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The intra- and interspecific relationships between abundance and distribution in helminth parasites of birds

ROBERT POULIN

Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand

Summary

1. Positive correlations between local abundance and distribution on a larger spatial scale are commonly observed among related species.

2. Within parasite species, the same relationship may be expected between prevalence and intensity of infection across host species used. Across parasite species, a positive relationship is expected between average abundance in a host population and the number of host species that can be exploited based on the resource breadth hypothesis. Trade-offs between the ability to exploit many host species and the potential for heavy infections, however, could result in a negative relationship.

3. Intraspecifically, using data on 51 helminth species parasitic in birds, prevalence and intensity of infection among host species used are generally only weakly correlated. Only in nematodes is there an overall positive relationship between prevalence and intensity.

4. A comparative analysis was performed on data from 389 species of cestodes, trematodes and nematodes parasitic in birds to determine how host specificity covaries interspecifically with abundance, measured both as prevalence and intensity of infection.

5. After controlling for phylogenetic influences and sampling effort, the number of host species used correlated positively with prevalence in all three parasite taxa, and with intensity of infection in trematodes only.

6. These results do not support the existence of a trade-off between abundance and the use of many host species, as has been found for fish parasites. Instead, whatever makes helminth parasites of birds abundant within a host population may facilitate their successful colonization of new host species.

Key-words: comparative analysis, host specificity, intensity of infection, phylogeny, prevalence.

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Introduction

The relationship between local abundance and geographical distribution is one of the best documented statistical patterns observed in nature (Brown 1984; Gaston & Lawton 1990; Maurer 1990; Gaston 1994, 1996; Gaston, Blackburn & Lawton 1997). As a rule, locally abundant species tend to be widespread on a geographical scale whereas locally rare species tend to be narrowly distributed. This generalization applies in a diversity of animal taxa from a variety of habitats and at several spatial scales (Gaston 1996). Several mechanisms are believed to act independently or jointly to produce positive correlations between abundance and distribution (Gaston *et al.* 1997).

The relationship is not restricted to free-living organisms. Among parasite species exploiting the same host population, positive correlations exist between the mean number of conspecifics per host individual (intensity of infection) and the percentage of hosts infected (prevalence of infection). In other words, parasite species 'locally' abundant in an individual host tend to be widespread among hosts in the population, the next scale up. This pattern has been reported among helminth species exploiting the same bird population (e.g. Bush & Holmes 1986; Stock & Holmes 1987). Studies at other scales are lacking,

Correspondence: Dr Robert Poulin, Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand. Fax: 643-479-7584. E-mail: robert.poulin@stonebow.otago.ac.nz

however. Within non-specific species, it is not known whether parasites achieve higher intensities of infection in host species in which they attain higher prevalence. The intraspecific relationship between abundance and distribution is also rarely examined in free-living species (but see Gaston & Curnutt 1998), although it could shed light on the underlying mechanisms causing interspecific relationships.

On an even larger scale, however, it is difficult to predict whether the pattern would be repeated. On the one hand, the resource breadth hypothesis (see Brown 1984; Gaston *et al.* 1997) suggests that the positive relationship between abundance and distribution of parasites should occur at all scales. One might expect that the characteristics that make a parasite species abundant within a host population would also lead that parasite species to successfully colonize several host species. This would result in locally abundant parasite species, i.e. those occurring at high prevalence and mean intensity, exploiting many host species, and in locally rare parasite species being more host specific. The parallel with free-living organisms should be made cautiously, since different host species would be analogous to different kinds of habitats rather than different patches of the same habitat, the largest scale at which studies on free-living organisms are usually performed. Still, by extrapolation, the resource breadth hypothesis would predict a positive correlation.

On the other hand, the other five biological mechanisms reviewed by Gaston *et al.* (1997) offer no clear prediction on what relation to expect between host specificity and abundance in parasites. In addition, a negative relationship between average abundance in host populations and the number of host species used might also exist. Parasites need different physiological and morphological adaptations to exploit different hosts and evade their immune responses. These adaptations are costly, and there may therefore be a trade-off between the number of host species that can be successfully exploited and the average abundance of parasites among their hosts (Poulin 1998a). A study of the relationship between parasite abundance and host specificity supports the trade-off hypothesis among metazoan parasites of freshwater fish (Poulin 1998b) but the generality of the pattern remains to be tested.

