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Do threatened hosts have fewer parasites? A comparative study in primates

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Summary

1. Parasites and infectious diseases have become a major concern in conservation biology, in part because they can trigger or accelerate species or population declines. Focusing on primates as a well-studied host clade, we tested whether the species richness and prevalence of parasites differed between threatened and non-threatened host species.

2. We collated data on 386 species of parasites (including viruses, bacteria, protozoa, helminths and arthropods) reported to infect wild populations of 36 threatened and 81 non-threatened primate species. Analyses controlled for uneven sampling effort and host phylogeny.

3. Results showed that total parasite species richness was lower among threatened primates, supporting the prediction that small, isolated host populations harbour fewer parasite species. This trend was consistent across three major parasite groups found in primates (helminths, protozoa and viruses). Counter to our predictions, patterns of parasite species richness were independent of parasite transmission mode and the degree of host specificity.

4. We also examined the prevalence of selected parasite genera among primate sister-taxa that differed in their ranked threat categories, but found no significant differences in prevalence between threatened and non-threatened hosts.

5. This study is the first to demonstrate differences in parasite richness relative to host threat status. Results indicate that human activities and host characteristics that increase the extinction risk of wild animal species may lead simultaneously to the loss of parasites. Lower average parasite richness in threatened host taxa also points to the need for a better understanding of the cascading effects of host biodiversity loss for affiliated parasite species.

Key-words: comparative analysis, host–parasite interactions, IUCN *Red List*, parasite species richness, wildlife conservation.

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Introduction

Infectious diseases play important roles in natural systems, from influencing host genetic diversity to altering species composition in ecological communities. Infectious diseases are also recognized as a source of threat for natural populations because they have been implicated as causing declines in previously thriving populations and in already imperilled species (Harvell *et al.* 1999, 2002; Daszak, Cunningham & Hyatt 2000; Dobson & Foufopoulos 2001; Jensen *et al.* 2002; Lafferty & Gerber 2002). Examples of infectious diseases causing notable mortality in threatened species include rabies in African wild dogs (Kat *et al.* 1995), canine distemper in black-footed ferrets (Dobson & Lyles 2000), withering disease in black abalone (Altstatt *et al.* 1996) and Ebola virus in chimpanzees and gorillas (Walsh *et al.* 2003; Leroy *et al.* 2004).

Identifying differences in parasites harboured by threatened and non-threatened host taxa represents one crucial step towards understanding the role of infectious agents in animal conservation. Infectious disease theory predicts that for many parasites, rates of

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spread should decline with decreasing host population size or density (Anderson & May 1979, 1991). From this perspective, threatened or endangered host populations should harbour fewer parasite species as a consequence of their limited geographical ranges and smaller, isolated populations (Lyles & Dobson 1993; Funk *et al*. 2001). Indeed, mathematical models show that directly transmitted parasites can be lost if host populations decline sharply, and that such parasites might not lead directly to host extinction (Anderson & May 1991; de Castro & Bolker 2005).

On the other hand, generalist parasites that can infect multiple host species, including more common reservoir hosts or domesticated animals, can cause severe population declines in sensitive hosts (e.g. McCallum & Dobson 2002; Holt *et al*. 2003). In mammals, for example, most declines or near-extinctions have been caused by generalist pathogens, rather than specialists (Dobson & Foufopoulos 2001; Gog, Woodroffe & Swinton 2002; de Castro & Bolker 2005). Furthermore, threatened host species may experience situations that predispose them to extinction risk, including fragmented, small populations and low genetic variability (Woodroffe 1999; Altizer *et al*. 2003). In some cases, these factors can increase host susceptibility and exposure to infectious diseases (Lyles & Dobson 1993); in other cases, infectious diseases might represent one of several factors that increases stochastic extinction risks (de Castro & Bolker 2005). Finally, it is often forgotten that parasites constitute biodiversity in their own right. Population declines and extinction of wildlife species may therefore have cascading negative effects on the biodiversity of affiliated parasites (e.g. Koh *et al*. 2004).

In this study, we used a comprehensive data set on the species richness and prevalence of infectious diseases in wild primates to investigate how patterns of parasitism vary in threatened and non-threatened host species. We focused on primates because they represent a diverse mammalian order whose behaviour, life history, phylogeny and ecology have been relatively well studied. This information makes it possible to control for other host traits that have been shown to correlate positively with both extinction risk and parasite species richness in mammals, including body size, population density and geographical range size (Nunn *et al*. 2003). Moreover, because of their close evolutionary relationship to humans, much is known about the parasites of primates, including microparasites such as viruses, protozoa, bacteria and fungi, and macroparasites such as helminths and arthropods.

