Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2007) **16**, 496–509

RESEARCH PAPER

Parasite species richness in carnivores: effects of host body mass, latitude, geographical range and population density

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ABSTRACT

Aim Comparative studies have revealed strong links between ecological factors and the number of parasite species harboured by different hosts, but studies of different taxonomic host groups have produced inconsistent results. As a step towards understanding the general patterns of parasite species richness, we present results from a new comprehensive data base of over 7000 host–parasite combinations representing 146 species of carnivores (Mammalia: Carnivora) and 980 species of parasites.

Methods We used both phylogenetic and non-phylogenetic comparative methods while controlling for unequal sampling effort within a multivariate framework to ascertain the main determinants of parasite species richness in carnivores.

Results We found that body mass, population density, geographical range size and distance from the equator are correlated with overall parasite species richness in fissiped carnivores. When parasites are classified by transmission mode, body mass and home range area are the main determinants of the richness of parasites spread by close contact between hosts, and population density, geographical range size and distance from the equator account for the diversity of parasites that are not dependent on close contact. For generalist parasites, population density, geographical range size and latitude are the primary predictors of parasite species richness. We found no significant ecological correlates for the richness of specialist or vector-borne parasites.

Main conclusions Although we found that parasite species richness increases instead of decreases with distance from the equator, other comparative patterns in carnivores support previous findings in primates, suggesting that similar ecological factors operate in both these independent evolutionary lineages.

Keywords

Biogeography, body mass, carnivores, comparative study, geographical range, parasite species richness, phylogeny, population density.

INTRODUCTION

Parasites play a major role in the lives of animals, with effects ranging from negative impacts on host population size to the evolution of host behaviours to combat parasites. For example, studies have shown that parasites regulate population sizes (Hudson *et al.*, 1998; Tompkins *et al.*, 2002) and may be responsible for extinction (or near extinction) of some host species (Warner, 1968; van Riper *et al.*, 1986; de Castro & Bolker, 2005). Through parasite-mediated competition, parasites might even influence the composition of host communities (Barbehenn, 1969; Price *et al.*, 1988). Parasites have also been proposed to account for a wide variety of behavioural and morphological traits (Moore, 2002), including sexually selected traits (Hamilton & Zuk, 1982), consumption of specific dietary items (e.g. medicinal plants; Lozano, 1998; Huffman, 2001) and grouping patterns to reduce attacks from flying insects (Mooring & Hart, 1992).

Despite the fundamental role of parasites in animal behaviour, ecology and evolution, we lack an understanding of which host traits correlate with the number of parasites that infect different species (i.e. parasite species richness; Poulin & Morand, 2004). Understanding such patterns can reveal the ecological processes

DOI: 10.1111/j.1466-8238.2006.00301.x

that underlie differences in parasite communities, while also shedding light on the evolutionary diversity of host and parasite traits. Previous studies of mammals have identified geographical range size, body mass and diet as factors influencing parasite species richness (reviewed in Poulin & Morand, 2004). Recent studies have also found support for an effect of basal metabolic rate (Morand & Harvey, 2000), latitude (Nunn *et al.*, 2005) and population density (Nunn *et al.*, 2003a). Some results have been sensitive to methodology, such as controlling for phylogeny (Poulin, 1995; Nunn *et al.*, 2003a). In order to understand the general factors that influence parasite diversity across all host species, it is essential to test a broad suite of hypotheses in multiple, evolutionarily independent clades. In addition, it is necessary to investigate patterns of parasite species richness in a phylogenetic context, with the goal to test whether evolutionary changes in host traits are associated with changes in parasite species richness. By focusing our tests on carnivores, a well-studied mammalian clade, we are able to assess a wide array of host traits that may account for variation in parasite diversity, while also controlling for host phylogeny. We organize our predictions around four main sets of variables involving body mass and life history, social contact, habitat use and biogeography (see also Nunn *et al.*, 2003a).

Body mass and life-history traits

A number of factors are predicted to produce a positive association between host body mass and parasite species richness. Larger-bodied hosts are expected to have more niches available for colonization by parasites, including a larger surface area for ectoparasites (Kuris *et al.*, 1980; Morand, 2000). Hosts with larger body mass also consume a greater quantity of food and may therefore ingest more endoparasites. Finally, larger-bodied carnivores have slower life histories (Gittleman, 1993), which could affect patterns of parasite species richness because lower host mortality rates increase the ability of parasites to become established in host populations (Anderson & May, 1979; Thrall *et al.*, 1993; De Leo & Dobson, 1996; Altizer & Augustine, 1997) and longer-lived hosts encounter more parasites throughout their lifetimes (Pacala & Dobson, 1988; Bell & Burt, 1991). Thus, we predict that associations between parasite diversity and host longevity remain statistically significant after controlling for body mass.

Social contact

Many parasites in populations of wild carnivores spread directly from one host to another without an intermediate developmental stage (direct transmission). Examples include the viruses that cause canine distemper and rabies (Funk *et al.*, 2001). Social interactions form the network through which these parasites spread in a population, as studied using epidemiological models based on the basic reproductive number, R_0 (Anderson & May, 1991). These models predict that a parasite will be maintained in a population when $R_0 > 1$. Thus, hosts living at high density or with frequent intraspecific contacts are expected to accumulate more parasite species. Similarly, any behaviours that involve increased contact among individual hosts will increase R_0, predicting increased parasite species richness (reviewed in Morand, 2000; Poulin & Morand, 2004). Such an effect is expected from epidemiological theory because, all else being equal, animals living at a higher density will tend to have a higher rate of encounter with conspecifics. To account for other sources of variation in social contact we also examine mating system.