The objectives of this study were to assess (i) the intraspecific relationship between intensity and prevalence of infection within species of parasites, and (ii) the interspecific relationship between abundance (measured as intensity and prevalence) and host specificity among parasite species. The study was performed on adult trematodes, cestodes, and nematodes parasitic in birds. A recent study indicates that measures of abundance are repeatable among populations of helminth parasites of the same species exploiting the same host species, making parasite abundance a true species character suitable for comparative analyses (Arneberg, Skorping & Read 1997). The present analysis also controlled for phylogenetic associations among parasite species and for uneven sampling effort. A positive interspecific correlation between average abundance and the number of host species used would mirror the relationship usually observed among free-living animals, whereas a negative correlation would support the trade-off hypothesis already illustrated by data on fish parasites.

Methods

Data were obtained from a survey of bird parasites in Azerbaidzhan, in which more than 6000 individuals from 158 bird species were examined for helminths (Vaidova 1978). For the bird species included in the present analysis (see below), the mean ± SE number of birds examined per species was 46 ± 12. Measures of host specificity, prevalence, and intensity were taken for each parasite species. For the analysis of intraspecific relationships, I only used parasite species for which at least 5 host species were recorded, and in which at least 20 birds per host species had been examined. Prevalence was calculated for each host species as the number of birds harbouring the parasite divided by the total number of birds examined. A range of intensity values (numbers of parasite individuals per bird) was given for each host species in which a parasite species was found; the mid-points of these ranges were used as estimates of parasite intensity for each host species. Because intensity values are unlikely to be normally distributed within a bird population, the mid-point scores may sometimes overestimate mean intensity, which could not be obtained. For each parasite species, Spearman's rank correlations were computed between prevalence and intensity across all host species in which it occurred. To test for a general direction among these relationships, an overall correlation coefficient was computed as the average of all individual Spearman's correlation coefficients, weighted for sample size. The ratio of the weighted average correlation coefficient to its standard deviation (Z score) allows the significance of the average correlation to be evaluated. More details on these statistical procedures and examples are given in Côté & Poulin (1995).

For the analysis of interspecific relationships, host specificity was recorded as the number of bird species in which the parasite was found. Using this estimate, the specificity of parasites of poorly sampled bird species could be overestimated because some suitable hosts would be missed; however, since these bird species (< 20 individuals examined) were excluded, the estimates of specificity are likely to be accurate. Prevalence of a parasite species was calculated in two ways: first as the number of birds harbouring the parasite divided by the total number of birds examined from all bird species in which the parasite occurred (parasite species with a number of birds examined smaller than 20 were excluded from the analyses); second as the average of prevalences computed independently for each host species. The second method makes it less likely that a single well-sampled host species will bias an estimate of overall prevalence. Intensity of infection was taken as the average, weighted for sample size, of the mid-points of ranges reported for each host species.

The method of phylogenetically independent contrasts was used to control for the potential effects of phylogenetic associations (Felsenstein 1985; Harvey & Pagel 1991). The method consists in deriving independent contrasts between sister parasite taxa and assessing relationships among variables using these contrasts. Data were first log-transformed to normalize their variance. Then computations were performed on transformed data using the CAIC program, version 2.0 (Purvis & Rambaut 1994) and following the procedures outlined by Garland, Harvey & Ives (1992). Phylogenies of the trematode, cestode and nematode species included in the analysis were constructed using the information in the appendix of Brooks & McLennan (1993) and in Anderson (1992). Separate analyses were performed for each of the three helminth groups.

Branch lengths were unavailable in the phylogenies. Analyses were therefore performed both on raw contrasts and on contrasts standardized for arbitrary branch lengths following Grafen (1989) and Garland *et al.* (1992). Since both approaches yielded almost identical results, only the results obtained using raw contrasts are presented here. All correlations and regressions are forced through the origin (see Appendix 2 in Garland *et al.* 1992). Estimates of intensity can be influenced by the number of hosts examined, as larger samples of hosts are more likely to include the rare heavily infected individuals (Gregory & Woolhouse 1993). When necessary, residuals of regressions of contrasts in intensity against contrasts in the number of birds examined were used as measures corrected for the confounding effect of sampling effort. Thus, a positive residual intensity score suggests a higher intensity than expected from sample size, and a negative residual score indicates a lower than expected intensity. Linear regressions were used as other functions did not provide a better fit to the data.