We tested three main predictions. First, we examined whether parasite species richness was lower in threatened primates relative to non-threatened primates, as might be expected if small or declining populations with narrow geographical ranges support fewer parasite species. Indeed, parasite species richness in wild primates has been shown to correlate positively with host population density and geographical range area (Nunn *et al*. 2003, 2005; Nunn & Altizer 2006). Secondly, we tested whether specialist parasites and those transmitted by direct host contact were relatively less common among threatened primates, based on the expectation that the spread of such parasites will be linked more tightly to the abundance of any single host species (McCallum & Dobson 2002). Finally, we examined whether the prevalence of selected pathogen groups increased or decreased in threatened primates. In general, prevalence might decline in threatened species if small, isolated host populations offer fewer opportunities for parasite transmission. Under some scenarios, however, prevalence could increase if threatened species show elevated susceptibility following the loss of genetic diversity or other stress-inducing factors, or if a lack of competition with other parasite species leads to higher prevalence of the remaining parasites.

Methods

PARASITE RECORDS

A database of parasitic organisms reported from free-living primate populations was compiled from records in the published literature by searching systematically major online reference databases for primate species Latin binomials (Nunn & Altizer 2005). For each parasite or infectious disease reported from a wild primate population, we recorded the type of parasite (virus, protozoan, fungus, arthropod, helminth or bacterium), parasite genus and species name, the number of hosts sampled, location and year of sampling, prevalence of infection and number of individual hosts or samples obtained. More details on how the data were compiled and a version of the data set are available at www.mammalparasites.org. The version of the database used here included 2173 lines of data, where each line was a record of a parasite species reported from a wild host population. A total of 934 unique host–parasite combinations were represented across 119 primate species and 386 parasites in 160 genera. The three best-represented parasite groups (viruses, helminths and protozoa) encompassed collectively 88% of all host–parasite combinations in the data set. Information on prevalence of infection (proportion of individuals infected) was available for 1352 records comprising 131 parasite genera and 100 host species.

HOST SPECIFICITY AND TRANSMISSION MODE

Information on the taxonomic range of naturally affected host species was compiled for all parasite species following protocols described in Pedersen *et al*. (2005). Parasites were assigned to one of two specificity categories: ‘specialists’ included parasites reported to infect hosts from a single species, genus or family, and ‘generalists’ included parasites that could infect hosts from multiple families or orders (or even, in some cases, non-mammals). For host groupings at the level of primate families, we followed the taxonomy of Corbet & Hill

(1991). Specificity scores were assigned based on the reported occurrence of parasites and pathogens in wild populations only, and we excluded reports from zoo animals or those used for biomedical research. A total of 55% of parasite species were specific at the level of host species, genus or family, and 45% were generalists reported from more than one family or order of hosts.

We also recorded information on the transmission mode for each parasite following the protocols of Pedersen *et al.* (2005). Parasites transmitted by physical contact between hosts, including biting, touching, sexual contact and vertical transmission, were classified as having transmission via 'close contact'. Parasites transmitted by any other means were assigned to the category 'mobile and non-close', which included any combination of transmission via arthropod vectors, intermediate hosts and contact with contaminated soil, food or water. The majority (70%) of all parasites could be transmitted by mobile and non-close contact, whereas 42% of parasite species in our data set were transmitted by close contact. The sum of these percentages is greater than 100% because the categories were not mutually exclusive, with over 20% of parasites being transmitted by multiple routes that included both categories.

PRIMATE THREAT STATUS AND HOST CHARACTERISTICS

To quantify primate conservation status, we classified host species according to threat levels reported by the 2002 IUCN *Red List of Threatened Species* (www.redlist.org). The IUCN *Red List* classifies species as threatened based primarily on three criteria: recent declines in population size, small or reduced geographical range area and considerable probability of near-term extinction (Hilton-Taylor 2002; IUCN 2002, 2004). In analyses of parasite richness that used threat levels as a dichotomous variable, species listed as vulnerable, endangered or critically endangered were designated as 'threatened', and species in the categories 'near threatened' and 'least concern' were designated as 'non-threatened'. Two species designated 'data deficient' were not included in our analyses. By these criteria, our database included 81 non-threatened and 36 threatened primate species, or 117 of the 119 primates for which parasite data were available.

To investigate the effects of host threat status relative to other factors that might influence parasite species richness in wild primates, we included host body mass, geographical range area and population density as covariates in a subset of analyses of parasite species richness. These variables have been shown to correlate positively with parasite species richness in a previous comparative study of anthropoid primates (Nunn *et al.* 2003). Moreover, for some species extinction risk is assigned based on geographical range area, and a previous analysis showed that measures of extinction risk correlate with low population density and slow life histories in mammals (Purvis *et al.* 2000). We therefore investigated whether variation in parasite richness could be explained more effectively by variation in body mass, geographical range size and population density relative to measures of threat status *per se*. We obtained data from previously compiled comparative databases of biological traits in primates (e.g. Nunn 1999; Nunn & van Schaik 2001). Body mass (available for 117 primate species) was estimated as mean female body mass (Smith & Jungers 1997) and population density (available for 99 primate species) was estimated based on field studies of local population density (measured as the mean number of animals per km^2). Geographic range area (in km^2; available for 117 primate species) was estimated from geo-referenced spatial maps of primate range distributions (Sechrest *et al.* 2002; Sechrest 2003), as used in previous studies (Nunn *et al.* 2003, 2004).

