1985). Contrasts were calculated using the computer program CAIC (Purvis and Rambaut 1995). Tests involving discrete substrate codes were analyzed using the "BRUNCH" algorithm in CAIC (Purvis and Rambaut 1995). The method of independent contrasts makes a number of assumptions regarding the evolutionary model, the phylogeny, and the quality of the data as representing valid species differences. We tested

Table 1: Results from the test for serial independence

Variable	*P* value
Total PSR, residuals based on WOS	.033
Total PSR, residuals based on RLG	.018
Total PSR, residuals based on animals sampled	.082
Helminth PSR, residuals based on WOS	.001
Protozoan PSR, residuals based on WOS	.006
Viral PSR, residuals based on WOS	.003

Note: The *P* values less than .05 indicate a significant association between the variable and primate phylogeny. Results are for anthropoid primates (monkeys and apes) only. PSR = parasite species richness, WOS = Web of Science, RLG = Research Libraries Group.

the assumptions of this method and performed sensitivity tests to determine how violations of these assumptions and different data sets affected the results (Harvey and Pagel 1991; Garland et al. 1992; Purvis and Rambaut 1995; Nunn and Barton 2001). Log-transformed data and branch lengths best met the assumptions of independent contrasts, but our analyses also revealed one or more outliers among the contrasts, which may indicate violations of assumptions in specific tests (Purvis and Rambaut 1995; Harvey and Rambaut 2000). We therefore conducted all analyses with and without outlying contrasts as determined by using Mahalanobis distance measures (JMP, version 4, Cary, N.C.).

A correlation between the traits of interest and phylogeny does not explain how the correlation came to be, and an alternative model of evolution can account for such correlations (Price 1997; Harvey and Rambaut 2000). We therefore also performed nonphylogenetic analyses using actual species values (Harvey and Rambaut 2000). Comparison of phylogenetic and nonphylogenetic results can often reveal the presence of confounding variables or grade shifts (Price 1997; Nunn and Barton 2001), which is critical for understanding the suite of traits that may influence PSR.

We used multiple regression to investigate the host traits that explain variation in PSR. A common problem with such analyses is reduced sample size because species are excluded from the analysis if they are missing data on any of the variables. For our data, samples sizes varied among predictor variables (see apps. A, B in the online edition of the *American Naturalist*), and overlap among variables was not perfect. We therefore balanced sample size against the number of variables included in the model by employing iterative stepwise regression and minimum adequate models. First, we conducted analyses of single predictor variables (focused tests). Because of the strong correlation between body mass and many of the host traits that we investigated (Clutton-Brock and Harvey 1977), we included body mass as a predictor variable in all multiple regression models that included life-history traits, population density, diet, terrestriality, and home range size. For each analysis, we included one measure of sampling effort as an independent variable.

Second, we performed iterative stepwise multiple regression analyses using all continuous predictors, repeated for each measure of sampling effort entered as an independent variable, to identify minimum adequate models. In this analysis, a variable was entered in forward inclusion (or removed in backward elimination) if its significance probability was less than (or greater than) 0.25. We then recalculated independent contrasts using only those variables that remained in the model, repeated the stepwise regressions using this new set of contrasts, and iterated this process until the model stabilized. In a final stage, to ensure that the model was complete, we reentered into the stepwise model variables that were found to be significant in focused tests but had dropped out in the early stages of model generation. We constructed a final multiple regression model based on the results of the minimum adequate models (calculated for both independent contrasts and species values and with each of the three measures of sampling effort, including all variables significant in two or more stepwise tests).

It is from the final multiple regression models that we drew conclusions about factors associated with PSR. We used the most conservative criteria possible for deciding that a variable influenced PSR; the variable had to account for significant variation in PSR in contrasts analyses after controlling for all three measures of sampling effort as well as other confounding variables, including body mass and other variables found to be significant in minimum adequate models.

In initial analyses, we found that including information on the percentage of time terrestrial in the stepwise regression model reduced the sample size considerably because this variable is available for the fewest number of species in our data set (see apps. A, B in the online editon of the *American Naturalist*). Thus, we investigated the influence of substrate use in separate multiple regression analyses by testing whether the percentage of time terrestrial and body mass independently explain variation in PSR. We also examined discrete transitions in substrate use to test the hypothesis that species that use both arboreal and terrestrial habitats are exposed to a greater diversity of parasites because categorical information on substrate use was available for all species in our data set (see app. B in the online editon of the *American Naturalist*). Finally, when testing specific predictions, we used directed tests rather than one-tailed tests because these enable detection of patterns that are opposite to predictions while retaining much of the statistical power of one-tailed tests (Rice and Gaines 1994). Directed tests allocate a disproportionate probability under the null hypothesis to the tail of the

distribution in the predicted direction (γ) while retaining a smaller probability in the opposite tail to detect unexpected deviations in the opposite direction ($\delta < \gamma$). Directed tests are subject to the constraint that $\delta + \gamma = \alpha$. We followed the guidelines in Rice and Gaines (1994) by setting γ/α to 0.8, giving values of $\gamma = 0.04$ and $\delta = 0.01$.

Results

Parasite Diversity in Wild Primate Populations

From our initial research, we can confirm Poulin's (1998) assessment of the availability of parasite data for free-living hosts (see Arneberg 1999). We found a large number of parasite records in all major primate radiations including prosimians, New World monkeys, Old World monkeys, and apes. Prosimian primates, however, were markedly underrepresented in our database, with an average of 1.8 parasite species recorded for each of 15 prosimians species as compared with an average of 9.3 parasite species recorded for each of 101 anthropoids (monkeys and apes). Even after controlling for sampling effort, the size of the parasite community remained smaller in prosimian species (fig. 1). Thus, compared with anthropoids, prosimians may have been sampled less thoroughly for parasites, which might be expected because of their generally nocturnal habits and greater phylogenetic distance from species that attract more interest, such as humans and threatened monkeys and apes. Because prosimians live in smaller groups and are smaller in body mass, the low diversity of parasites reported from prosimians had the potential to bias the results of some analyses. We therefore removed this small number of host-parasite records from the comparative tests ($n = 27$ records). The remaining data set of 941 records was largely composed of helminths (338 unique host-parasite records, mainly nematodes), protozoa (335 records), viruses (162 records), arthropods (63 records), bacteria (39 records), and fungi (four records). Information was available on a total of 231 parasite species in 138 genera, with parasite species spanning a wide variety of life histories and transmission modes.