Results

The data set comprised 93 species of cestodes, 195 species of trematodes and 101 species of nematodes. Both the frequency distributions of prevalence and intensity values indicate that the majority of these parasites are not very abundant (Figs 1 and 2). Both methods of computing prevalence yielded very similar results; only results using the first method are presented here. Depending on the parasite taxon, between half and two-thirds of species occurred in fewer than 10% of hosts and at intensities of fewer than 10 individual worms per host. The trend toward rarity is also apparent at a higher scale: about two-thirds of parasite species occur in either one or two host species only (see Fig. 3 in Gregory, Keymer & Harvey 1991).

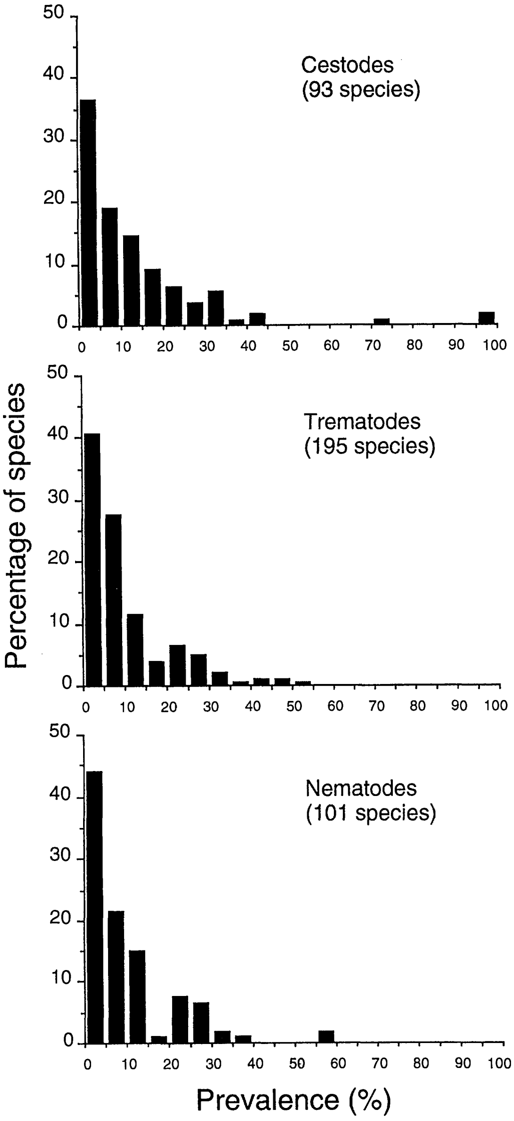

Fig. 1. Frequency distribution of prevalence values among species of helminths parasitic in birds.

In the intraspecific analysis, correlation coefficients between prevalence and intensity across host species could be obtained for 51 parasite species. The majority of those coefficients were positive (Fig. 3). Most were not statistically significant, probably due to the fact that most parasite species do not exploit much more than the 5 host species required for inclusion in the analysis (mean = 6·9 host species per parasite, range 5–15). The overall average correlation coefficient was positive but not significantly different from zero (r = 0·239, P = 0·147). When the three parasite taxa were considered separately, no significant overall correlations between prevalence and intensity across hosts were observed for cestode species (r = 0·333, n = 12, P = 0·189) and trematode species (r = 0·201,

