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Rodent sociality and parasite diversity

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The risk of parasitism is considered to be a general cost of sociality and individuals living in larger groups are typically considered to be more likely to be infected with parasites. However, contradictory results have been reported for the relationship between group size and infection by directly transmitted parasites. We used independent contrasts to examine the relationship between an index of sociality in rodents and the diversity of their macroparasites (helminths and arthropods such as fleas, ticks, suckling lice and mesostigmatid mites). We found that the species richness of directly transmitted ectoparasites, but not endoparasites, decreased significantly with the level of rodent sociality. A greater homogeneity in the biotic environment (i.e. a reduced number of cohabiting host species) of the more social species may have reduced ectoparasites' diversity by impairing ectoparasites transmission and exchange. Our finding may also result from beneficial outcomes of social living that include behavioural defences, like allogrooming, and the increased avoidance of parasites through dilution effects.

Keywords: rodents; sociality; parasite species richness; ectoparasites

1. INTRODUCTION

Infectious and parasitic diseases play a major role in mammalian demography (Tompkins *et al.* 2001) and in the emergence of immunological and behavioural counterstrategies to avoid or eliminate infection (Moore 2002). Social (or group living) species are expected to have higher parasitic loads or disease prevalence because parasite transmission is usually density dependent (Arneberg *et al.* 1998; Côté & Poulin 1995; Altizer *et al.* 2003). Thus, parasites are expected to create a 'cost' of sociality (Alexander 1974). This theoretical prediction has been confirmed in several empirical studies that found positive correlations between group size (or densities) and parasitic loads (i.e. abundance, prevalence or parasite species richness (PSR)) for a variety of directly transmitted ectoparasites or helminths (Arneberg *et al.* 1998; Stanko *et al.* 2002), as well as for vector-borne arthropods (Nunn & Heymann 2005). Other studies that focused on investment in immune function as an indirect measure of parasitic pressures have also found positive relationships between the group size and the level of immunological investment (Møller *et al.* 2001; Brown & Brown 2002).

Notably, however, some studies have failed to find such positive correlations (Arnold & Lichtenstein 1993; Van Vuren 1996; Ezenwa *et al.* 2006), and recent theoretical studies suggest that spatial segregation of individuals into social groups can actually reduce the spread of disease (Wilson *et al.* 2003). Group size alone is a somewhat imprecise measure of sociality because it does not recognize more complex social relationships (Wey *et al.* in press).

The aim of this study was to identify, in rodents, the relationship between host sociality and PSR using an index of sociality. We expected to find a positive relationship between the level of host sociality and the species richness of directly transmitted ectoparasites, because a main determinant of ectoparasite species richness is host density (Stanko *et al.* 2002). By contrast, the relationship between host sociality and the species richness of indirectly transmitted endoparasites is difficult to predict, as these parasites are transmitted by animals ingesting them. The main determinants of their species richness are host diet, prey abundance and diversity, and host density (Šimková *et al.* 2003).

2. MATERIAL AND METHODS

(a) *Parasitic data*

Data for both ecto- and endoparasite species richness were obtained from published studies. We used only surveys where sample size was given and rejected descriptive parasitic reports for a given host species. We used PSR—the number of parasite species found in a host species—as a measure of parasitic load. For endoparasites we focused on helminths (nematodes, cestodes, trematodes and acanthocephalans) and for ectoparasites we focused on fleas, suckling lices, ticks and mesostigmatid mites. We obtained endoparasite species richness for 46 rodent species and data for both the endo- and the ectoparasites for 33 species (electronic supplementary material 1).