Ecology and habitat use

Animals acquire parasites from the environment, including through faecal contamination of water and food sources, exposure to vectors and consumption of paratenic, transport and intermediate hosts (collectively referred to in this paper as intermediate hosts). An animal with a larger home range size should come into contact with more parasites, leading to increased parasite species richness (e.g. Mohr & Stumpf, 1964). Similarly, consumption of animals, including insects, is likely to lead to increased risk of infection with indirectly transmitted parasites, including *Toxoplasma gondii* and a wide variety of helminths (Woodroffe *et al.*, 2004). Thus, we predict that parasite diversity in carnivore hosts increases with home range size, day range length and increasing percentage of animals in the diet.

Biogeography

Biogeography may influence patterns of parasite species richness if disease risk varies among geographical locations, or if a host is exposed to a wider diversity of habitats at the population and species level (as compared to the individual level for predictions involving home range size). Thus, a host species with a larger geographical range may occupy more different habitats, or come into contact with a larger number of other host species, leading to higher parasite species richness. Alternatively, a larger geographical range may indicate that a species has a larger number of host individuals, increasing the likelihood that more parasites become established (Bagge *et al.*, 2004). Latitude is a major biogeographical factor that might influence parasite diversity, with parasite species richness expected to follow the latitudinal gradient found in free-living species (Poulin & Rohde, 1997; Møller, 1998; Guernier *et al.*, 2004; Nunn *et al.*, 2005). Thus, we also predict that parasite diversity increases closer to the equator.

Many of these hypotheses apply differently to different subdivisions of parasites, including both taxonomic subdivisions and subdivisions based on parasite transmission mode and host specificity. We predict that parasites that require close contact among hosts for transmission will be more numerous in species that exhibit a greater level of social contact, while the same is not expected for parasite species that are less dependent on transmission by close contact. Similarly, generalist parasites that can infect a wide range of species should closely map onto hosts having high population density and large geographical range size. Specialist parasites should also correlate with these host traits, but the effects should be stronger for patterns of generalist parasite richness.

For comparison with previous studies, and to maximize sample size, we focused on measures of diversity involving the total

number of parasites (parasite species richness). Other approaches are available to quantify parasite diversity, including phylogenetic distinctness of the parasite community and nestedness (e.g. Poulin & Morand, 2000; Webb *et al.*, 2002; Guernier *et al.*, 2004; Guégan *et al.*, 2005). Application of these methods, however, would have entailed a substantial reduction in our sample sizes (number of host species) due to exclusion of parasite data for which we lacked suitable measures of phylogenetic relatedness and occurrence. Sampling biases can also affect the number of parasites documented in different host species, with variation in parasite species counts attributable to how well each host species has been sampled for parasites (Gregory, 1990; Arneberg, 2002). Thus, a parasite may be missing from a host because it does not occur or because the host has been sampled insufficiently to discover the parasite. Similarly, parasite species diversity may be more similar among closely related hosts (e.g. Nunn *et al.*, 2003a), thus requiring information on host phylogeny to identify independent evolutionary changes in parasite richness (Poulin, 1995; Morand, 2000). We therefore implemented controls for both sampling effort and phylogeny in our comparative tests of parasite richness.

Carnivores are an excellent group for investigating these variables because they provide the intrinsic variation required for testing a wide range of predictions across species: carnivores exhibit greater variation in body size than any other mammalian order (Gittleman, 1985), reproduce as slowly as one young every 5–7 years (e.g. giant panda, *Ailuropoda melanoleuca*) or as fast as two litters a year with up to 12 young in a litter (e.g. least weasel, *Mustela nivalis*; Gittleman, 1993), inhabit nearly every habitat or vegetational zone (Sunquist & Sunquist, 1989) and reside on all continents except Antarctica (Gittleman & Gompper, 2005). Further, carnivores exhibit substantial variation in both mating system (polygyny, monogamy, promiscuity and polyandry) and social group size, ranging from strictly solitary in most carnivore species to as many as 80 individuals in spotted hyenas, *Crocuta crocuta* (Gittleman, 1989; Creel & Macdonald, 1995). The magnitude of this interspecific variation is substantially greater across than within species, providing higher statistical power for testing hypotheses.

MATERIALS AND METHODS

Data on host–parasite combinations

We collected data on microparasites (viruses, bacteria, protozoa and fungi) and macroparasites (helminths and arthropods) naturally occurring in wild carnivore populations by conducting a systematic search of the literature. The data were compiled using the online data base Web of Science (http://isi3.isiknowledge.com) from 1986 to 2002, which provided over 812 references. We searched for Latin binomials following the taxonomy of Wilson & Reeder (1993) and using common generic synonyms. We compiled abstracts from this search, and based on abstracts and titles we identified publications to obtain and include in the data base. Both primary and secondary data sources were used to construct the data base, but only data from wild populations were entered into the data base. The large amount of information available on parasites in carnivores limited our ability to search other online data bases, including those that might provide additional information. For similar reasons, we did not search books and book chapters that are not indexed in online data bases. Even by limiting our search to 16 years of literature, we had almost four times as much data as was gathered for 119 species of primates (for which the literature was searched extensively across all years and available resources; Nunn & Altizer, 2005).

For each host–parasite combination in these sources, we recorded parasite taxonomy (helminth, protozoan, virus, arthropod, bacteria and fungus), sampling locality, dates of sampling and information on the number of animals sampled. Parasites were scored into transmission categories of 'close' or 'non-close' based on whether close/direct host-to-host contact is required for successful parasite transmission. Parasites transmitted by physical contact between hosts, including sexual and vertical transmission, were classified as having transmission via 'close contact', while parasites transmitted by fomites (surfaces contaminated by infected material) or contact with contaminated soil, food or water were classified as having transmission via 'non-close contact'. Vector transmission was assigned to parasites that require an arthropod vector for transmission. Further, 'indirectly' transmitted parasites are those transmitted via vector and intermediate hosts and which thus do not require contact between two hosts of the same species, while 'directly' transmitted parasites are transmitted via social or sexual contact, vertically from mother to offspring, through contact with fomites or by other forms of non-close contact. The categories of 'close' and 'non-close' contact are not mutually exclusive and are not equivalent to 'direct' versus 'indirect' transmission – the former classification refers to spatial requirements for transmission, while the latter refers to the parasite's life cycle. Given that transmission categories overlap and parasites are capable of being spread via different transmission routes, a parasite could belong to several categories.