Before controlling for uneven sampling effort, parasites were highly aggregated among host taxa, with a few well-studied hosts harboring 40 or more parasite species and most hosts having records of eight or fewer parasite species (fig. 2*A*; a similar pattern was found by Raibut et al. 1998). As expected, we found a strong association between the degree to which each host species was studied and the number of parasite species recorded in our database, and this was true for all three measures of sampling effort and parasite type (e.g., overall parasite number: WOS $t_{99} = 7.96$, RLG $t_{99} = 5.99$, animals sampled $t_{99} = 15.8$, $P < .0001$ in all tests, two-tailed tests). Similar patterns have been documented in previous studies of parasite diversity (e.g., Gregory 1990; Poulin 1995; Walther et al. 1995; Poulin and Rohde 1997; Morand and Harvey 2000; Arneberg 2002). After controlling for sampling effort by taking residuals, our measures of PSR more closely resembled a normal distribution (fig. 2*B*).

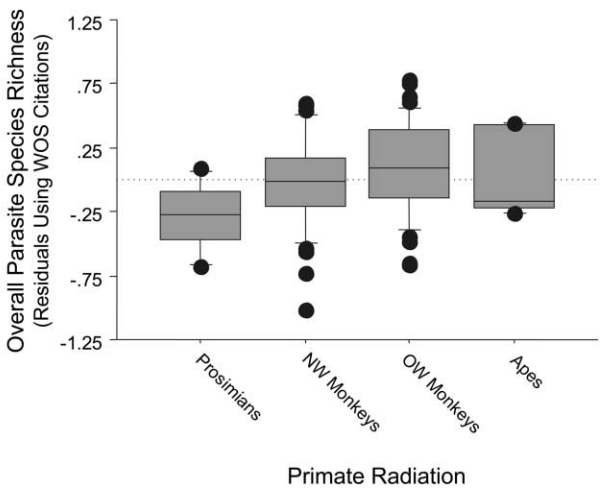

Figure 1: Overall parasite diversity in each of the four major primate radiations after controlling for sampling effort using Web of Science (WOS) citations. Box plots show tenth, twenty-fifth, fiftieth (median), seventy-fifth, and ninetieth percentiles, with points outside the extreme percentiles plotted individually. As compared with anthropoids (monkeys and apes), prosimian primates had consistently lower values for overall parasite species richness (PSR). In analyses of specific types of parasites, this pattern was repeated for protozoa and helminth PSR. For viruses, however, Old World monkeys exhibited highest parasite diversity (not shown).

Residuals from all three measures of sampling effort were highly correlated, as expected if the three measures assess the degree to which host taxa have been studied for parasites. Correlations were highest among the residuals calculated from the two citation indices ($r = 0.94$, $n = 101$ species, $P < .0001$), although all pairwise correlations exceeded 0.54 ($P < .0001$, $n = 101$ species). We also found strong positive relationships between all measures of sampling effort and the diversity of the three most commonly reported parasite types (helminths, viruses, and protozoa). Finally, we compared residuals calculated for each of the three major parasite groups separately. Protozoan PSR was positively correlated with diversity of helminths and viruses ($r > 0.80$, $P < .0001$, using all measures of sampling effort). However, helminth PSR was not correlated significantly with virus PSR (e.g., for WOS, $r = 0.11$, $P = .28$).