(b) *Sociality data*

It is remarkably difficult to obtain consistently collected data that allow broad-scale comparative study of sociality. Thus, many researchers use group size as a metric of sociality. Social behaviour, however, is more complex than simply the number of potentially interacting individuals. Therefore, we used a three-level index of sociality that tried to focus on the nature and complexity of social interactions (*sensu* Blumstein & Armitage 1998), but was independent of group size or density. For this study, rodent species were classified into one of the three groups: group 1, species that are essentially solitary; group 2, species that aggregate only seasonally, that nest communally during the breeding season or that aggregate to form colonies but in which all members of the colony live individually; and group 3, species living in well-established groups throughout their active season continually sharing space. Group sizes were highly variable in this third, most social, category. In total, we obtained data for 46 rodent species from eight families that represented the full range of sociality (electronic supplementary material 1).

(c) *Comparative analysis*

We used independent contrasts to study the coevolution of sociality and parasite abundance. The phylogeny and its sources are presented in electronic supplementary material 2. We used the brunch option in CAIC 2.0 (Purvis & Rambaut 1995) to calculate contrasts. For marmots, we used Armitage & Blumstein (2002) as the source of average body mass of males and females. For all other species we obtained similar data from Novak (1991). Body masses were log-transformed before calculating contrasts. PSR may be biased by sampling effort which could create confounding variation

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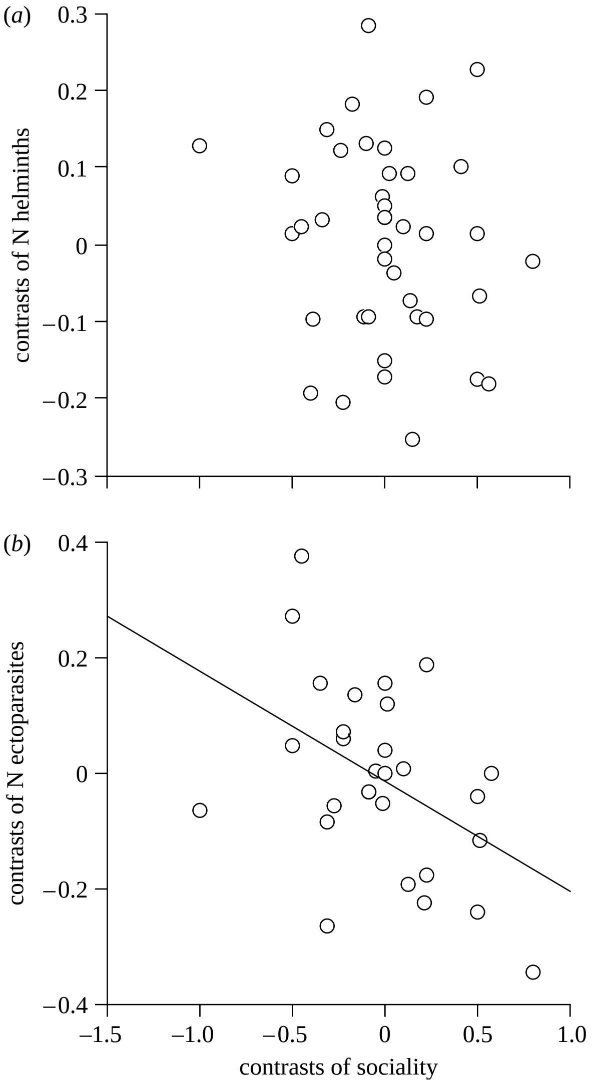

Figure 1. Bivariate relationships between phylogenetically independent contrasts of host sociality and parasite species richness for (*a*) endoparasitic helminths and (*b*) ectoparasites. N=Number.

(Poulin & Morand 2004). Additionally, host body size may be associated with parasites' diversity (Ezenwa *et al.* 2006). To account for these potential source of variation, we fitted two multiple regression models on the independent contrasts to explain variation PSR. The models regressed host mass, the sample size of hosts studied and host sociality against either log-transformed ectoparasite species richness or endoparasite richness.