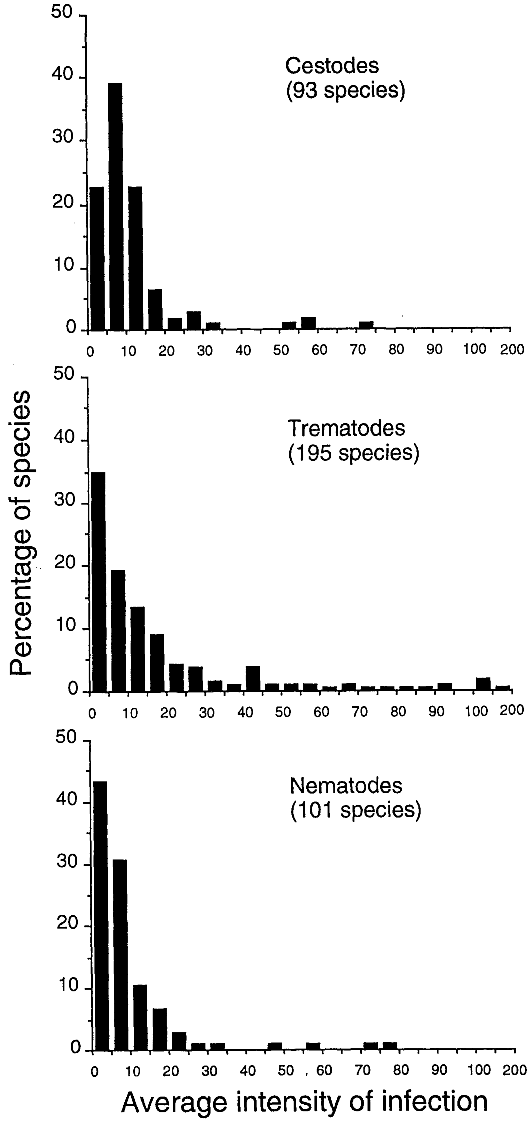

Fig. 2. Frequency distribution of intensity of infection values (mean number of parasites per host individual) among species of helminths parasitic in birds.

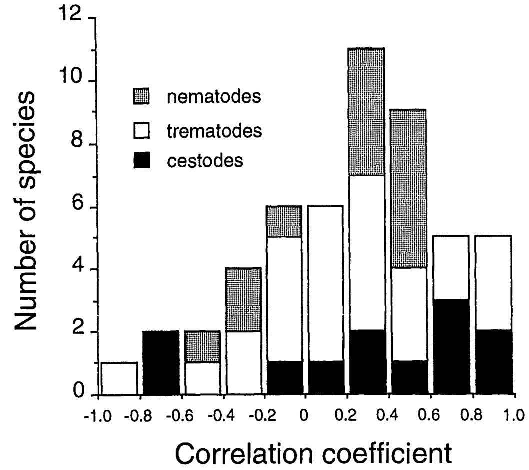

Fig. 3. Frequency distribution of correlation coefficients computed between prevalence and intensity among host species, for 51 species of helminths parasitic in birds.

$n = 26$, $P = 0{\cdot}176$). In nematodes, where individual correlation coefficients are less variable (Fig. 3), the overall correlation was positive and significant ($r = 0{\cdot}248$, $n = 13$, $P < 0{\cdot}001$).

In the interspecific analysis using phylogenetically independent contrasts, the number of birds examined did not correlate significantly with prevalence in any of the three parasite taxa. However, the number of birds examined correlated positively with intensity in both trematodes ($r = 0{\cdot}324$, $n = 98$, $P < 0{\cdot}001$) and nematodes ($r = 0{\cdot}586$, $n = 47$, $P < 0{\cdot}001$). Corrected intensity measures (residuals) are thus used in all further analyses. In all three parasite taxa, prevalence and intensity tended to correlate positively but not always significantly (cestodes: $r = 0{\cdot}318$, $n = 32$, $P < 0{\cdot}10$; trematodes: $r = 0{\cdot}430$, $n = 98$, $P < 0{\cdot}001$; nematodes: $r = 0{\cdot}251$, $n = 47$, $P < 0{\cdot}10$).

Overall, prevalence and intensity within host populations correlated positively with the range of host species used. Among cestodes, the number of host species used by a parasite species correlated positively with prevalence, but not with intensity (Fig. 4).