We also classified parasites as being either 'generalists' or 'specialists'. Generalist parasites were those that had been recorded as infecting more than one family within the Carnivora, or as infecting carnivores in addition to species in other mammalian orders. Specialist parasites were those that had been recorded only from species within a single family within the Carnivora and for which there are no records of them infecting non-carnivores. As for the parasite species richness data, only records from nature were used for classifying parasites into generalist and specialist categories; artificial or experimental infections were not included.

To deal with variation in the number of parasites recorded due to differential sampling effort, we followed previous studies by including a measure of sampling effort in the analyses (Poulin, 1995, 1998; Walther *et al.*, 1995; Poulin & Rohde, 1997; Morand, 2000; Morand & Harvey, 2000; Arneberg, 2002), specifically by using the number of citations for each species (Gregory, 1990; Nunn *et al.*, 2003a, 2004, 2005; Vitone *et al.*, 2004). For the broad-scale analysis conducted here, citation counts offer several advantages over other approaches for controlling for sampling effort: they are easy to calculate in a consistent way for each host species; they help to deal with differences in studies carried out

for different purposes (which can affect sample sizes); and citation counts deal with ambiguity in whether sample size reflects the number of animals or the number of samples (e.g. in studies that collect faecal samples, or when populations are sampled in which animals are not individually identified). In addition, sample sizes were not provided for all studies; thus, such studies would have been excluded (or sample sizes estimated) if we relied on sampling effort measured as the summed sample sizes from the studies on a particular species.

To obtain data on citation counts, we noted the total number of references found for each host species in the Web of Science bibliographic data base. This measure was highly correlated with other estimates of sampling effort, such as the number of citations per host species using only citations that involve studies of parasites (regression $P < 0.001$), or the number of individuals sampled in the studies for each species ($P = 0.009$). We report only results using the total number of citations per host to correct for sampling effort as a covariate in multivariate tests; this variable explained 60% of the variance in overall parasite species richness ($P < 0.001$, $R^2 = 0.602$). No lower limit for inclusion was enforced on the citation counts. Since the inclusion of lower citation counts can be expected to increase the noise in the data simply by chance, we checked for potential problems by repeating all non-phylogenetic multivariate analyses using only species in which citation counts were larger than 10. Introducing this limit did not alter the results qualitatively; we therefore present results from analyses with all data included. In the tests on the presence of phylogenetic signal and to represent parasite species richness in bivariate plots, we used residual parasite species richness, which was calculated by regressing the number of parasites onto the number of citations per host.

Because the number of citations and measures of parasite species richness deviated significantly from a normal distribution, these measures were $\log_{10}$-transformed prior to analysis. Moreover, the relationship between sampling effort (citation counts) and the total number of parasites revealed a nonlinear pattern in non-phylogenetic tests. This nonlinear relationship held in the subdivisions of the data among different groups of parasites, with the exception of helminths, viruses and vector-borne parasites. In terms of host taxonomic divisions, nonlinearity was found only in fissiped (largely terrestrial) carnivores (Fig. 1). To investigate the consequences and degree of nonlinearity, we included a quadratic term for citation counts in multivariate analyses (see below) and conducted statistical tests to determine whether inclusion of this term explained significant variation in the multivariate model (Quinn & Keough, 2002). A significant influence of the quadratic term was found only for bacterial parasite species richness, and inclusion/exclusion of the quadratic term in this case did not change the significance levels of the other variables. From these results, we concluded that nonlinearity had little effect on the statistical results, and we therefore present analyses using a linear model. For tests of phylogenetic signal, however, we utilized residuals calculated including a quadratic term in the cases where it was significant, but its inclusion/exclusion had no influence on the conclusions of the test.

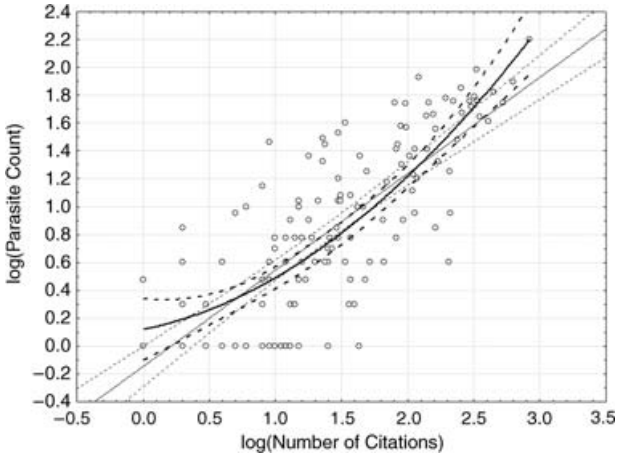

Figure 1 Parasite counts plotted against citation counts for fissiped carnivores. The linear regression is significant (thin line; $P < 0.001$), but an added quadratic term is also significant (thick line; $P = 0.002$) indicating a nonlinear component in the relationship between the two variables. Due to this, the influence of a quadratic term is tested in multivariate analyses. Dashed lines indicate 95% confidence intervals.