STATISTICAL ANALYSES

Non-phylogenentic tests

We used analysis of variance (ANOVA) to examine the association between dichotomous measures of host threat status and parasite richness. We controlled for uneven sampling effort among host taxa by including a measure of sampling effort as a covariate in statistical analyses of parasite richness (Walther *et al.* 1995; Gregory, Keymer & Harvey 1996; Nunn *et al.* 2003). As the primary measure of sampling effort, we used the number of citations (with the Latin binomial for each primate species as the key search term) from the PrimateLit bibliographical database (primatelit.library.wisc.edu). This source provides the most complete reference information for journal articles and books on primates and matches most closely the sampling period (1940–present) during which most of the studies in our database were published. Initial tests were run once with only threat status and sampling effort as independent variables, and were repeated by including host traits as covariates (model: parasite richness = threat status + citation count + body mass + geographic range + population density). For analyses with more than two predictors, we performed model simplification following Crawley (2002).

To evaluate the importance of host specificity, we examined how (a) the proportion of generalist parasites (of all parasites reported from that species) and (b) the species richness of both generalist and specialist parasites examined separately depended on host threat status. To examine the role of parasite transmission strategies, we tested whether threatened and non-threatened hosts differed according to: (a) the proportion of parasites with 'mobile and non-close' transmission and (b) the species richness of parasites with 'close contact' vs. 'mobile and non-close' transmission. Analyses of host specificity and transmission mode were run with and without the covariates mentioned above. Proportions were arcsine-square root-transformed prior to analysis to normalize the error variance, whereas all other variables were log-transformed.

Controlling for host phylogeny

Comparative analyses were repeated using methods that controlled for host phylogeny. We used Felsenstein's (1985) independent contrasts method as implemented in the computer program CAIC (Comparative Analysis by Independent Contrasts) (Purvis & Rambaut 1995), with contrasts calculated using a composite estimate of primate phylogeny (Purvis 1995). Branch-lengths were set to unity, as this best corresponded to the assumptions of CAIC for this data set. To control for sampling effort when using independent contrasts, we obtained a measure of residual parasite species richness based on least squares regression through the origin of contrasts of the number of parasites and contrasts of the number of citations. With non-threatened species coded as 0 and threatened species coded as 1, we predicted that parasite richness contrasts (residuals) would decrease with transitions to increasing threat. We performed the CAIC analyses using the BRUNCH algorithm to identify contrasts with a change in the discrete trait. We excluded all contrasts with no change in threat status, and tested whether the mean residual parasite richness of the remaining contrasts was significantly different from zero.

Directed tests

We used directed tests (Rice & Gaines 1994) in phylogenetic and non-phylogenetic analyses involving parasite richness based on a priori directional predictions for the effects of host threat status. 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 opposite to predictions ($\delta < \gamma$; where $\delta + \gamma = \alpha$). We followed the guidelines in Rice & Gaines (1994) by setting γ/α to 0·8, giving values of $\gamma = 0{\cdot}04$ and $\delta = 0{\cdot}01$. We had no directional predictions for analyses of parasite prevalence (described next) and therefore used two-tailed tests.

Differences in parasite prevalence

We compared the prevalence of infection among pairs of primate species that differed in their threat status. For non-phylogenetic analyses of prevalence, we focused on 14 parasite genera for which data on prevalence were available for at least eight primate species, with two or more of the primate species threatened based on dichotomous threat categories. To maximize the number of contrasts in phylogenetic tests, we used transitions in any of the four ranked threat classes (non-threatened, vulnerable, endangered and critically endangered). Analyses were conducted using untransformed prevalence data in three steps. First, we identified those parasites with information on prevalence for multiple hosts that varied in their threat status (for a total of 47 genera, Appendix S1, supplementary material). Secondly, we used the Purvis (1995) primate phylogeny to identify comparisons of host species that differed in threat status (Fig. 1). For clades of hosts with the same threat status, we selected primate species with the greatest number of animals sampled. If sample sizes were equivalent among closely related hosts with the same threat status, we used the median prevalence across hosts with equal sample sizes. We worked from the tips of the tree to deeper nodes to maximize the number of comparisons. We eliminated comparisons with samples sizes of fewer than eight animals before running analyses, and examined variation within the three major parasite groups, transmission categories and specificity categories using matched-pairs *t*-tests. For 81% of comparisons within parasite genera, prevalence data were obtained using similar sampling regimens (e.g. sero-prevalence based on detection of antibodies, prevalence based on fecal egg counts or oocysts, or prevalence based on examination of tissues or blood samples).