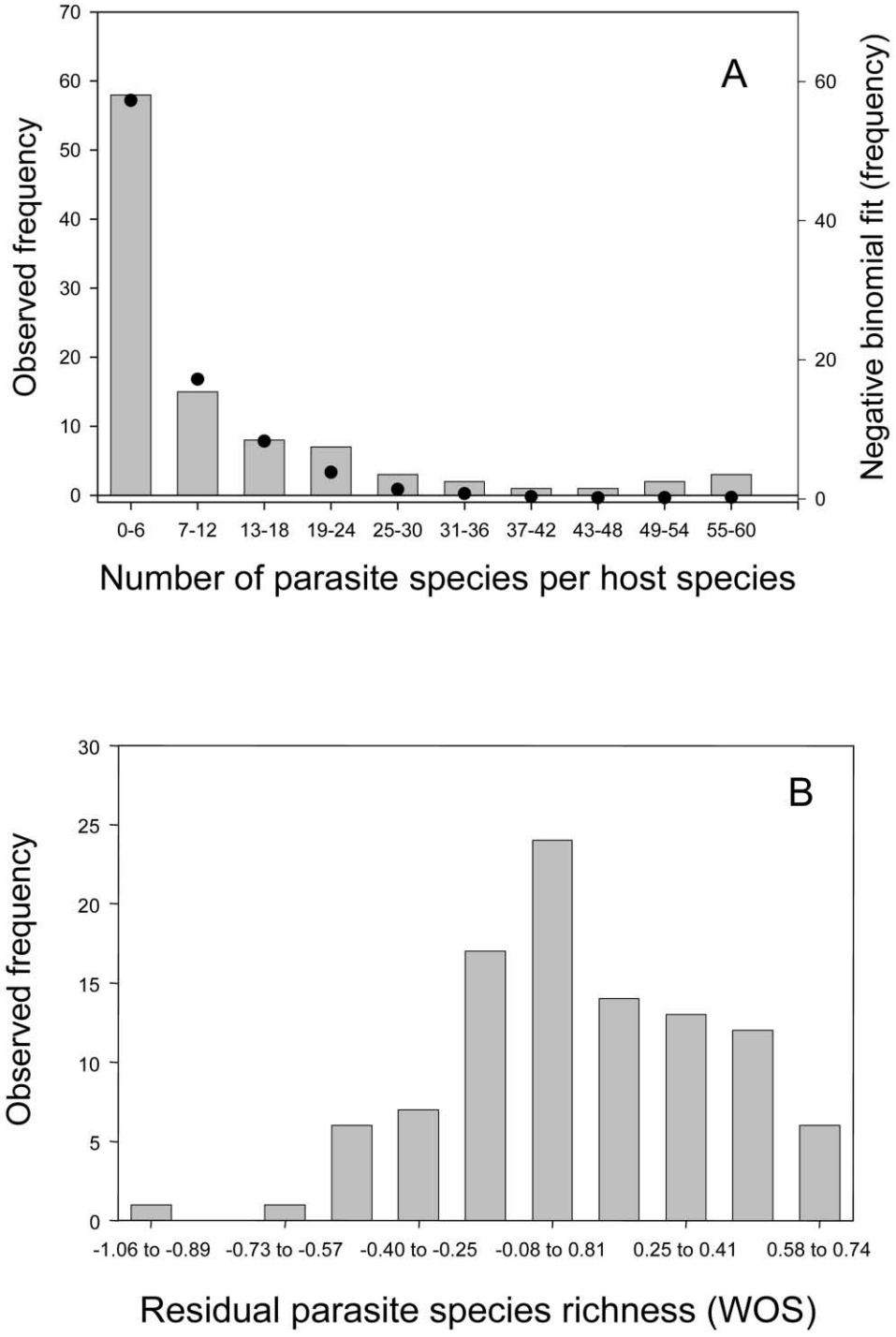

Figure 2: Distribution of parasite species among primate hosts. *A*, Raw data on parasite species counts before controlling for sampling effort. *B*, After controlling for sampling effort using Web of Science (WOS) citations. The distribution of parasites before controlling for sampling effort was highly aggregated, with most hosts having six or fewer parasites (e.g., three *Saguinus* species had 0 parasites) and a few host species having 40 or more parasites (e.g., three *Papio* species had 57–60 parasite species each). Although superficially similar to a negative binomial distribution, which is the pattern observed for aggregation of parasites on individual hosts, the observed distribution was significantly different from this distribution ($K = 0.0617$, mean = 9.30, likelihood ratio $G2 = 64.7$, $P = .0001$). After controlling for sampling effort, the distribution of parasite diversity was consistent with a normal distribution (Kolmogorov-Smirnov test statistic = 0.069, df = 101, $P = .20$).

Overall Parasite Species Richness

In focused tests (table 2), population density showed a clear positive relationship with overall PSR (both with and without controlling for host phylogeny and for all three measures of sampling effort; fig. 3). Other significant results depended on the method of analysis, with body mass and group size significant in all tests that used species values but not independent contrasts (table 2; fig. 4). In focused phylogenetic tests, the percentage of leaves in the diet and geographic range size explained variation in overall PSR in two tests, longevity was a significant predictor in one test, and home range size was negatively related to overall PSR in another analysis (table 2). In the iterative stepwise regression model using species values, body mass and population density were consistently entered. Results were similar for analyses of independent contrasts, with body mass significant in two tests and population density significant in three tests. Geographic range was found to be significant in one phylogenetic and one nonphylogenetic test, in both cases when controlling for sampling effort using RLG citations.

We constructed a multivariate model using variables significant in two or more phylogenetic and nonphylogenetic stepwise tests (table 3). In multiple regression tests that did not control for host phylogeny, both body mass and population density were statistically significant predictors of overall PSR. Geographic range remained significant in one test that used RLG citations to control for sampling effort. Population density was the only variable that was significant in all analyses of independent contrasts (table 3), with geographic range again significant when using RLG citations to control for sampling effort. Thus, population density was the primary variable that explained variation in overall PSR.

To assess whether more terrestrial species of primates possessed larger parasite communities, we regressed overall PSR on body mass, the percentage of time terrestrial and sampling effort. In analyses of species values and independent contrasts, however, terrestriality failed to explain significant variation in overall PSR for all measures of sampling effort (e.g., WOS, species values: $b_{\%\ \text{terrestrial}} = -0.070$, $F = 0.51$, df $= 1, 33$, $P = .95$; WOS, independent contrasts: $b_{\%\,\text{terrestrial}} = 0.037$, $F = 0.12$, df $= 1, 32$, $P = .46$, directed tests). We also tested whether primate species that more commonly use a mixture of terrestrial and arboreal substrates experience increased contact with infectious parasites, but we found no significant association (e.g., for WOS, only five of 13 contrasts were positive over transitions to mixed substrate use, $t_{12} = -0.31$, $P = .78$, directed test).

Helminth Parasite Species Richness

Body mass was the strongest predictor of helminth PSR in focused tests that did not control for host phylogeny, and group size was significant in two tests (table 2). In analyses of independent contrasts, population density was statistically significant regardless of how we controlled for sampling effort but only when outliers were included (for RLG and WOS measures of sampling effort). Conversely, for body mass, results became nonsignificant when outliers were included (also for RLG and WOS). This instability between population density and body mass is unsurprising given that these variables are negatively correlated (con-

Table 2: Focused tests of parasite species richness

	Overall parasite species richness		Helminth species richness		Protozoan species richness		Virus species richness	
Variable	Species	Contrasts	Species	Contrasts	Species	Contrasts	Species	Contrasts
Mass	3		3	2	3	2	3	
Age at first reproduction[a]								
Longevity[a]		1		1		1		2
Population density[a]	3	3		3	3	3	3	3
Group size	3		2		2		3	
Testes mass[a]								
Percent insects[a]							1	
Percent leaves[a]		2		2				
Geographic range		2				2	2	2
Home range size[a]		(1)		(1)				
Day range length				(2)			1	1

Note: Numbers indicate the number of tests for which a variable was statistically significant in sensitivity tests that used each of three measures of sampling effort (Web of Science citations, Research Libraries Group citations, and animals sampled). Values in parentheses indicate variables for which the slope was negative.