Data on host characteristics

We obtained data on adult body mass (g), maximum longevity (months), population density (individuals km^{-2}), home range area (km^2), day range length (km) and mating system (polyandrous, monogamous, promiscuous or polygynous) from the PanTHERIA v.1 data base (K.E. Jones *et al.*, in prep.), which has been compiled to summarize key comparative variables among mammal species, including body size, behaviour, life-history traits and geographical distribution. PanTHERIA contains 99,720 lines of data from over 3300 primary and secondary sources collected over a 2-year period by a collaboration of three academic institutions. Data were entered using a standardized data input protocol and source papers were found systematically from the most relevant journals and secondary sources (e.g. *Journal of Mammalogy*, *Mammalia*, *Journal of Zoology*; Hayssen *et al.*, 1993). Further sources for particular variables, clades or individual species were found using the electronic search engine Web of Science (http://isi3.isiknowledge.com). Taxonomic accuracy was ensured by referring to Wilson & Reeder (1993), which is the most current taxonomic source that matches the phylogeny used for the analysis (Bininda-Emonds *et al.*, 1999) and also includes species synonyms (taxon names that are no longer valid). Synonyms are crucial in order to collate species data into a common taxonomic reference for analysis from different sources. We checked the entries for inconsistencies and complemented the data set when additional data were available (see Kitchener, 1991; Creel & Macdonald, 1995; Nowell & Jackson, 1996; Mills & Hofer, 1998; Creel & Creel, 2002; Sunquist & Sunquist, 2002; Macdonald & Sillero-Zubiri, 2004). All these variables were $\log_{10}$-transformed prior to analysis to meet the assumption of normally distributed data.

Table 1 Host traits used in the analyses. Sample sizes were confined to those species with estimates of parasite species richness

Variable	*n* carnivores	*n* fissipeds	*n* pinnipeds
Body mass (g)	146	116	30
Maximum longevity (months)	130	101	29
Population density (km^{-2})	87	72	15
Diet (% animal)	68	68	—
Home range area (km^2)	42	42	—
Day range length (km)	24	24	—
Geographical range size (km^2)	144	114	30
Average latitude (degrees)	111	111	(30)*
Mating system (PA, Mon, Prom, Pol)†	73	44	29

*Midpoint latitude.

†PA, polyandrous; Mon, monogamous; Prom, promiscuous; Pol, polygynous.

Species were classified as having one of four mating systems. These were ordered into degrees of increasing potential intramale sexual selection (polyandry, monogamy, polygynandry and polygyny) and treated as a continuous variable in statistical tests. This introduces an assumption of ordered evolution into the phylogenetic analyses, since mating systems coded this way are assumed to progress in changes through the different stages in an ordered way, e.g. from monogamy to polygyny via polygynandry, with changes from monogamy to polygyny thus being of larger magnitude than changes from monogamy to the other two classes. We therefore checked our results by also using mating system as a categorical variable with the BRUNCH option in CAIC (Purvis & Rambaut, 1995; see below). As no substantial differences were found, we report the results from the continuous analyses here.

A measure of dietary composition (proportion of vertebrate and invertebrate animals in the diet) was obtained (Gittleman & Harvey, 1982; Carbone & Gittleman, 2002), as were data on geographical range sizes and average latitudes. Diet was measured as a percentage and deviated significantly from a normal distribution; thus, it was arcsine square-root transformed prior to analysis. Geographical ranges were compiled using published primary and secondary literature for each species (W. Sechrest, unpublished). The composite range maps were digitized into a geographical information system (GIS) and an equal-area projection (Behrmann) was used to calculate range size. Values were then cube-root transformed to make them normally distributed. Average latitudes were calculated by converting the ranges into 0.5° cells and then averaging latitudes of the centre of all cells. The absolute values of the average latitudes were square-root transformed prior to analysis to get a normally distributed measure of each species' average distance from the equator. Midpoint latitudes (rather than averages) were used for pinnipeds due to difficulties of quantifying the geographical range for these wide-ranging, migratory species.

Table 1 summarizes the variables that we obtained for use in this analysis, along with information on sample sizes. Sample sizes were confined to those species that had some estimate of parasite species richness.

Comparative methods and statistics

We analysed the data using standard statistical tests that treated each species value as statistically independent (non-phylogenetic tests), and then repeated the analyses using phylogenetically independent contrasts (Felsenstein, 1985). Phylogenetic information was obtained from Bininda-Emonds *et al.* (1999). The method of independent contrasts assumes that trait values are shared among closely related species through common descent. The primary data in our analyses — counts of the number of parasite species — are not shared through common descent via the same biological mechanisms as other traits, such as body mass. We therefore tested the assumption that more closely related species share more similar trait values using the method suggested by Blomberg *et al.* (2003), as implemented in the MATLAB program PHYSIG. We found a significant, or almost significant, phylogenetic signal for all host traits except mating system, geographical range size and average distance from the equator, and no phylogenetic signal in the parasite species richness estimates (after controlling for citation counts using residuals), except for tendencies towards significant effects among parasites transmitted via close or non-close contact (Table 2).

These results point to difficulties in the interpretation of the analyses of the influence of host traits — many with significant indicators of phylogenetic signal — on parasite species richness — where such a signal is largely absent for this group of mammals. To make certain that our conclusions are robust, we therefore focus on the findings where the phylogenetic and non-phylogenetic analyses yield the same results, which was the case in a surprisingly large subset of our results (see below).

Independent contrasts were calculated using the computer program CAIC (Purvis & Rambaut, 1995). We tested the assumptions of CAIC, as recommended by Garland *et al.* (1992) and in the CAIC manual. We found that log-transformed branch lengths best met the assumptions of independent contrasts and therefore report those results.