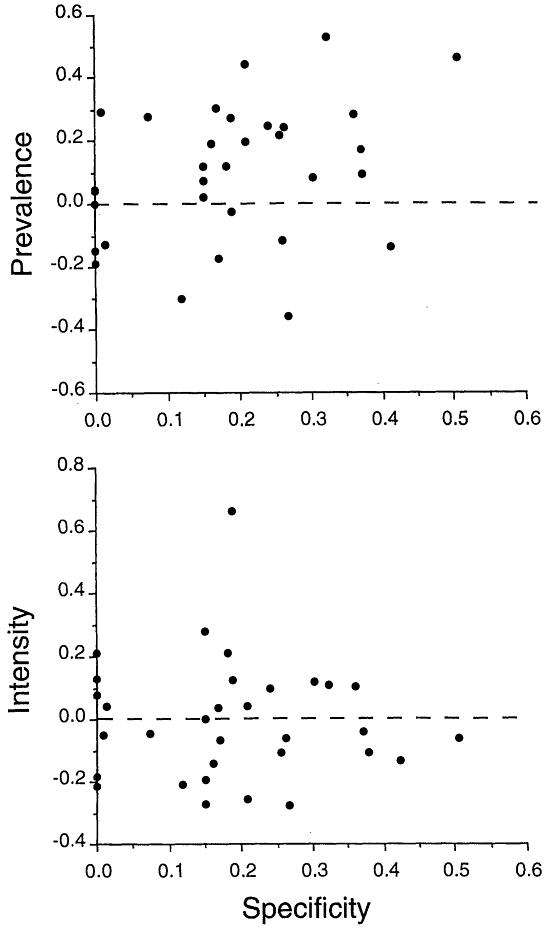

Fig. 4. Relationship between phylogenetically independent contrasts in host specificity (number of host species used by a parasite species) and contrasts in both prevalence ($r = 0{\cdot}399$, $n = 32$, $P < 0{\cdot}05$) and intensity of infection ($r = -0{\cdot}053$, $n = 32$, $P > 0{\cdot}50$), among cestodes parasitic in birds.

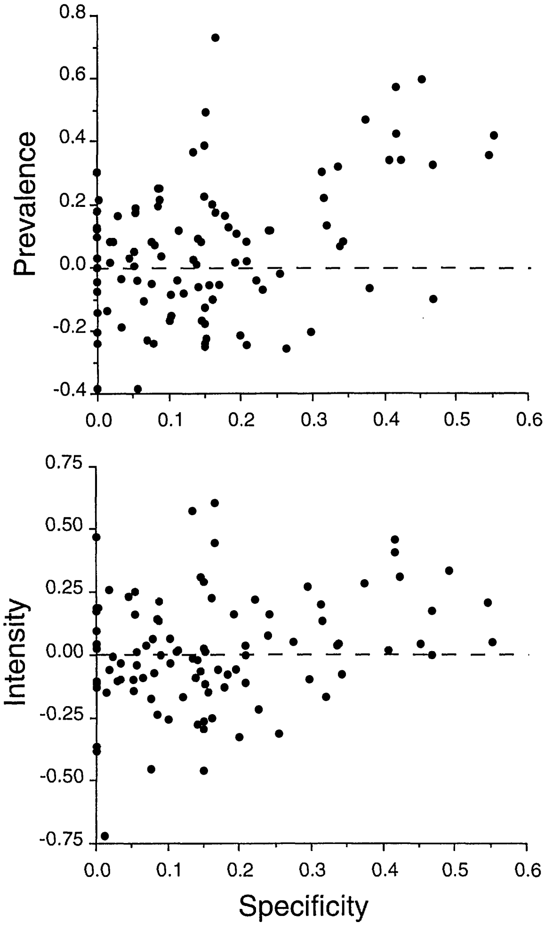

Fig. 5. Relationship between phylogenetically independent contrasts in host specificity (number of host species used by a parasite species) and contrasts in both prevalence ($r = 0{\cdot}434$, $n = 98$, $P < 0{\cdot}001$) and intensity of infection ($r = 0{\cdot}199$, $n = 98$, $P < 0{\cdot}05$), among trematodes parasitic in birds. Contrasts in intensity are corrected for the number of birds examined.

Among trematodes, the number of host species used by a parasite species was positively correlated with both prevalence and intensity (Fig. 5). Finally, among nematode species, only prevalence correlated with the number of host species used (Fig. 6).

Discussion

Several biological mechanisms have been proposed to explain why organisms common in many habitat patches also achieve high abundance in these patches (Gaston *et al.* 1997). The results presented here do not allow precise mechanisms to be determined, but they do provide support for the resource breadth hypothesis (Brown 1984). It is possible that either the niche or life-history characteristics that allow certain parasites to attain high intensities and infect a high proportion of hosts in a population also facilitate the colonization and exploitation of several host species. Thus, abundant parasite species found in many host species are so because they can use a wide range of host resources. Whatever the nature of the mechanisms behind it, the general pattern observed among helminth parasites of birds is identical to those reported for most free-living organisms.

Intraspecifically, there was some variation in prevalence and intensity among host species used. Prevalence and intensity were not always positively related, and the overall pattern was one suggesting only a weak positive relationship between prevalence and intensity among host species. Some of the mechanisms proposed to explain the interspecific relationship between abundance and distribution can also be applied to intraspecific patterns (Gaston *et al.* 1997). Given the weak and inconclusive intraspecific pattern observed here, however, it is difficult to discriminate among these mechanisms.