[a] Body mass was controlled.

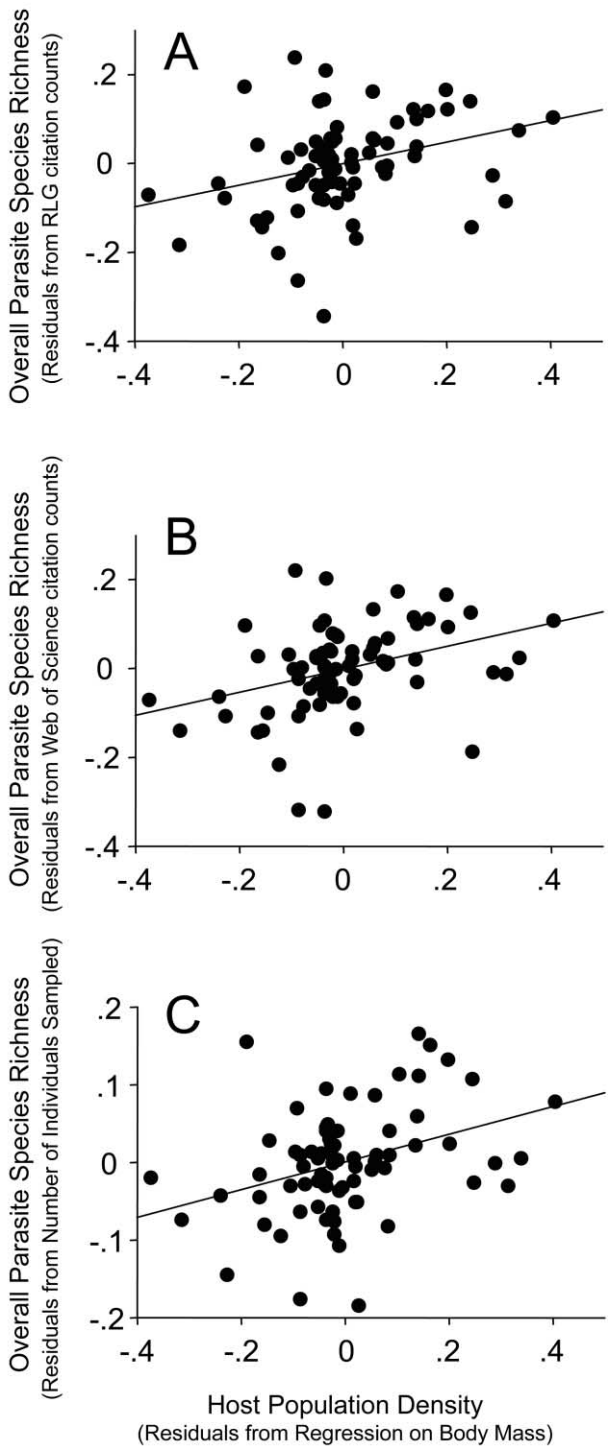

Figure 3: Relationship between population density and overall parasite species richness. *A*, Using Research Libraries Group (RLG) citations. *B*, Web of Science citations. *C*, Animals sampled. Plots show relationship between population density (controlling for body mass by taking residuals) and the size of the parasite community (controlling for three measures of sampling effort by taking residuals).

trasts: $r_s = -0.24$, $n = 74$, $P = .043$, two-tailed test) but are both expected to influence PSR positively. Home range size and day journey length were negatively associated with helminth PSR, and we found one or more positive associations in phylogenetic tests involving longevity, body mass, and percentage of leaves in the diet (table 2).

In iterative stepwise regression analyses using raw species values, body mass alone was significant for only one measure of sampling effort (RLG). In iterative stepwise regression using independent contrasts, sampling effort was the only variable consistently entered in all three tests. Other variables found to be significant in fewer tests included population density, day range length (negative), group size, home range size (negative), and body mass. Among the phylogenetic and nonphylogenetic tests, only body mass was statistically significant in more than one analysis. Because results involving body mass and population density were sensitive to outliers in focused analyses, we included both variables in the final model (table 4). In nonphylogenetic multiple regression analyses, only body mass was significant. In phylogenetic tests, results were again sensitive to inclusion of outliers. Thus, when outliers were excluded, only one test involving population density was significant (controlling for number of animals sampled, $t_{66} = 1.89$, $P = .04$, directed test). When using all contrasts, however, population density was a significant predictor of helminth PSR for all measures of sampling effort (table 4), with body mass also significant when using WOS citations to control for sampling effort. Thus, results depended strongly on the method of analysis, with body mass of greater importance in nonphylogenetic tests and population density significant for all measures of sampling effort once phylogeny was taken into account.

We tested whether more terrestrial primate species possess larger helminth parasite communities. However, we found no support for an effect of terrestriality using all measures of sampling effort in phylogenetic and nonphylogenetic tests (e.g., WOS, species values: $b_{\%\,\text{terrestrial}} = 0.0078$, $F = 0.01$, df $= 1, 33$, $P = .59$; independent contrasts: $b_{\%\,\text{terrestrial}} = 0.10$, $F = 0.96$, df $= 1, 31$, $P = .21$, directed tests). We also assessed whether dual use of arboreal and terrestrial substrate use increased helminth PSR, but we found no support for this hypothesis (e.g., using WOS citations: seven of 13 contrasts positive, $t_{12} = -0.31$, $P = .78$).