For both the phylogenetic and non-phylogenetic tests, we used multiple regression methods to identify predictor variables that best account for variation in parasite species richness. We

Table 2 Significance levels and *K* statistics for tests of phylogenetic signal. For this test, all measures of PSR (parasite species richness) were calculated as residuals after correcting for the effect of sampling effort. Only host species with data on parasite species richness were included in this analysis

Variable	*P* value	Blomerg *et al.*'s *K*	Variable	*P* value	Blomerg *et al.*'s *K*
Overall PSR*	0.299	0.083	No. of citations	0.378	0.072
Helminth PSR	0.353	0.083			
Bacteria PRS*	0.709	0.070	Body mass	0.000	0.584
Protozoan PSR*	0.538	0.064	Maximum longevity	0.000	0.237
Virus PSR	0.856	0.118	Population density	0.000	0.252
Close PSR*	0.067	0.111	Diet	0.005	0.280
Non-close PSR*	0.189	0.090	Home range area	0.011	0.217
Direct PSR*	0.065	0.112	Day range length	0.042	0.229
Indirect PSR*	0.382	0.074	Geographical range size	0.334	0.086
Vector PSR	0.718	0.092	Average latitude	0.003	0.134
Generalist PSR*	0.173	0.095	Mating system	0.000	0.726
Specialist PSR*	0.927	0.042			

*Residuals from a second-degree polynomial.

performed two main sets of analyses. First, we conducted 'focused' tests in which we investigated whether particular host traits individually accounted for variation in parasite species richness after controlling for sampling effort and body mass. Second, we addressed the possibility that multiple host traits influence parasite diversity by analysing the data with a stepwise multiple regression model. We used a forward stepwise model with all variables initially removed, since including all variables reduced the sample size of our data set to only 12 species with data on all of the variables in Table 1. We then sequentially added variables with significance levels of $P < 0.1$, and removed entered variables when significance exceeded this value. In order to control for correlations between body mass and other traits, as well as the links between sampling effort and parasite counts, body mass and citation counts were forced into the model at all steps. To deal with correlations among traits, including citation counts, we also calculated variance inflation factors (VIF). In all cases, however, VIFs were below 10, indicating that collinearity was unlikely to have a major impact on the stability of the multiple regression models (see Petraits *et al.*, 1996; Quinn & Keough, 2002). It is from these final multiple regression models, both phylogenetic and non-phylogenetic, that we identified host traits that correlate with parasite species richness.

Although the Carnivora are a well recognized monophyletic clade (Bininda-Emonds *et al.*, 1999), functional differences between the terrestrial (fissiped) and aquatic (pinniped) carnivores have been noted in previous comparative studies (Bininda-Emonds & Gittleman, 2000). From the focused tests (see Appendices S1–S3 in Supplementary Material), we observed that the causal agents explaining differences in parasite species richness differed between pinnipeds and fissipeds (terrestrial carnivores). Since we found no significant explanatory factors that account for variation in pinniped parasite species richness, we present the results for fissipeds only. For clarity, only significant or nearly significant ($0.05 < P < 0.10$), correlates of parasite species richness in the best possible multiple regression model are presented. Results of focused tests on all variables examined separately, as well as results for pinnipeds, are available in Appendices S1–S3.

RESULTS

General patterns

The final data base provided 7166 records of host–parasite combinations, with 2419 unique combinations representing 146 host species and 980 parasite species. Table 3 describes the data base with the parasites broken down in subgroups, while Table 4 describes the data with the host species broken down by family. The main carnivore family to be sampled for parasites was canids, accounting for 2456 positive parasite matches, with the red fox (*Vulpes vulpes*) accounting for 963 entries (159 parasites) on its own. Other well-sampled families were mustelids (1209 entries) and phocids (1193 entries). In contrast, herpestids, procyonids and viverrids were relatively poorly sampled for parasites (Table 4).

After controlling for sampling effort by calculating the residual overall parasite species richness from a regression of overall parasite species richness on the number of citations for each host species, we found significant differences among families of carnivores (ANOVA $P = 0.029$), with Fisher's LSD test indicating that bears and hyenas have significantly lower numbers of parasites than felids, canids, mustelids and otariids (Fig. 2).

Parasite type

The stepwise regression analysis using species values revealed that the significant predictors of overall parasite species richness in fissiped carnivores involve body mass, distance from the equator and geographical range (Table 5). As with other studies of parasite species richness (Poulin & Morand, 2004), sampling

Table 3 General information on the carnivore parasite data base by parasite type

	Unique host–parasite combinations	Number of host species	Number of parasite species
Total	2419	146	955
Helminths	1103	100	421
Bacteria	410	72	158
Viruses	333	93	97
Arthropods	288	61	147
Protozoa	264	81	117
Fungi	21	14	15
Close transmission	806	120	270
Non-close transmission	745	99	289
Direct transmission	827	121	278
Indirect transmission	1758	133	693
Vector transmission	168	73	73
Generalists	1596	137	519
Specialists	457	92	261

Table 4 General information on the carnivore parasite data base by host order

Host family	Number of recognized host species	Number of host species with parasite data	Unique host–parasite combinations	Total number of data points
Canidae	34	26	590	2456
Felidae	36	24	387	824
Herpestidae	37	9	47	100
Hyaenidae	4	3	12	32
Mustelidae	65	35	582	1209
Procyonidae	18	5	111	386
Ursidae	9	8	150	403
Viverridae	34	6	40	110
Odobenidae	1	1	8	43
Otariidae	14	11	177	410
Phocidae	19	18	315	1193
Carnivora	271	146	2419	7166

effort accounted for the most variation in parasite counts. Population density approached significance. All variables were in the predicted direction with the exception of latitude, with parasite diversity actually increasing with distance from the equator. Stepwise regression of independent contrasts revealed a similar pattern, with overall parasite diversity increasing with body mass, population density, geographical range size and distance from the equator (Table 5). When using independent contrasts, population density became highly significant, and the overall amount of variation explained increased.

