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Ranging patterns and parasitism in primates

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Competing hypotheses exist concerning the influence of ranging patterns on parasitism. More intensive use of a home range could result in greater exposure to infectious agents that accumulate in the soil. Alternatively, when more intensive ranging is associated with territorial defence, this could decrease home range overlap and produce lower levels of parasitism. We tested these hypotheses using phylogenetic comparative methods and parasite richness data for 119 primate species. Helminth richness increased with the defensibility index, a quantitative measure of home range use that correlates with the degree of territoriality in primates. This association was independent of other host traits that influence parasite richness in primates. Results involving non-vector transmitted helminths produced the most significant results, suggesting that the relationship between territorial behaviour and parasitism is driven by accumulation of parasites in defended home ranges. In addition, costs associated with greater ranging could increase susceptibility to infectious agents.

Keywords: parasite species richness; day range; home range; primates

1. INTRODUCTION

Infectious disease plays a major role in the lives of mammals, with parasites responsible for massive fatalities in some populations of wild primates (Chapman *et al.* 2005; Nunn & Altizer 2006) and the driving force behind an incredible array of behavioural counterstrategies to avoid or eliminate infections (Hart 1990; Moore 2002). A key question in disease ecology concerns the factors that influence patterns of parasitism. The spread of disease in mammalian populations is widely thought to increase with group size and measures of social contact within groups (Møller *et al.* 1993; Loehle 1995; Altizer *et al.* 2003), but empirical and theoretical research suggests that spatial separation of individuals into social groups can actually reduce the spread of disease (Watve & Jog 1997; Wilson *et al.* 2003).

By mediating contact between groups in socially structured populations, ranging patterns could impact the spread of infectious disease in the following ways:

(i) More intensive use of a home range could elevate exposure to parasites already present in the range (Stoner 1996; Ezenwa 2004). This hypothesis predicts a positive association between range use intensity and parasitism.
(ii) When range use intensity increases due to greater territorial defence, the resulting physical separation of groups could prevent the spread of directly transmitted parasites (Loehle 1995; Wilson *et al.* 2003; Cross *et al.* 2005). This hypothesis predicts a negative association between range use intensity and measures of parasitism. Under this hypothesis, we also predict a positive association between home range overlap and parasitism, since shared habitats in undefended ranges could allow parasites to spread between groups, including ectoparasites and parasites in faecal matter.

We tested these hypotheses in non-human primates by examining quantitative measures of home range use and parasite species richness. We present results for multiple measures of parasite richness, but focused particularly on parasites that survive as infectious stages outside the host, such as helminths (Hausfater & Meade 1982). This class of parasites has an added advantage in this context, as they are probably less likely to spread through direct physical contact during territorial aggression, as compared to parasites transmitted in saliva, blood or in the air. We also controlled for sampling effort, phylogeny and host traits that have been shown to influence parasite richness in primates.

2. MATERIAL AND METHODS

We used parasite data from the *Global Mammal Parasite Database*. Details on how this database was constructed are reported in Nunn *et al.* (2003), Nunn & Altizer (2005) and Pedersen *et al.* (2005). Data on helminths, protozoa and viruses collectively represented 825 unique host–parasite combinations involving 330 parasite species reported from 119 primate species (both anthropoids and prosimians). We examined the richness of these three taxonomic groups of parasites, and calculated in two taxonomy–transmission mode categories: direct transmission in all parasites combined and non-vector transmission in helminths. As noted above, the strongest tests of the hypotheses involved the two measures of helminth richness (Hausfater & Meade 1982). For completeness, however, we included analyses using other measures of parasitism to detect additional transmission modes, such as physical contact during inter-group encounters (e.g. viruses).

We quantified range use intensity with the ‘defensibility index’ (D-index; Mitani & Rodman 1979). The D-index measures the intensity of range use by examining day journey length relative to home range size (assuming a circular range). In a comparative study of 33 populations from all major lineages of primates, Mitani & Rodman (1979) found that the D-index correlated positively with territoriality across species, indicating a propensity to defend areas when it is easier to patrol the range. We obtained data on the D-index from Nunn & van Schaik (2001) and home range overlap values (the percentage overlapping with surrounding groups) from Nunn & Barton (2000).

Using information on primate phylogeny (Purvis 1995), we calculated independent contrasts with the computer program CAIC (Purvis & Rambaut 1995). To best meet the assumptions of independent contrasts, all data and branch lengths were log-transformed prior to running phylogenetic tests, as in previous analyses using this dataset. We also re-ran focused tests after excluding outlier contrasts and we conducted non-phylogenetic analyses. Based on previous results that revealed phylogenetic signal in measures of parasite richness (Nunn *et al.* 2003), we based our primary conclusions on the phylogenetic analyses. Statistical tests were conducted with a significance level of $\alpha = 0.05$ using two-tailed tests. We corrected for multiple tests using false discovery rate control (Verhoeven *et al.* 2005).

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Table 1. Effect of D-index, home range overlap and body mass on parasite richness. (Analyses used independent contrasts with $n=63$ for the D-index and $n=36$ for home range overlap. Parasite richness served as the dependent variable in a model, with D-index or home range overlap, body mass and sampling effort as predictor variables. Sampling effort was significant in all analyses involving the D-index, but not in all tests of home range overlap (possibly due to smaller sample sizes). Removing sampling effort and body mass from the model produced largely similar results for two analyses of overlap in which sampling effort was non-significant (helminths and protozoa).)