Protozoan Parasite Species Richness

In focused tests of species values, body mass, population density, and group size were significantly associated with protozoan PSR (table 2). Of these variables, however, only population density and body mass were significant in phylogenetic tests, with geographic range and longevity sig-

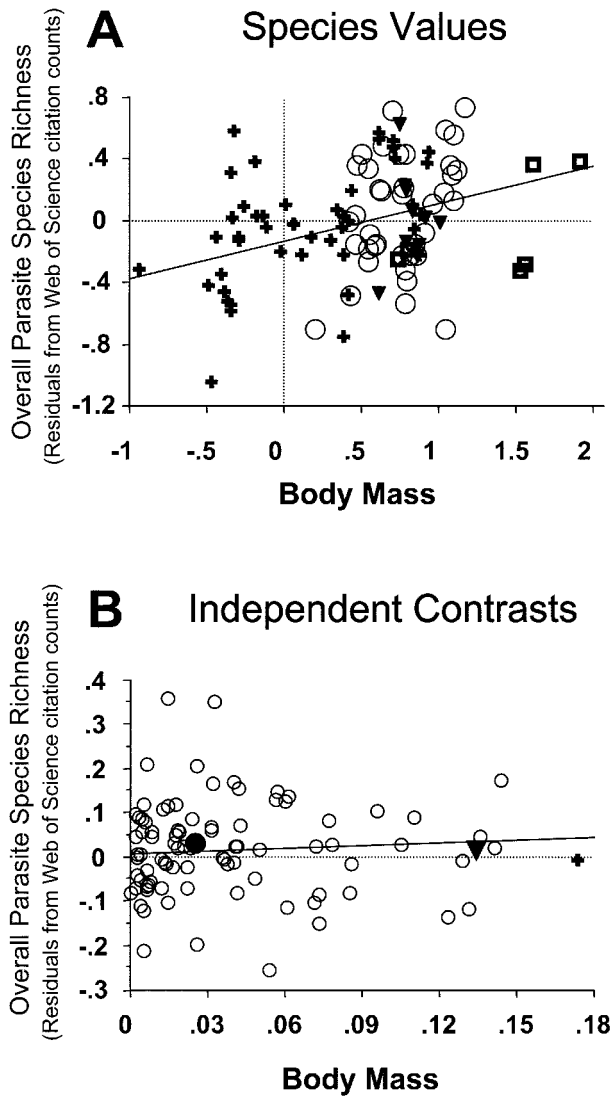

Figure 4: Relationship between body mass and overall parasite species richness. *A*, Results from nonphylogenetic analysis of species values ($b = 0.24$, $F = 13.8$, df $= 1, 97$, $P = .0002$, directed test). *B*, Results using independent contrasts ($b = 0.22$, $F = 1.39$, df $= 1, 83$, $P = .15$, directed test). In both plots, sampling effort was controlled by using residuals from regression of total parasites recorded regressed on Web of Science citation counts, but results were similar when using other measures of sampling effort and multiple regression to control for sampling effort. Primate lineages are indicated by symbols as follows. In *A*, plus sign = New World monkeys, circle = cercopithecine monkeys, triangle = colobine monkeys, square = apes. In *B*, plus sign = contrast between Old World and New World anthropoids, triangle = contrast between monkeys and apes, and filled circle = contrasts between ceropithecines and colobines (the latter being primarily folivorous). This striking difference in the association between body mass and parasite diversity when using species values versus independent contrasts was also found for protozoan and viral parasite species richness.

nificant in a smaller number of analyses. Results involving body mass were significant only when outlier contrasts were excluded. By comparison, population density was significant in all analyses regardless of the measure of sampling effort used and inclusion of outliers.

In stepwise regression models, population density and longevity were entered and statistically significant in two or more analyses that included body mass as a covariate. Results for multivariate models that included these three variables again differed for phylogenetic and nonphylogenetic tests. In analyses of independent contrasts, longevity and population density were statistically significant

Table 3: Multivariate analysis of overall parasite species richness

	Nonphylogenetic analyses (species values, $N = 79$)			Phylogenetic analyses (independent contrasts, $N = 74$)		
	Body mass	Density	Geographic range	Body mass	Density	Geographic range
RLG	3.60***	1.98*	1.97*	.96	2.76**	2.63**
WOS	3.65***	2.27*	1.11	.92	3.81***	.84
Animals sampled	3.79***	2.04*	1.13	1.60	4.09***	1.28

Note: Model is overall parasite species richness = host body mass + population density + geographic range + sampling effort. Multiple regression models were based on factors significant in stepwise regression analyses. Table provides *t*-statistics, with the direction of the *t*-statistic indicating the sign of the regression coefficient. Results are shown for tests based on both raw species values (nonphylogenetic) and independent contrasts (phylogenetic analyses) and for three different measures of sampling effort (RLG = Research Libraries Group database, WOS = Web of Science citations). Sampling effort was statistically significant in all tests (results not shown in table). Significance is based on directed tests.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

regardless of the method of controlling for sampling effort (table 5). The significance of results for longevity depended strongly on an outlier representing a large difference in longevity between the common chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) so that removal of this single data point eliminated longevity as a significant predictor. Thus, the primary predictor of protozoan PSR was host population density.

In multiple regression analyses of the effects of body mass and percentage of time terrestrial, terrestriality was a nonsignificant predictor of protozoan PSR in contrasts analyses for all measures of sampling effort (e.g., WOS: $b_{\%\,\text{terrestrial}} = 0.012$, $F = 0.01$, df $= 1, 32$, $P = .68$). Similarly, in analysis of species values, the percentage of time terrestrial was not significant for all measures of sampling effort (WOS: $b_{\%\,\text{terrestrial}} = -0.077$, $F = 0.71$, df $= 1, 33$, $P = .99$). Finally, we found no support for an increase in protozoan PSR among species that are more likely to use both terrestrial and arboreal substrates (for WOS, six of 13 contrasts were positive, $t_{12} = 0.60$, $P = .88$).