Next, we investigated patterns in four groups of parasites reported in carnivores: helminths, protozoa, bacteria and viruses (Table 5). Arthropods were not examined separately because too few data points were available. The analyses revealed that helminth parasite species richness is higher in carnivores with larger geographical ranges and with increasing distance from the equator. As was the case for overall parasite species richness, analysis of independent contrasts revealed that population density was a significant predictor for helminth richness. For bacterial parasite species richness, fewer patterns emerged, with bacterial parasite species richness significantly lower in species with larger home ranges, but only when controlling for phylogeny. Protozoan parasite species richness showed a positive association with geographical range and, in the species analyses, with population density. No consistent correlates could be found for virus richness.

Parasite transmission mode

In tests that recalculated parasite species richness according to transmission mode, we found that the species richness of directly transmitted parasites and those spread by close contact were mainly associated with smaller home ranges, as indicated by the negative *t*-statistic in Table 6. Indirectly transmitted parasite

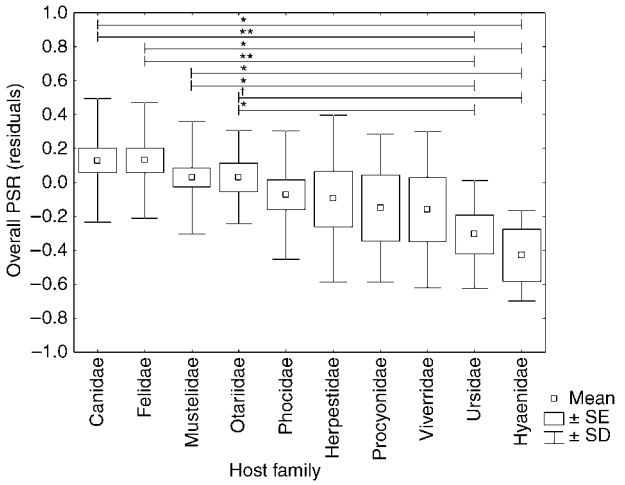

Figure 2 Overall parasite species richness (PSR) in 10 carnivore families (Odobenidae excluded because it contains only one species, the walrus) after controlling for sampling effort using least-squares residuals. The box plots show the means, standard errors and standard deviations. Lines marked with asterisks (*) indicate statistically significant differences (*indicates $0.01 < P < 0.05$, and ** indicates $0.001 < P < 0.01$), while †indicates $P = 0.051$ (Fisher's LSD tests). Ursids and hyenas have consistently fewer parasites and pathogens than do canids, felids, mustelids and otariids.

species, in contrast, are more numerous in host species with higher densities, larger geographical ranges and greater distance from the equator. This pattern is weakly replicated in the species analyses of non-closely transmitted parasites, with these three variables approaching significance ($P < 0.1$), while the only variable that showed a significant correlation in the phylogenetic analyses was geographical range size. Finally, we found that parasites spread through vector transmission are more numerous in species that consume fewer animals, although this test was not significant in the phylogenetic analyses.

In conclusion, the strongest results involved body mass and home range size (for parasites spread by close contact or by direct transmission), and geographical range size and population density (for parasites spread through non-close contact or indirectly).

Parasite host specificity

In analyses of specialist and generalist parasites, multivariate tests revealed that the richness of generalist parasites was correlated with population density, average latitude and geographical range size (the latter only approaching significance, $P < 0.01$, in non-phylogenetic tests; Table 7). Results for specialist parasites depended on the type of analysis conducted, with population density, geographical range size and diet statistically significant in the non-phylogenetic tests, and body mass (a negative effect) and day range length significant in the phylogenetic tests (Table 7).

DISCUSSION

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. Our analyses of fissiped carnivores showed that overall parasite species richness is higher in host species that are larger bodied, exhibit higher population densities, live further from the equator and cover larger geographical ranges. These results were obtained from both phylogenetic and non-phylogenetic tests. However, we also found that no general explanation for parasite diversity in carnivores exists, but rather that the determinants differ among different parasite groups, both in

Table 5 Parasite species richness (PSR) of different parasite types — multivariate analyses

	Overall PSR		Helminth PSR		Bacterial PSR		Protozoan PSR		Virus PSR	
Variable	Species	Contrasts	Species	Contrasts	Species‡	Contrasts	Species	Contrasts	Species	Contrasts
Body mass	2.251*	2.440*	−0.609	0.628	0.733	1.469	1.147	−1.138	2.760**	0.353
Maximum longevity										
Population density	1.930†	3.507***		2.745**			2.024*			
Mating system										
Home range area						−4.290***				
Day range length										
Diet										
Geographical range size	2.219*	2.419*	2.202*	1.722†			2.648*	2.452*		
Average latitude	2.374*	3.591***	2.319*	4.148***						
Adjusted model R^2	0.653***	0.716***	0.552***	0.668***	0.394***	0.556***	0.322***	0.356***	0.456***	0.337***

Numbers given are *t* values, significance levels are indicated by the number of asterisks: *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$; †indicates a variable included in the model where $0.05 < P < 0.1$. The sign indicates the direction of the effect, i.e. slope in the regression analysis. Body mass and sampling effort (results not shown but always significant) were forced into the stepwise analyses. 'Species' indicates results of non-phylogenetic analyses, whereas 'Contrasts' indicates results of phylogenetic analyses.

‡For bacterial PSR, the quadratic term of the citation counts was significant in the non-phylogenetic analyses. Its inclusion did not alter the results from the linear analysis as presented here, however.