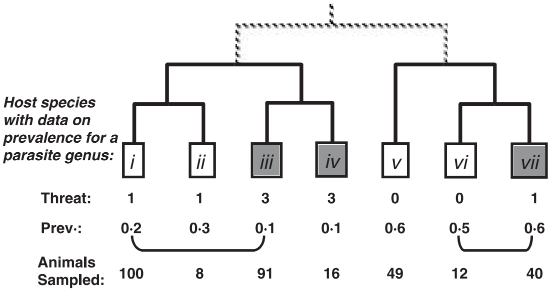

Fig. 1. For independent comparisons involving prevalence we examined primates sampled for a given parasite genus, and used ranked threat categories from 0 (not listed/least concern) to 3 (critically endangered). For sister species (e.g. vi and vii) we compared more threatened species (shaded boxes) to less threatened species (white boxes), and pruned each pair of species from the tree after making a comparison. When two or more closely related species shared the same threat category (e.g. i and ii; iii and iv), we used information on sample size to resolve which species to compare, thus avoiding reconstruction of ancestral states. For example, by preferring species with the largest sample sizes, we compared species i (sample size = 100) and species iii (sample size = 91). In this case, prevalence is higher in the less threatened primate species (0·2 vs. 0·1). A similar approach based on sample size was used when more than one prevalence estimate was available for a given host species. Further details are provided in the Methods.

Results

PREDICTION 1: PARASITE SPECIES RICHNESS AND HOST THREAT STATUS

Non-phylogenetic tests

Fewer parasite species were reported from threatened primate species relative to non-threatened primates. When not controlling for sampling effort, threatened primates had a mean of 5·17 (± 1·38) and median of two parasite species per host, whereas non-threatened primates had a mean of 7·72 (± 1·24) and median of four parasite species per host. In analyses of total parasite

Table 1. Analysis of variance results (non-phylogenetic tests) for effects of primate threat status (coded as 0/1) on log-transformed parasite species richness (PSR) for all parasites combined, and for helminths, protozoa and viruses tested separately. For each measure of parasite richness, the mean for threatened primates was lower than for non-threatened species. Citation counts (not shown) were associated positively with parasite richness and this effect was highly significant in each case ($P < 0{\cdot}0001$). P-values are shown for directed tests as described in the Methods

Dependent variable	Non-phylogenetic analyses (species values, $n = 117$)			Phylogenetic analyses (independent contrasts, $n = 27$)		
	Mean square	F	P	Mean square	F	P
Total PSR	0·611	4·83	0·019	0·071	4·76	0·024
Helminth PSR	0·265	2·40	0·076	0·025	2·55	0·061
Protozoa PSR	0·384	3·64	0·037	0·052	6·02	0·011
Virus PSR	0·198	2·82	0·048	0·024	3·39	0·039

Table 2. Model simplification results for effects of primate threat status (coded as 0/1) and three host traits (body mass, geographical range area, and population density) on measures of parasite richness (PSR). In each of these non-phylogenetic tests, threatened hosts had lower mean parasite richness and other covariates were associated positively with parasite richness. Our measure of sampling effort (citation counts, not shown) was also highly significant in each case ($P < 0{\cdot}0001$). Adjusted R^2 values for the final reduced models ranged from 0·30 to 0·46, and final sample sizes ranged from 98 to 116. P-values are shown for directed tests as described in Methods

Dependent variable	Independent variable							
	Threat status		Body mass		Density		Geogr. range	
	F	P	F	P	F	P	P	F
Total PSR	12·0	0·001	24·43	< 0·0001	–	–	–	–
Helminth PSR	4·99	0·018	9·21	0·002	–	–	–	–
Protozoa PSR	–	–	11·35	0·001	–	–	8·74	0·003
Virus PSR	–	–	14·89	< 0·0001	4·49	0·023	8·59	0·003

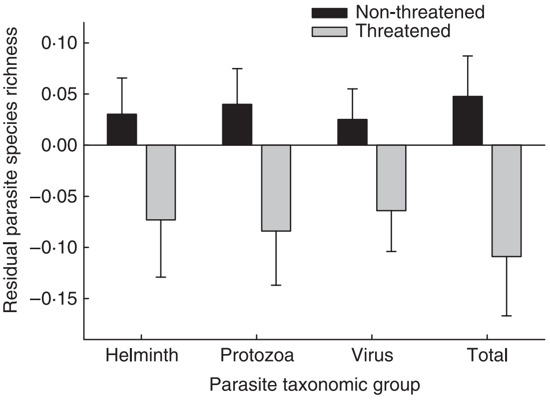

Fig. 2. Parasite species richness in threatened and non-threatened primate species, shown as residuals from regression of parasite richness on sampling effort (for all parasites combined, and for helminths, protozoa and viruses separately). Error bars show standard errors.

species richness that controlled for sampling effort, this difference was statistically significant (Table 1). Similar results were obtained when viruses, protozoa and helminths were investigated separately (Fig. 2; Table 1). For both total parasite richness and helminth parasite richness, the effect of threat status remained significant in an analysis that included other host traits as covariates (Table 2), with body mass retained as a significant predictor variable. Threat status became non-significant in analyses of protozoa and virus parasite richness with body mass, geographical range area and population density retained in the final models (Table 2).