Viral Parasite Species Richness

In focused nonphylogenetic tests of viral diversity, body mass, population density, and group size were statistically significant regardless of the measure used to control for sampling effort (table 2). Geographic range size was a significant predictor of viral PSR for two of three methods for controlling sampling effort. In phylogenetic tests, population density was statistically significant when using all three measures of sampling effort, with longevity significant in two tests. Geographic range was statistically significant in all three tests but only when outliers were included.

In the stepwise regression models using contrasts and species values, body mass, day range length, geographic

Table 4: Multivariate analysis of helminth parasite species richness

	Nonphylogenetic analyses (species values, $N = 79$)		Phylogenetic analyses (independent contrasts, $N = 74$)	
	Body mass	Density	Body mass	Density
RLG	2.29*	.73	1.66	2.19*
WOS	2.23*	.85	1.89*	2.43*
Animals sampled	1.69	.18	1.42	2.41*

Note: Model is helminth parasite species richness = host body mass + population density + sampling effort. Multiple regression models were based on factors significant in stepwise regression analyses. Table provides *t*-statistics, with the direction of the *t*-statistic indicating the sign of the regression coefficient. Results are shown for tests based on both raw species values (nonphylogenetic) and independent contrasts (phylogenetic analyses) and for three different measures of sampling effort (RLG = Research Libraries Group database, WOS = Web of Science citation). Sampling effort was statistically significant in all tests (results not shown in table). Significance is based on directed tests.

* $P < .05$.

Table 5: Multivariate analysis of protozoan parasite species richness

	Nonphylogenetic analyses (species values, $N = 51$)			Phylogenetic analyses (independent contrasts, $N = 49$)		
	Mass	Longevity	Density	Mass	Longevity	Density
RLG	−.43	2.20*	1.35	−.26	2.59**	2.35*
WOS	−.19	1.88*	1.47	−.03	2.35*	2.62**
Animals sampled	−.014	1.76	1.70	−.61	2.44*	3.22**

Note: Model is protozoan parasite species richness = host body mass + longevity + population density + sampling effort. Multiple regression models were based on factors significant in stepwise regression analyses. Table provides *t*-statistics, with the direction of the *t*-statistic indicating the sign of the regression coefficient. Results are shown for tests based on both raw species values (nonphylogenetic) and independent contrasts (phylogenetic analyses) and for three different measures of sampling effort (RLG = Research Libraries Group database, WOS = Web of Science citations). Sampling effort was statistically significant in all phylogenetic tests (results not shown in table) but in only one nonphylogenetic test (for number of animals sampled). Significance is based on directed tests.

* $P < .05$.

** $P < .01$.

range size, and population density were entered in two or more tests. These variables were therefore used in the final multivariate model. All four host traits explained significant variation in virus PSR in two or more tests (table 6). However, only population density was statistically significant in all phylogenetic and nonphylogenetic tests, regardless of the measure of sampling effort used. Body mass was highly significant in analyses of species values, but this variable became nonsignificant once phylogeny was taken into account. Day journey length was significant in all three phylogenetic tests. When outliers were included in the phylogenetic tests, geographic range, day journey length, and population density were significant regardless of the method used to control for sampling effort.

Finally, we examined the role of substrate use in explaining variation in virus PSR. In multiple regression analyses, terrestriality was not a significant predictor of virus PSR for any measures of sampling effort (e.g., WOS: independent contrasts, $b_{\%\,\text{terrestrial}} = 0.053$, $F = 0.53$, df $= 1, 32$, $P = .29$; species values, $b_{\%\,\text{terrestrial}} = -0.042$, $F = 0.42$, df $= 1, 33$, $P = .93$, directed tests). We tested whether a combination of terrestrial substrates and wooded habitats leads to increased virus PSR but again found no significant effects for all measures of sampling effort (WOS: seven of 13 contrasts positive, $t_{12} = -0.51$, $P = .86$, directed test).

Discussion

Patterns of parasite community diversity in anthropoid primates indicate that several features of host ecology and life history may affect the colonization, spread, diversification, and persistence of parasites. This observation is consistent with a growing number of comparative studies that have demonstrated links between parasite diversity and host traits such as body size, group size, and popu-

Table 6: Multivariate analysis of viral parasite species richness

	Nonphylogenetic analyses (species values, $N = 69$)				Phylogenetic analyses (independent contrasts, $N = 64$)			
	Mass	Geographic range	Day journey length	Density	Mass	Geographic range	Day journey length	Density
RLG	3.74***	2.02*	1.60	2.28*	1.09	1.27	2.23*	3.22**
WOS	3.85***	1.32	1.66	2.45*	1.56	.36	2.10*	3.75***
Animals sampled	3.19**	2.03*	2.63**	2.33*	1.34	1.17	2.64**	3.27**

Note: Model is viral parasite species richness = host body mass + geographic range + day journey + population density + sampling effort. Multiple regression models were based on factors significant in stepwise regression analyses. Table provides *t*-statistics, with the direction of the *t*-statistic indicating the sign of the regression coefficient. Results are shown for tests based on both raw species values (nonphylogenetic) and independent contrasts (phylogenetic analyses) and for three different measures of sampling effort (RLG = Research Libraries Group database, WOS = Web of Science citations). Sampling effort was statistically significant in all tests (results not shown in table). Significance is based on directed tests.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

lation density (e.g., Davies et al. 1991; Poulin 1995; Gregory et al. 1996; Morand and Poulin 1998; Arneberg 2001). Our study extends this general approach by investigating a broader taxonomic range of parasites and using multiple measures of sampling effort. Moreover, primates are a well-studied mammalian clade, and the data set we compiled enabled us to investigate the effects of multiple host traits in a phylogenetic framework. Such an approach is essential for analyses of PSR because the hypotheses are not mutually exclusive, factors predicted to have strong effects often covary, and host traits, such as body size, are shared through common descent and often are correlated with other traits under consideration.