	D-index				home range overlap			
	slope: D-index	*F*-ratio	*p*-value	mass significant?	slope: range overlap	*F*-ratio	*p*-value	mass significant?
parasite taxonomic groups								
all combined	0.47	3.58	0.063	no	0.046	0.11	0.75	no
helminths	0.58	6.39	0.014[a]	no[b]	−0.044	0.09	0.77	no
viruses	0.43	5.07	0.028	no	0.081	0.63	0.43	no
protozoa	0.46	3.59	0.063	no	0.083	0.38	0.54	no
parasite transmission modes								
direct (all combined)	0.5	4.23	0.044	no[b]	0.00	0.00	≈1.0	no
non-vector (helm.)	0.79	12.2	0.0009[a]	yes	−0.043	0.01	0.76	no

[a] Significant after implementing false discovery rate control (Verhoeven *et al.* 2005).

[b] $p<0.1$.

Regional or taxonomic sampling biases pose a challenge to studies of parasite diversity, with better-studied host species having more parasites reported in the literature. We therefore followed previous researchers (Gregory 1990; Nunn *et al.* 2003) by including a measure of sampling effort in all tests. We used citation counts from the database PrimateLit (http://primatelit.library.wisc.edu/), as this source provides the most complete reference information for journal articles and books on primates, and it most closely matches the sampling period (1940–present) during which most of the parasite studies were published.

In a set of 'focused' multivariate analyses, we controlled for body mass and sampling effort (independent variables) in a multivariate model that included one measure of parasite richness as the dependent variable and the D-index as an independent variable. We included body mass in this model because it correlates negatively with the D-index (independent contrasts: $b=-0.51$, $F_{1,62}=23.0$, $p<0.0001$, see also Nunn & van Schaik 2001), and because larger-bodied hosts are larger 'islands' for parasites and can acquire more parasites through greater energy requirements (Poulin & Morand 2004).

To control for other host traits, additional multivariate tests were run for each measure of parasite richness. These tests included the following independent variables: host body mass, age at first reproduction, geographical range size, latitude, population density, group size and home range size. In a stepwise regression model, we entered and retained variables that were significant at $p\leq 0.10$ to construct a model of the factors that influence parasite richness, with body mass and sampling effort forced into the model at all steps; variables were considered significant if $p\leq 0.05$. Body mass was estimated as mean female body mass (Smith & Jungers 1997), and age at first reproduction was measured as age at first birth in years (Ross & Jones 1999). Geographical range size and latitude were compiled using the published literature to establish a digitized map of occurrence for each species (W. Sechrest, used in Nunn *et al.* 2003, 2004, 2005). We obtained data on group size (mean number of individuals), population density (animals per km^2) and home range size (hectares) from the published literature on primate behaviour and ecology (Nunn & van Schaik 2001).

3. RESULTS

Analyses based on phylogenetically independent contrasts found that parasite richness correlated positively with the D-index in analyses of helminth and viral richness (table 1). In tests that examined parasite richness among taxonomy–transmission categories, significant results were obtained in analyses of directly transmitted parasites and non-vector helminths. Results involving helminths explained the most variation ($r^2=0.19$–0.28) and remained significant after excluding outliers and when implementing the correction for multiple tests. In non-phylogenetic tests, however, the D-index was no longer statistically significant (see electronic supplementary material).

In phylogeny-based tests that investigated additional covariates (see §2), the D-index was included in analyses of helminths and non-vector helminths, with both results remaining significant after controlling for multiple tests. Non-phylogenetic tests produced similar results, with strongest support for the D-index in analyses of helminth richness (e.g. non-vector helminths: $b=0.47$, $F_{3,64}=3.58$, $p=0.06$; $p=0.017$ when restricted to $n=49$ species with data on all variables). Full multivariate results for the phylogenetic tests are presented in the electronic supplementary material.

In analyses based on independent contrasts, tests of home range overlap produced non-significant results (table 1). Home range overlap exhibits a positive association with home range size in primates (phylogenetic test: $b=0.33$, $F_{1,35}=10.6$, $p=0.0026$), but overlap remained non-significant when range size was included as a covariate. Similarly, home range overlap was not entered in the multivariate models that controlled for other potentially confounding variables (see electronic supplementary material). In support of linkage between range use intensity and home range overlap, groups exhibit greater overlap as range use intensity declines ($b=-0.78$, $F_{1,31}=4.73$, $p=0.04$).

4. DISCUSSION

We found that parasite richness correlated positively with range use intensity in primates when controlling for phylogeny, sampling effort, body mass and other host traits. Because the strongest results involved helminth richness, the positive association probably reflects increased risk from accumulation of parasites in more heavily used ranges, which often occurs in the context of territorial defence (Ezenwa 2004). The results failed to support the hypothesis that territorial behaviour reduces disease risk, with home range overlap also failing to reach significance as a predictor of parasite richness. The costs of ranging and territoriality could lead to greater susceptibility to disease (Ezenwa 2004), further increasing risks from exposure to parasites that accumulate in the soil.

Few studies have investigated the effects of ranging behaviour on the spread of infectious agents (Loehle 1995). One notable exception involved a study of African ungulates (Ezenwa 2004), which showed that parasitism correlated with territoriality both across species and among individual gazelles. Theoretical models have investigated the importance of contact between groups for the establishment of infections (Thrall *et al.* 2000; Wilson *et al.* 2003; Cross *et al.* 2005). Our results suggest that contact among primate groups may be sufficiently high to overcome constraints on the spread of disease in socially structured populations. Such contact could occur through regular dispersal between groups, sexual contact among individuals in different groups and shared use of resources.

In conclusion, we found support for increased range use intensity leading to increased parasitism. This result appears most consistent with exposure to more parasites that accumulate in defended home ranges, and could also reflect increased susceptibility to disease in species that use their ranges more intensively. The comparative approach provides a means to assess the role of ranging behaviour in other species. To investigate the mechanisms responsible for this relationship, field research could quantify parasitism in relation to between-group movement (dispersal), range use intensity and inter-group contact during territorial encounters.

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