Phylogenetic tests

More-threatened primate taxa had significantly lower parasite richness (based on residual values) than their less-threatened sister-taxa (Table 1). Among the three major parasite groups this trend was in the same direction, and the effect of host threat status was significant for both viruses and protozoa (Table 1).

PREDICTION 2: PARASITE SPECIFICITY AND TRANSMISSION MODE

Non-phylogenetic tests for host specificity

Differences in parasite species richness between threatened and non-threatened primates were similar for both generalist and specialist parasites (Fig. 3a). Accordingly, we found no significant effect of host threat status on the proportion of generalist parasites per host species ($F_{1,115} = 0{\cdot}05$; $P = 0{\cdot}811$). These results remained unchanged when we included only those host species for which three or more parasite species had been reported ($F_{1,71} = 0{\cdot}25$; $P = 0{\cdot}620$).

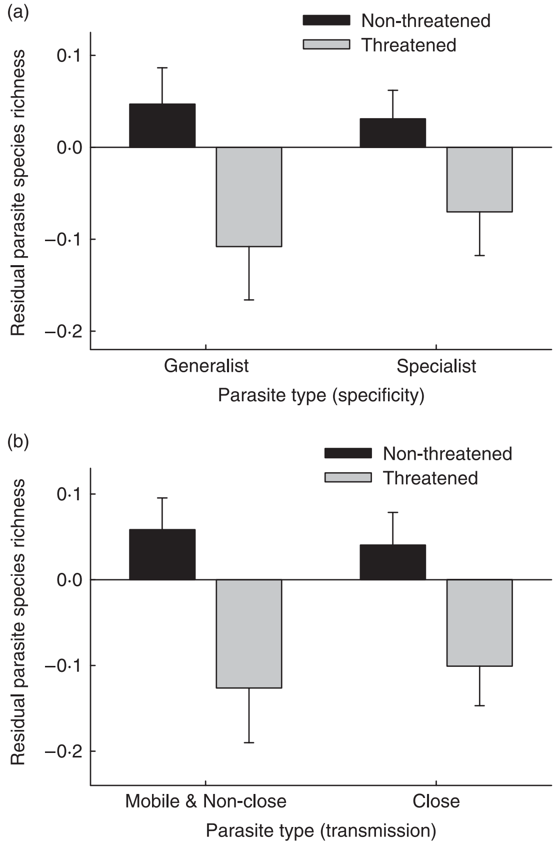

Fig. 3. (a) Parasite species richness in threatened and non-threatened primate species, shown as residuals from regression of parasite species richness on sampling effort. (a) Specialist vs. generalist parasites. Specialist parasites were specific to single host families, genera or species, whereas generalists could infect hosts from multiple families or orders. (b) Mobile and non-close (arthropod vectors, non-close contact and intermediate hosts) vs. close contact transmission modes. Error bars represent standard errors.

We also tested the effect of host threat status on the log-transformed numbers of specialist and generalist parasites in separate ANOVAS that included citation counts as a continuous covariate. Results showed that both generalist ($F_{1,114} = 4·68$; $P = 0·021$) and specialist parasite richness ($F_{1,114} = 3·18$; $P = 0·048$) were lower in threatened host species. In multivariate analyses that included host threat status and three additional host traits as covariates, estimates of generalist and specialist parasite richness remained lower among threatened host species (Table 3), although the trend for generalist parasite richness became non-significant. Moreover, generalist parasite richness increased significantly with body mass and geographical range size, but not with population density (Table 3). For specialist parasites, richness increased significantly with body mass and population density, but not geographical range size (Table 3).

Phylogenetic tests for host specificity

Threatened primate species harboured significantly fewer specialist parasites ($F_{1,26} = 4·64$, $P = 0·026$). This trend was in the same direction but non-significant for generalist parasites ($F_{1,26} = 2·40$, $P = 0·083$). Moreover, there were no significant differences in the proportion of generalist parasites for threatened and non-threatened primates (MS = 0·018, $F_{1,26} = 0·52$, $P = 0·477$).

Non-phylogenetic tests for parasite transmission

We found no significant effect of host threat status on the proportion of parasites that could be transmitted by ‘mobile and non-close’ routes in relation to ‘close contact’ ($F_{1,115} = 0·167$; $P = 0·684$). Results remained unchanged when we included only those host species for which three or more parasite species had been reported ($F_{1,71} = 0·15$; $P = 0·70$). Measures of richness for parasites having ‘close contact’ were significantly lower in threatened primates in tests that included citation counts as a continuous covariate ($F_{1,114} = 4·51$; $P = 0·036$; Fig. 3b). Similar results were observed for parasites with ‘mobile and non-close contact’ transmission ($F_{1,114} = 6·79$; $P = 0·010$). Finally, in multivariate analyses that included host threat status and three additional host traits as covariates, estimates of richness