In our study, the strongest results emerged from analyses of the effects of population density, with the diversity of all three major classes of parasites increasing with greater host density. Our analyses therefore demonstrate that epidemiological processes operating within populations provide explanations for broad patterns of parasite biodiversity across species. Epidemiological models of directly transmitted parasites predict that host density is of central importance to the transmission of infectious diseases because this variable often sets the threshold for successful parasite invasion and spread. Among these parasites, for example, expressions for R_0 (the basic reproductive number that governs parasite establishment) depend on the density of susceptible hosts, a transmission coefficient, and the duration of infectiousness for individual hosts (Anderson and May 1991; Roberts et al. 2002). Comparative studies in other host-parasite systems also have demonstrated the importance of increased host density in explaining higher parasite prevalence and species richness (e.g., Morand and Poulin 1998; Arneberg 2001) when testing a smaller number of predictor variables. Within-species studies support a similar trend, with greater parasite prevalence or incidence associated with increasing numbers of susceptible animals (Dobson and Meager 1996; Packer et al. 1999). By governing transmission rates within host populations, host density may be of overriding importance in predicting which host species are most heavily parasitized in free-living populations.

Body mass was correlated with the size of the parasite community in most nonphylogenetic tests, although many of these results became nonsignificant once host phylogeny was taken into account (fig. 4). Host body size has been shown to explain the diversity of parasitic arthropods and helminths infecting birds, fish, and some mammals (e.g., Kuris et al. 1980; Guegan et al. 1992; Poulin 1995; Gregory et al. 1996; Morand and Poulin 1998; Clayton and Walther 2001). A previous study of parasites in vertebrates also found that results involving body mass differed in phylogenetic and nonphylogenetic analyses, depending on host taxa examined (Poulin 1995; Morand and Poulin 1998).

Several factors may account for differences that emerge when body mass is examined using independent contrasts and species values. First, predictions involving body mass involve many different factors, including niches available for parasite colonization, ingestion of parasites through increased metabolic needs, and the correlated effects of life history (see "Body size and life history" in the introduction to this article). Better control of such factors may provide more consistent results in phylogenetic and nonphylogenetic tests. In our multivariate analyses, however, results often remained different in analyses of species values and independent contrasts. Second, collinearity among the predictor variables may lead to unstable statistical models, possibly affecting nonphylogenetic and phylogenetic tests differently. Such problems can be detected with variance inflation factors (VIF) greater than 10 (Petraitis et al. 1996). In our contrasts analyses, however, VIF_{max} was always less than 7, whereas analyses of species values produced a $\text{VIF} > 20$ for body mass in some tests that included multiple predictor variables. Thus, our contrasts analyses are unlikely to be affected by unusually high collinearity, consistent with some expectations that the method of independent contrasts controls for confounding variables (for discussion of this issue, see Price 1997; Nunn and Barton 2000, 2001). Finally, differences in phylogenetic and nonphylogenetic tests may be due to grade shifts (i.e., a similar allometric exponent but different *y*-intercept), which will impact nonphylogenetic tests to a greater extent than tests that control for phylogeny (Nunn and Barton 2000, 2001). Thus, New World monkeys tended to be smaller in body mass and have slightly lower overall PSR (see figs. 1, 4). Independent contrasts controls for this grade shift by reducing the many data points for New World monkeys in figure 4*A* to a single contrast with Old World primates in figure 4*B* (see figure legend), but this contrast was not indicative of a large-grade shift. Thus, further research is needed to investigate the factors that cause body mass to become nonsignificant when phylogeny is taken into account.

In addition to body mass and population density, several other variables were significant in multivariate models. The positive effect of habitat diversity, as measured by day journey length and geographic range size, was supported in tests of viral PSR. Geographic range also was significant in focused tests of protozoa. Both of these factors are likely to increase the duration or geographic area over which hosts come into contact with new parasites. In fact, a large number of viruses in our data set are generalists (capable of infecting hosts in different families or orders), such as flaviviruses (St. Louis encephalitis, yellow fever virus) and bunyaviruses (Manzanilla, Melao, and Oropouche fevers).

Geographic range size has been shown to correlate positively with the diversity of helminths and ectoparasites in birds, reptiles, fish, and some mammals (e.g., Aho 1990; Gregory 1990; Feliu et al. 2001). However, few previous studies have examined this variable using phylogenetic comparative methods. An important variable to investigate in future research is geographic range overlap among primate species and other mammalian taxa. In particular, wide-ranging species are more likely to overlap with other host taxa, increasing the probability of host shifts (for specialist parasites) or host sharing (for generalist parasites) and thus increasing the size of the parasite community.

Total population size is an important variable to include in future comparative tests of parasite diversity because this may influence the size of the parasite community through island biogeographic effects. Estimates of total population size are unavailable for most primate species, but this variable can be estimated as geographic range size multiplied by population density. We chose not to analyze this derived variable in this article because the results would not be independent of results involving population density and geographic range size. Given our significant results with population density and geographic range size (table 2), however, total population size should be included in future tests when independent estimates of this variable become available.

In several analyses, we found support for positive effects of host longevity on PSR, but these results depended on the inclusion of outliers. These analyses therefore highlight the importance of examining contrasts plots closely because single data points (species differences) may have high leverage, leading to spurious results when patterns are not general to the broader group of species being investigated (Nunn and Barton 2000). Nonetheless, a limited number of previous studies have found significant links with host life history and parasite diversity. Among freshwater fish, for example, longevity has been shown to correlate positively with the diversity of helminths (Morand 2000). A study of mammalian parasites found that the prevalence of infection increased with body mass and that sex biases in prevalence were correlated with sexual dimorphism and male-biased mortality (Moore and Wilson 2002).