Table 6 Parasite species richness (PSR) of parasites differing in transmission mode — multivariate analyses

	Close PSR		Non-close PSR		Direct PSR		Indirect PSR		Vector PSR	
Variable	Species	Contrasts	Species	Contrasts	Species	Contrasts	Species	Contrasts	Species	Contrasts
Body mass	2.004†	2.343*	1.229	−1.503	2.051*	2.388*	1.574	0.694	−0.587	−0.890
Maximum longevity										
Population density			1.978†				3.001**	3.344**		
Mating system										
Home range area	−1.893†	−2.575*			−1.923†	−2.624*				
Day range length										
Diet									−1.701†	
Geographical range size			1.761†	2.111*			2.497*	2.290*		
Average latitude			1.896†				2.259*	3.503***		
Adjusted model R^2	0.615***	0.551***	0.589***	0.538***	0.617***	0.557***	0.613***	0.691***	0.207**	0.142**

Numbers given are *t* values, significance levels are indicated by the number of asterisks: *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$; †indicates a non-significant variable included in the model where $0.05 < P < 0.1$. Body mass and sampling effort (results not shown but always significant) were forced into the stepwise analyses. 'Species' indicates results of non-phylogenetic analyses, whereas 'Contrasts' indicates results of phylogenetic analyses.

Table 7 Parasite species richness (PSR) of generalist and specialist parasites — multivariate analyses

	Generalist PSR		Specialist PSR	
Variable	Species	Contrasts	Species	Contrasts
Body mass	1.725†	2.583*	−0.108	−3.026**
Maximum longevity				
Population density	2.246*	3.746***	2.330*	
Mating system				
Home range area				
Day range length				3.386**
Diet			1.729†	
Geographical range size	1.832†	2.498*	1.715†	
Average latitude	2.616*	3.678***		
Adjusted model R^2	0.623***	0.682***	0.545***	0.369*

Numbers given are *t* values, significance levels are indicated by the number of asterisks: *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$; †indicates a non-significant variable included in the model where $P < 0.1$. Body mass and sampling effort (results not shown but always significant) were forced into the stepwise analyses. 'Species' indicates results of non-phylogenetic analyses, whereas 'Contrasts' indicates results of phylogenetic analyses.

terms of parasite taxonomy and among categories of parasites categorized according to specificity and transmission mode.

Larger-bodied hosts have previously been hypothesized to represent larger 'islands' for parasites to colonize, predicting that more parasites will be found in larger-bodied hosts. In addition, larger-bodied hosts require a greater intake of resources, potentially exposing these hosts to more infectious stages of parasites through incidental ingestion. Body mass was found to be significant in previous studies (reviewed in Poulin & Morand, 2004). In some studies, however, effects of body mass became non-significant after controlling for phylogeny (Poulin, 1995; Morand & Poulin, 1998; Nunn *et al.*, 2003a). In our study, body mass was significantly correlated with overall parasite species richness in both phylogenetic and non-phylogenetic tests. We also found that geographical range size was an important determinant of overall parasite diversity, possibly reflecting that a species covering a larger area encounters more parasite species. This lends support to previous studies of fish, birds and mammals that have found associations between parasite species richness and geographical range size — although not all studies have supported this association (Poulin & Morand, 2004).

Higher population density is a factor identified in epidemiological models as influencing the ability of a parasite to become established in a host population (Anderson & May, 1991; Roberts *et al.*, 2002). Poulin & Morand (2004) review the general epidemiological principles that potentially underlie this relationship and could lead to variation in parasite richness, and they review studies that have found an association between host density and parasite species richness (see also Morand & Poulin, 1998; Arneberg, 2002). Lending support to these models, we found

consistent significant effects of host density on overall parasite diversity, especially when controlling for phylogeny (results only approached significance in non-phylogenetic tests). Previous work on primates also found support for an effect of population density (Nunn *et al.*, 2003a). We found no evidence that mating system had an impact on patterns of parasite species richness, with no support for the hypothesis that monogamous host species harbour fewer parasite species, including those acquired through close contact (Loehle, 1995; Nunn *et al.*, 2000, 2003b; Thrall *et al.*, 2000). This might reflect that sexually transmitted diseases are generally understudied (Lockhart *et al.*, 1996) and are therefore missing from our comparative data base on close-contact parasites of carnivores.

In contrast to predictions, distance from the equator was positively correlated with overall parasite diversity. Although species further from the equator tend to have larger geographical ranges (Gittleman & Gompper, 2005; Lomolino *et al.*, 2005), this is an unlikely explanation for our results on latitude because geographical range size was included in our analyses. This unexpected pattern could also represent a bias in sampling effort, with host species that live further from the equator having been sampled more intensely for parasites, especially given that carnivores inhabit areas of industrialized countries in the Northern Hemisphere. We controlled for sampling effort in our analyses, but the possibility of geographical biases will require further investigation, including research into developing geographically based measures of sampling effort. Future research could also help to resolve this issue by investigating environmental factors, such as precipitation and temperature, and by examining whether similar patterns occur within species, i.e. in carnivore hosts that exhibit a wide latitudinal gradient. In primates, latitude showed the opposite correlation, with increased richness of protozoa closer to the equator (Nunn *et al.*, 2005). Geographical sampling biases may be less linked to latitude in primates than in carnivores because primates are mainly tropical.

In addition to mating system, two variables were consistently non-significant – maximum longevity and day range length. The absence of maximum longevity from our final models could indicate the existence of a limit to the number of parasite species an individual host acquires during its lifetime, that parasites and pathogens in general colonize carnivore hosts rather quickly after birth or that life histories of carnivores are so slow in comparison to their parasites that life-history variation has little effect on the ability of parasites to become established in different host species. Additionally, maximum longevity could be a poor measure of temporal exposure to parasites, but better measures, such as average age of individuals, are not available for most species. That day range length was not identified as significant, while home range size and geographical range in many cases were, suggests that the overall area covered by a species is more relevant than daily ranging patterns by individuals.