Table 3. Model simplification results for effects of primate threat status and three host traits (body mass, geographical range area and population density) on (i) generalist and specialist parasite richness, and (ii) parasites with close contact vs. mobile and non-close transmission (as described in Methods). In each of these non-phylogenetic tests, threatened hosts had lower mean parasite richness and other covariates were associated positively with parasite richness. Our measure of sampling effort (citation counts, not shown) was also highly significant in each case ($P < 0·0001$). Adjusted R^2 values for the final reduced models ranged from 0·329 to 0·448, and final sample sizes were from 98 to 116. *P*-values are shown for directed tests as described in Methods. Parasite species richness is abbreviated as PSR

	Independent variable							
	Threat status		Body mass		Density		Geogr. range	
Dependent variable	*F*	*P*	*F*	*P*	*F*	*P*	*P*	*F*
Generalist PSR	2·46	0·075	12·01	< 0·0001	–	–	1·87	0·106
Specialist PSR	8·61	0·003	26·65	< 0·0001	3·58	0·039	–	–
Close contact PSR	11·40	0·001	29·30	< 0·0001	3·56	0·039	–	–
Mobile and non-close PSR	11·20	0·001	10·76	0·001	–	–	–	–

Table 4. Prevalence comparisons from non-phylogenetic tests. 'Direction of effect' indicates whether more threatened species had higher (+) or lower (–) prevalence than non-threatened primate hosts

Parasite	Type	*F*-statistic	*P*-value	Direction of effect
Alphavirus	Virus	$F_{1,11}$ = 0·86	0·37	–
Ascaris	Helminth	$F_{1,10}$ = 0·25	0·63	–
Balantidium	Protozoan	$F_{1,7}$ = 6·86	0·034	–
Entamoeba	Protozoan	$F_{1,12}$ = 2·74	0·12	–
Hepatocystis	Protozoan	$F_{1,9}$ = 2·00	0·19	–
Iodamoeba	Protozoan	$F_{1,7}$ = 2·13	0·19	–
Lentivirus	Virus	$F_{1,15}$ = 1·95	0·18	+
Necator	Helminth	$F_{1,9}$ = 1·48	0·25	+
Oesophagostomum	Helminth	$F_{1,13}$ = 0·25	0·63	+
Plasmodium	Protozoan	$F_{1,44}$ = 2·03	0·16	+
Deltaretrovirus	Virus	$F_{1,34}$ = 0·04	0·85	–
Strongyloides	Helminth	$F_{1,20}$ = 0·06	0·81	–
Trichuris	Helminth	$F_{1,18}$ = 1·10	0·31	–
Trypanosoma	Protozoan	$F_{1,14}$ = 0·37	0·55	–

for parasites in each transmission category remained lower among threatened host species (Table 3). Thus, the effect of host threat status approached significance for parasites transmitted by 'mobile and non-close' routes (Table 3), and body mass was the only significant covariate. For parasites transmitted by 'close contact' richness was significantly lower in threatened hosts, and body mass and population density were positively associated with parasite richness in the final model (Table 3).

Phylogenetic tests for parasite transmission

Parasites transmitted by 'close contact' were reported less commonly in threatened species ($F_{1,26}$ = 5·50, *P* = 0·017), and a similar pattern was found for parasites with 'mobile and non-close' transmission ($F_{1,26}$ = 3·89, *P* = 0·030). Analysis of the proportion of parasites with 'mobile and non-close' transmission showed no significant difference between threatened and non-threatened primate taxa ($F_{1,26}$ = 1·97, *P* = 0·172).

PREDICTION 3. PARASITE PREVALENCE AND HOST THREAT STATUS

Non-phylogenetic tests of prevalence were conducted for a total of 14 parasite genera for which there were a minimum of eight prevalence estimates and at least two threatened hosts. In 10 of 14 tests that used dichotomous threat categories, there was a tendency for more threatened host species to have lower parasite prevalence (Table 4). Only one of these tests reached significance, however, and this result was no longer significant after controlling for multiple tests using a Bonferroni correction (corrected α = 0·0036).

After deleting 12 comparisons in which sample sizes of one or both of the compared host species was less than eight, phylogenetic analyses involving prevalence data were based on 78 independent comparisons involving 47 parasite genera and 53 primate hosts (Appendix S1). Mean prevalence of infection across all parasites examined in threatened hosts was 15·3%, whereas prevalence in non-threatened hosts was 19·1%. This slight difference was not statistically significant in a matched pairs *t*-test (t_{77} = 1·02, *P* = 0·31, two-tailed). The trend for viruses was in the opposite direction, with higher prevalence in more threatened species (means of 19·7% and 9·4%), but results were not significant for any tests that investigated major parasite groups separately (helminths: t_{35} = 1·46, *P* = 0·15; protozoa: t_{17} = 1·85, *P* = 0·083; viruses: t_{21} = –1·51, *P* = 0·15, all tests two-tailed). Results were similar when analyses were restricted to 63 comparisons with a single sampling regime (described in Methods). In this subset of the data, overall prevalence was 15·9% in threatened primate species and 17·3% in non-threatened host species (t_{62} = 0·34, *P* = 0·73).