A recent analysis showed that mating promiscuity in primates is associated with elevated leukocyte counts, suggesting that promiscuous species experience greater risk of infection by sexually transmitted parasites (Nunn et al. 2000; Nunn 2002). In our study, we found no effect of mating promiscuity on parasite diversity, but this may simply reflect that little is known about sexually transmitted diseases (STDs) in wild primates. Records of STDs in natural populations are mainly from Old World monkeys and apes in which viral STDs, such as simian immunodeficiency virus and simian T-lymphotropic virus, are well characterized (Lockhart et al. 1996; Nunn and Altizer, in press). Thus, an effect of mating system may be found when more is known about STDs across a diverse array of primates.

Previous research has shown effects of habitat type on parasite diversity (e.g., Dobson and Pacala 1992; Dobson et al. 1992), but we found no effect of substrate use or terrestriality on primate parasites and infectious diseases. We also found no consistent effects of diet on the diversity of primate parasites. Diet has been shown to be an important predictor of helminths in birds and fish, with omnivory associated with greater parasite diversity (e.g., Bell and Burt 1991; Guegan and Kennedy 1993; Galaktionov 1996). It is perhaps not surprising that we found no effects of insects in the diet because the majority of parasites in our data set were directly transmitted and not linked with trophic transmission. Moreover, by removing prosimians from analyses, we excluded a major group of insectivorous primates. Further tests involving the effect of insectivory should focus specifically on parasites with intermediate hosts or complex life cycles.

More detailed studies are needed to better understand the links between host traits and parasite diversity. In our study, for example, population density had an overriding influence on PSR, but other measures of social contact involving group size and mating promiscuity were largely nonsignificant, particularly in multivariate and phylogenetic tests. Previous studies have shown that host gregariousness or sociality as measured by schooling behavior in fishes has significant positive effects on the diversity of gill parasites and ectoparasites (e.g., Caro et al. 1997; Raibaut et al. 1998). Moreover, a meta-analysis of mammalian parasites showed that social group size was significantly associated with parasitism within species (Côté and Poulin 1995). One explanation for our failure to identify social and mating parameters as important predictors of parasite diversity is that highly social host species, such as primates, may exhibit a range of defense mechanisms to limit disease spread. Thus, host species with high parasite pressure may have evolved immune defenses to limit parasite transmission or physiological resistance to infection on exposure. Studies of leukocyte counts, however, found no association between basal white blood cell counts and measures of host sociality (Nunn et al. 2000; Nunn 2002; Semple et al. 2002). Behavioral defenses are another means of reducing the risk of acquiring infectious disease (Hart 1990; Møller et al. 1993). Behavioral counterstrategies are poorly studied in wild primates (Nunn 2003; Nunn and Altizer, in press), and further research is needed to explore the relationships between parasite transmission, sociality, host defenses, and patterns of parasitism.

An additional factor that may have obscured effects of

group size is that our analyses lumped together parasites exhibiting a wide diversity of transmission modes and patterns of host specificity. Even among the subgroups of parasites that we examined, such as viruses or helminths, infectious agents spanned a broad diversity of transmission strategies, degrees of host specificity, and effects on host fitness. Thus, an important next step is to categorize parasites according to their primary transmission modes to more clearly identify processes affecting disease invasion and persistence. For example, parasites in most major classes can be spread through aerosol or direct contact, by biting vectors, in contaminated water or soil, by sexual transmission, or by other routes. A more mechanistic prediction to test, then, is that social group size should correlate with the diversity of parasites transmitted by direct contact. Such distinctions between social factors associated with directly versus indirectly transmitted parasites have been demonstrated previously in a meta-analysis of mammalian parasites (Côté and Poulin 1995).

A final factor relevant to the effects of sociality concerns the scale of the analysis. In our study, we examined patterns across species, but investigation of within-species variation may reveal different patterns. For example, the effects of population density on parasite persistence are predicted to arise from individual social interactions within populations. Although such processes can explain the interspecific variability examined here, intraspecific analyses may provide new insights into the mechanisms that underlie global cross-species patterns. Until recently, most parasitological studies of primates have not provided the kinds of detailed information on host characteristics, such as local population density or group size, needed to examine patterns within species. But it is possible to examine PSR in primate communities that have been particularly well sampled by primatologists and parasitologists, such as those in biological reserves (V. Ezenwa, S. Altizer, and C. Nunn, unpublished data).

Understanding patterns of PSR is critical for conserving biodiversity, including the natural diversity of parasites themselves. Parasites are an important factor driving the current human-induced global biodiversity crisis, although research on their impacts has been scarce. Threats include introductions of parasites into native ecosystems and increases in native parasites because of climate warming or other ecological changes (Daszak et al. 2000; Dobson and Foufopoulus 2001). Environmental changes, especially climatic changes, will likely influence the decline and extinction of species through increased disease risk (Daszak et al. 2001; Harvell et al. 2002). A broad comparative approach is essential for understanding the natural role of parasites in biodiversity research and for developing predictive models to identify species at greatest risk from infectious diseases.

In summary, our analyses of PSR in a well-studied host group demonstrated that broad patterns of parasite diversity were explained by a relatively small number of host characteristics, especially host population density and to a lesser degree body mass, geographic range size, day journey length, and longevity. Thus, several processes central to host biology are likely to generate and constrain the diversity of host-parasite systems. A better understanding of these processes should provide insights to the types of diseases that affect rare or threatened species. Moreover, further details on parasite characteristics, including specificity, transmission mode, and effects on host fitness, will allow us to investigate the role of a larger number of predictor variables and test process-oriented hypotheses about host-parasite combinations that occur in wild populations.

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