Perhaps the most interesting feature of the present results is that they are in sharp contrast to those obtained in a similar study on fish parasites (Poulin

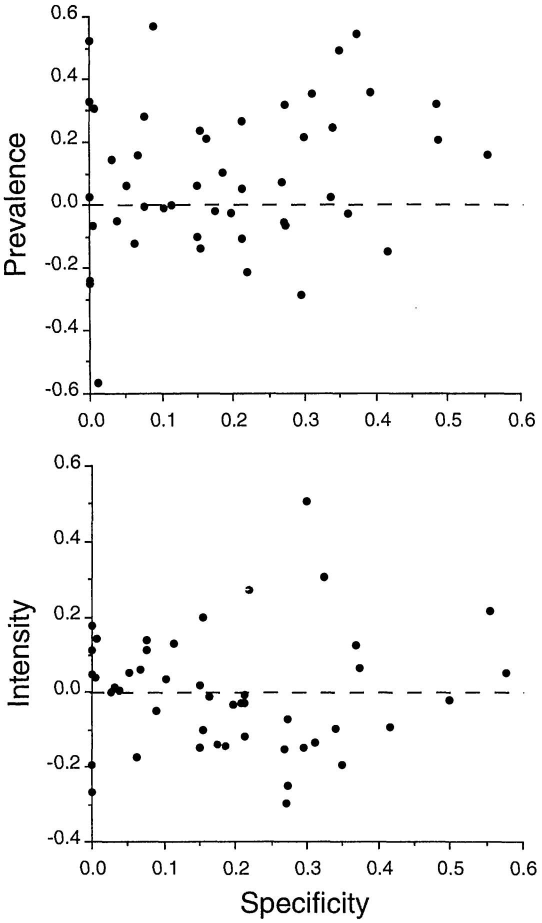

Fig. 6. Relationship between phylogenetically independent contrasts in host specificity (number of host species used by a parasite species) and contrasts in both prevalence ($r = 0{\cdot}298$, $n = 47$, $P < 0{\cdot}05$) and intensity of infection ($r = 0{\cdot}022$, $n = 47$, $P > 0{\cdot}50$), among nematodes parasitic in birds. Contrasts in intensity are corrected for the number of birds examined.

1998b). Among fish parasites, there appears to be a trade-off between the ability to exploit many host species and the potential for heavy infections in local host populations. Among bird parasites, these two traits are instead positively linked. What is so different between fish and bird parasites? Birds tend to harbour richer, denser and more diverse helminth communities than fish (Kennedy, Bush & Aho 1986; Bush, Aho & Kennedy 1990). Reasons for this include the greater complexity of the avian alimentary canal, the greater vagility of birds and their broader diets relative to fish (Kennedy *et al.* 1986). The biology of birds thus means that they are exposed to a wider range of helminth species than fish, and that they provide a greater variety of gastrointestinal habitats than fish. Colonization of new host species may be more likely by bird parasites than by fish parasites. In bird parasites, traits that lead to high prevalence and intensity of infection could simultaneously increase the probability of colonizing new hosts; in fish parasites, traits that influence prevalence and intensity may have little effect on colonization of new hosts. With the success of colonization enhanced in bird hosts relative to fish hosts, the positive relationship reported here between abundance and the number of host species used becomes predictable.

The relationship between abundance and distribution has implications for the risk of extinction (Lawton 1993). Bush & Kennedy (1994) identified some ecological features of parasites that make their extinction unlikely, at least on a geographical scale. Low host specificity and high prevalence are two of these features protecting parasite species from global disappearance. The positive relationship between abundance and the number of host species used found among bird parasites suggests that the parasite species occurring at high prevalence are also the ones with low host specificity. There may thus be a large number of species of bird parasites that are rare on both scales and thus in potential danger of extinction, and only a minority of common species in no danger of extinction (see Figs 1 and 2, as well as Fig. 3 in Gregory *et al.* 1991). In their essay, Bush & Kennedy (1994) concluded that parasites in general were unlikely candidates for extinction as either low host specificity or high prevalence would serve as hedges against extinction. The implications of the results presented here on helminth parasites of birds have some limitations. They suggest, however, that rarity (regardless of exactly how it is defined; Gaston 1994) at all scales is a property of the majority of parasite species, and that extinction is often a possible outcome of the vagaries in host abundance.

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