After excluding 24 comparisons for which parasite genera could not be assigned exclusively to 'generalist' or 'specialist' categories, approximately two-thirds of the comparisons involved generalist parasites (Appendix S1). There was no significant difference in the mean prevalence of generalist parasites between less threatened (15·2%) and more threatened (17·2%) primate species (t_{34} = –0·76, *P* = 0·46, two-tailed). The difference in prevalence was more striking when restricted to specialist parasites (prevalence of 23·0% in less threatened vs. 12·2% in threatened), but again this difference was not statistically significant (t_{18} = –0·33, *P* = 0·75, two-tailed). We also examined prevalence among parasites with different transmission modes and again found no difference in prevalence between host threat categories when the analysis was restricted to 'close contact' transmission (t_{29} = 1·08, *P* = 0·29, two-tailed) or to parasites with 'mobile and non-close' transmission (t_{47} = 0·40, *P* = 0·69, two-tailed).

Discussion

Results presented here showed that threatened primate species harbour fewer parasite species than non-threatened primate species. This pattern was remarkably similar across three major parasite taxonomic groups – helminths, protozoa and viruses – and results were consistent for analyses with and without controlling for host phylogeny. Host threat status could correlate negatively with parasite richness for several reasons. First, primate species innately vulnerable to extinction might naturally harbour less diverse pathogen populations. This effect may arise because population size and geographical range area are key variables used to ascertain primate conservation status, and are also important determinants of parasite establishment in natural populations (Gregory 1990; Arneberg *et al.* 1998; Morand & Poulin 1998). For example, Nunn *et al.* (2003) showed that parasite richness was greater among anthropoid primates with larger geographical ranges and higher population densities. Furthermore, local population density and body mass have been shown to correlate significantly with parasite richness in primates (although body mass was significant in non-phylogenetic test only; Nunn *et al.* 2003) and with mammalian extinction risk (Purvis *et al.* 2000). In support of this explanation, our analyses of virus and protozoan parasite richness showed that inclusion of host population density, body mass and geographical range size rendered the effects of host threat status non-significant.

Lower parasite richness in threatened hosts could also result from the direct loss of parasite species in declining host populations. Many epidemiological models of directly transmitted parasites in single host populations predict that parasites will decline or 'fade out' when host population size falls below a critical threshold density (Anderson & May 1991; McCallum 1994; Lloyd-Smith *et al.* 2005). Thus, as population sizes of threatened species decline, their parasites might go extinct long before the hosts (Gompper & Williams 1998). In that sense, processes such as habitat fragmentation, isolation of populations and over-exploitation may negatively impact populations of parasites above and beyond intrinsic host traits that increase or decrease parasite richness. In support of this hypothesis, threat status remained a significant predictor in some analyses of parasite species richness that included host traits as covariates, including those involving total and specialist parasite richness, and the richness of parasites with different transmission routes.

Finally, it is possible that more scientific research has focused on threatened primates, which could inflate citation counts for these species and generate lower measures of residual parasite richness. However, our data showed that average log-citation counts were nearly identical for threatened (mean = 1·72 ± 0·105 SE) and non-threatened (mean = 1·69 ± 0·082 SE) primate species. These citation counts did not differ statistically among hosts in these two threat categories ($t_{115} = -0{\cdot}210$, $P = 0{\cdot}834$, two-tailed).

We predicted that specialist parasites or parasites that rely on host-to-host contact for transmission would be under-represented in threatened hosts, compared to parasites with broader host ranges and patterns of transmission that are decoupled from host contact. Thus, although specialist parasites might be lost from shrinking populations of threatened hosts, generalist parasites with a broad host range could be maintained by exposure to large heterospecific reservoir populations (Woodroffe 1999; Cleaveland, Laurenson & Taylor 2001; Woolhouse, Taylor & Haydon 2001; Foufopoulos, Altizer & Dobson 2002). In carnivores, for example, more disease-related population declines have been caused by generalist pathogens (such as rabies and morbilliviruses) than by specialists (Woodroffe 1999). Less is known about pathogen exposure in non-human primates, although evidence is accumulating that wild primates may encounter infectious diseases from humans in the context of field research and ecotourism (reviewed in Nunn & Altizer 2006), and from fruit bats in the case of Ebola haemorrhagic fever (Leroy *et al.* 2005). In terms of transmission mode, parasites transmitted via mobile vectors or contaminated soil or water could present higher risks to small populations of threatened hosts by spreading quickly among multiple host species in favourable environmental conditions (Woolhouse *et al.* 2001).