3. RESULTS

There was no relationship between rodent sociality and endoparasite species richness ($B=0.015$; $p=0.746$, partial $\eta^2=0.003$; figure 1) after controlling for non-significant variation explained by host weight ($B=-0.052$, $p=0.254$, partial $\eta^2=0.034$) and significant variation explained by host sample size ($B=0.328$, $p<0.001$, partial $\eta^2=0.415$). This model explained 44.3% of the variation in the number of parasites ($p<0.001$). There was, however, a substantial and significant effect of sociality on ectoparasite species richness ($B=-0.178$; $p=0.010$, partial $\eta^2=0.230$; figure 1) after explaining variation accounted for by host weight ($B=-0.199$; $p=0.014$, partial $\eta^2=0.212$) and host sample size ($B=0.204$; $p=0.019$, partial $\eta^2=0.195$). This model explained 46.4% of the variation ($p=0.001$) in the number of parasites.

4. DISCUSSION

We found no relationship between sociality and endoparasite species richness. We expected this because many macroendoparasites are transmitted indirectly and thus rely on several determinants, including intermediate hosts, host diet and host local aggregation in transmission foci (Vicente *et al.* 2006).

We found a significant relationship between sociality and ectoparasite species richness. Importantly, however, this relationship was significantly negative. We expected to find a significant positive relationship because more social contacts should be associated with the risk of being infected by directly transmitted parasitic arthropods. We suggest two possible non-mutually exclusive explanations for this counterintuitive finding.

First, ectoparasite species richness may depend on the host's environment (Krasnov *et al.* 2004). Host environment refers not only to several abiotic factors (e.g. temperature, humidity, burrow structure) that may affect ectoparasite survival but also to some biotic components (e.g. the number of potential hosts and the number of other ectoparasites) that may affect competitive interactions between ectoparasites. Our negative relationship between sociality and ectoparasite richness may be interpreted in the light of ectoparasite species coexistence and transmission on a shared resource (i.e. the host species). Environmental heterogeneity associated with less social host species may favour a greater diversity of parasite species (shared with other host species), while environmental homogeneity (from the parasite's perspective) is expected in more social host species. Greater environmental homogeneity may favour co-infection, and if parasite coexistence is regulated by competition, competitive exclusion may reduce ectoparasite diversity. Thus, ectoparasite transmission may be reduced in social species compared with solitary ones, and this may lead to fewer species of ectoparasites. Ectoparasite coexistence is also favoured in heterogeneous environments and may lead an increase in the number of ectoparasite species (Krasnov *et al.* 2004). If this explanation is true, we expect that the specificity of ectoparasite species should be higher in social host species compared with less social ones.

Second, social species may have evolved defensive strategies to control ectoparasite transmission (Moore 2002). Both removal of ectoparasites (via auto- and allogrooming) and parasite avoidance by grouping to produce a 'dilution effect' have been described as effective means to reduce ectoparasite loads (Mooring & Hart 1992; Sánchez-Villagra *et al.* 1998). By reducing transmission rate, behavioural defences reduce parasite invisibilities, affecting primarily the less-transmissible ones and consequently the number of ectoparasite species. Our results may then suggest that the evolution of sociality in rodents could be associated with: (i) an increase in allogrooming, which in turn may have reduced ectoparasite species richness and/or (ii) parasite avoidance whereby individuals in social groups have 'diluted' infection risks. Another possible mechanism for our finding is that a higher immune investment against ectoparasites has evolved in social species compared with solitary ones. Indeed most studies have considered only the potential effect of a single parasite species on the physiology, defence or behaviour of a given host. The hypothesis that the influence of parasitism should increase with the diversity of parasites faced by a given host has not been fully investigated. However, recent studies have shown that an increase in genetic diversity at immune genes (MHC) is correlated with the increase in PSR (Wegner *et al.* 2003). If defensive gene diversity is correlated with the diversity of parasite species, we could also hypothesize that the investment in behavioural defences should also be correlated with the parasite diversity. PSR could be a good predictor of the extent to which the evolution of host life-history traits and host immune defence has been shaped by parasitism (Poulin & Morand 2004).

Whatever the explanation, for a variety of rodents, our findings suggest that one potential cost of sociality related to parasitism remains to be investigated.

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