We found no consistent host correlates of parasite species richness in pinnipeds, which could relate to complications of quantifying host traits for these aquatic mammals, particularly population density, geographical range characteristics, home range area and day range length. Temporal variation might also be relevant, particularly seasonal variation. For example, highly polygynous pinnipeds may primarily exchange parasites during the breeding season when they aggregate on beaches in high densities to give birth and mate. The elevated stress levels during these periods may further increase their susceptibility to parasitic infection. The absence of significant correlates for pinnipeds in this study could therefore be viewed as reflecting fundamental differences between fissipeds and pinnipeds (see Bininda-Emonds & Gittleman, 2000), or as simply reflecting difficulties in collecting relevant ecological data for pinnipeds.

Parasite type, transmission mode and host specificity

Species richness of different types of parasites was determined by different factors, with no single host trait emerging as a primary determinant in all parasite groups. Splitting the parasites according to taxonomy showed that, for helminths, the main determinants of species richness were host geographical range size and population density, while for protozoa only geographical range was statistically significant (although some tests also suggested that population density was a significant determinant of parasite species richness for protozoa). Analyses of viral species richness produced no consistent results. This variation among particular parasite taxonomic groups could indicate that different transmission mechanisms and levels of host specificity drive these patterns.

Parasite species that require close contact for their transmission exhibited higher richness in larger-bodied hosts and those with smaller home ranges. The same factors also correlated with the diversity of directly transmitted parasites. Home range size and body mass are variables describing characteristics of individuals, while other factors, such as geographical range, latitude and density, characterize populations or species. Thus, our results indicate that morphology and behaviour of individual hosts, rather than species characteristics, can determine the species richness of parasites with a direct life cycle and those transmitted via close host-to-host contact.

For non-closely and indirectly transmitted parasites and pathogens, the scenario was reversed, with variables describing species level traits emerging as more important predictor variables. Thus, for parasites not dependent on close host-to-host contact for transmission or those with an indirect life cycle, geographical range size, distance from the equator and population density were the main predictors of parasite species richness. For vector-borne parasites, we found no consistent correlates of parasite species richness. This could indicate that we did not include the variables crucial to understanding the diversity of vector-borne parasites, that different ecological processes affect the ability of different vector-borne parasites to establish, or that processes determining the establishment of these parasites are stochastic. One approach for resolving these (and other) inconclusive results would be to examine variation in transmission mode and specificity within particular taxonomic groups (helminths, protozoa and viruses). In primates, for example, Pedersen *et al.* (2005) found that vector-borne viruses have a broad host range (generalists), while vector-borne protozoa are relatively host specific.

We examined the effects of host specificity, as generalist parasites could be influenced by a wider range of host variables than species-level host traits, such as overall levels of diversity of other mammalian hosts with overlapping geographical ranges. For generalist parasites and pathogens, body mass, population density, geographical range size and distance from the equator contributed significantly in the phylogenetic and non-phylogenetic analyses. Why more parasites should be encountered further from the equator is, as pointed out above, a pattern counter to expectations and deserves further analyses, focusing particularly on the climatic mechanisms that could drive patterns of parasite species richness (Guernier *et al.*, 2004).

For specialist parasites, on the other hand, we could find no host trait that correlated with parasite species richness in both the phylogenetic and non-phylogenetic tests. Non-phylogenetic tests indicated that population density, geographical range and diet were of importance, while phylogenetic tests indicated that body mass and day range length were significant predictors. Given that specialist parasites are associated with a single host species to a higher degree that generalists, this may simply reflect an inadequacy of non-phylogenetic methods to discern coevolutionary associations between hosts and their parasites. In that case, the results on specialist parasites indicate that smaller species with longer day ranges harbour significantly more specialist parasites than do other hosts.

CONCLUSIONS

In summary, the results presented here provide support for an effect of geographical range size, body mass and population density in predicting patterns of parasite species richness in carnivores. Latitude also accounted for variation in parasite species richness, although in a direction that was opposite to predictions. These results offer similarities to previous studies of primates that investigated a similar suite of predictions, and which found support for the effects of population density, latitude and geographical range size on parasite species richness (Nunn *et al.*, 2003a, 2004, 2005). However, the direction of the latitudinal effect diverged in these two mammalian groups, effects of body mass were more dependent on the method of analysis in primates, and differences were found among different taxonomic groups of parasites. Further research is needed to address the underlying ecological mechanisms that drive differences in these two host clades, particularly regarding the effect of latitude and possible geographical sampling biases, while a better understanding of the mechanisms driving patterns involving body mass, particularly diet and resource intake, could help to account for differences due to methodology and variation among host species.

ACKNOWLEDGEMENTS

This work was supported by the Swedish Research Council (P.L.), National Science Foundation (NSF) grant DEB-0212096 (C.N.), and was conducted as part of the 'Host Behavior' working group supported by the National Center for Ecological Analysis and Synthesis (NCEAS), funded by the NSF, the University of California and the Santa Barbara campus, and through funding from the Center for Applied Biodiversity Science at Conservation International. J.L.G., K.E.J. and W.S. acknowledge support from NSF (DEB-0129009), and K.E.J. also acknowledges support from The Earth Institute of Columbia University. We also wish to thank Jenny Fulford for help with the classification of parasite transmission mode and specificity, Olof Leimar for advice on multivariate statistics and Justin O'Dell for calculating average latitudes. Further, we thank Per Arneberg and one anonymous referee for comments on previous drafts of this manuscript.

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BIOSKETCHES

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Editor: Tim Blackburn

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Parasite species richness of different parasite types – multivariate analyses with forced inclusion of the number of citations and average body mass.

Appendix S2 Parasite species richness of parasites differing in transmission mode – multivariate analyses with forced inclusion of the number of citations and average body mass.

Appendix S3 Parasite species richness of generalist and specialist parasites – multivariate analyses with forced inclusion of the number of citations and average body mass.

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