Counter to these predictions, however, specificity and transmission mode generally had no discernible effect on the association between primate threat status and parasitism in our analyses. Parasites across all categories tended to be less diverse in threatened primate hosts, including those predicted to be more tightly linked to the abundance of a particular host species. One explanation for this pattern could be that even pathogens with broad host ranges or those whose transmission is decoupled from direct host contact are limited by host isolation and lack of contact with biotic and abiotic reservoirs. In terms of host range, the underlying biological factors affecting generalists and specialists could differ, even though the end result is the same. For example, the richness of specialist parasites increased with host population density, but the richness of generalists increased with host geographical range size. Threatened species could be both less dense and have smaller ranges, leading to a net loss of parasites from both groups. Another explanation might be that our results were affected by sampling biases and inaccurate knowledge of parasite taxonomy and host range. For example, improved information could result in some parasites that are currently classified as generalists being split into multiple host-specific species. Conversely, some parasites classified as specialist may be identified at a later date as infecting additional host species. Thus, patterns reported here could change with improved understanding of parasite taxonomy and the range of hosts that parasites can infect.

The prevalence of selected agents was generally lower among threatened primate species, following a similar directional trend as parasite richness. However, this effect of host threat status was small and non-significant, and in some cases (e.g. for viruses and generalist parasites) average prevalence was higher among threatened hosts. These results are not surprising for several reasons, including the fact that prevalence estimates can vary tremendously among populations within a species, across seasonal cycles and over longer time-periods – all of which could add 'noise' to observed patterns and make differences among host species more difficult to detect. For example, although prevalence comparisons were conducted within parasite genera, it is possible that some genera included both endemic parasites that persist at constant levels and epidemic diseases that cause notable outbreaks. Furthermore, in fragmented and declining host populations, reduced opportunities for transmission (which could lower prevalence) might be offset by increased host susceptibility due to stress or reduced genetic variability. Finally, predictions are less clear-cut for the effect of prevalence, with some factors potentially increasing prevalence in threatened hosts and others having the opposite effect. If different factors play a role in different lineages and at different times, this could make it difficult to detect overall patterns of prevalence. Focused efforts to monitor the prevalence of targeted agents in wild primate populations will probably provide a better understanding of mechanisms that influence parasite dynamics in threatened and non-threatened hosts.

Other studies have investigated the links between threat status and host traits (Purvis *et al.* 2000), and between threat status and prevalence of specific diseases (e.g. spondyloarthropathy: Nunn, Rothschild & Gittleman 2007). To our knowledge, however, our study represents the first comprehensive analysis to address whether broad patterns of parasitism differ among threatened and non-threatened animal species. Because parasites can threaten already-reduced populations, and because infectious diseases can trigger catastrophic declines in otherwise robust host populations, understanding and managing infectious disease will become increasingly important in wildlife conservation (e.g. Cleaveland *et al.* 2002; Lafferty & Gerber 2002). Comparative studies such as this one can play a key role in examining parasite-related threats to wildlife, and in identifying host and parasite traits associated with host extinction risk. Interestingly, the IUCN *Red List* (Hilton-Taylor 2002) provides only limited records of parasites that threaten wild host species, even though many listed species are known to have experienced recent declines from infectious diseases (Smith, Sax & Lafferty 2006). Moreover, it is interesting to note that as of 2006, no primate species were listed as threatened due to parasites or infectious diseases, although this is certainly expected to change as biologists learn more about the impacts of Ebola on apes in equatorial Africa (Walsh *et al.* 2003; Leroy *et al.* 2004). In our data set, five threatened primate species had unusually high parasite species richness after controlling for sampling effort – these included *Mandrillus sphinx* L., *Alouatta fusca* Geoffroy, *Macaca sinica* L., *Saimiri oerstedii* Reinhardt, *Pan troglodytes* Blumenbach and *Gorilla gorilla* Savage & Wyman. Determining whether these species experience greater susceptibility or are unusually affected by human encroachment will be important for future conservation management efforts.

Finally, the above discussion is skewed towards pathogens as threats to wild primates and other mammals. It is also important to recognize that losses in the number of mammal species will impact negatively the biodiversity represented by their parasites (Koh *et al.* 2004). Many microparasites that live uniquely on endangered or threatened mammals are expected to go extinct long before their specific hosts (Gompper & Williams 1998), although as with most taxa, we do not have accurate numbers of how many species of parasitic organisms might be affected by future mammalian extinctions. A relevant question at the interface of conservation biology and disease ecology involves whether the loss of parasites is harmful or helpful to a host population. For example, hosts that lose their parasites during population bottlenecks or in captive breeding programmes may also lose their genetic ability to respond to future disease threats (Lyles & Dobson 1993; Altizer, Harvell & Friedle 2003). The debate over positive vs. negative effects of parasites is likely to intensify as more research is published on the interactions between different parasitic organisms within host communities, and the relationships between parasites species richness, host defences and disease. From a related perspective, coevolution between hosts and parasites may be a major force determining the earth's biodiversity (Thompson 1999; Stockwell, Hendry & Kinnison 2003; Nunn *et al.* 2004; Poulin & Morand 2004). Conservation strategies that result in loss of parasites by failing to recognize this potential could ultimately rob host populations of behavioural, physical and immune defences needed to respond to future ecological changes.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com

Appendix S1. List of parasite genera used in phylogenetic comparisons of prevalence.