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The relationship between specialization and local abundance: the case of helminth parasites of birds

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Abstract Positive relationships are commonly observed between the abundance of a species in a locality and the frequency of its occurrence among localities on a larger scale. This pattern may not hold for parasitic organisms when the average abundance of a parasite among its hosts is related to the number of host species in which it occurs, because of the additive investment in specific adaptations to counter host immune responses required for each host species in a parasite's repertoire. For a rigorous test of the hypothesis that there is a trade-off between the number of host species that can be successfully exploited and the average abundance of parasites in those hosts, one needs to take into account the phylogenetic (or taxonomic) distances among the host species used by a parasite. Differences in immune responses are likely to increase with increasing phylogenetic distances. The trade-off hypothesis was tested in a comparative analysis of 393 species of trematodes, cestodes and nematodes parasitic in birds surveyed from the same geographical area, using an index of host specificity that measures the average taxonomic distances between a parasite's known host species. After correcting for the influences of parasite phylogeny and other potential confounding variables, mean abundance was negatively correlated with the average taxonomic distance among host species for nematodes, and with the variance in taxonomic distances among hosts for cestodes. In the case of trematodes, these variables covaried positively. The trade-off between average infection success and how taxonomically distant a parasite's host species are from each other was only found in two of the three groups of helminths investigated, possibly because of compensating features in trematodes, such as their ability to multiply asexually in intermediate hosts. These results provide empirical evidence consistent with the hypothesis that specialization allows greater local adaptation and therefore greater local population abundance, supporting key predictions regarding the evolution of ecological specialization.

Keywords Comparative analysis · Host specificity · Phylogeny · Taxonomic distinctness · Trade-off hypothesis

Introduction

The positive relationship between the abundance of a species in a locality and either its geographical range or the frequency of its occurrence among localities has emerged as one the most ubiquitous and best documented patterns in nature (Brown 1984; Gaston and Lawton 1990; Gaston 1996; Gaston and Blackburn 2000). Locally abundant species are usually also found in many localities within a larger area. The pattern applies to most free-living taxa, and several mechanisms may act jointly to generate it (Hanski et al. 1993; Gaston et al. 1997; Gaston and Blackburn 2000). More generally, the positive relationship between abundance and distribution indicates that whatever features give a species the ability to achieve high abundance locally do not limit its potential for dispersal and colonization of new localities.

The situation may be different for parasitic organisms. If we consider the different host species within a higher taxon as the spatial scale on which parasites can expand, then colonization of new localities, i.e. new host species, will be costly. The physiological and morphological adaptations required by parasites to overcome host defences may occur to the detriment of their ability to successfully exploit alternative host species. Because the immune defences of different host species are not

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identical, parasites must invest more in immune evasion each time they add a host species to their repertoire; this may occur at the expense of their ability to achieve high abundance in any of these hosts. Indeed, host specialization (the exploitation of a single host species) has long been thought to limit gene flow among parasite populations and enhance local adaptation (Futuyma and Moreno 1988; Thompson 1994). We might thus expect a trade-off between the number of host species that can be successfully exploited and the average abundance of parasites in those hosts: parasites capable of exploiting several host species may be jacks of all trades, but masters of none. Support for this trade-off hypothesis came from a comparative analysis of host specificity and abundance in metazoan parasites of freshwater fish (Poulin 1998). This study was based on data collected from literature sources, however, and later studies based on field data have found opposite patterns. For instance, Barger and Esch (2002) found a positive relationship between average local abundance and the number of host species infected among 22 species of fish parasites from several North Carolina streams. Similarly, Poulin (1999) observed positive relationships between the number of host species used and one or both components of parasite abundance (percentage of host individuals parasitized, and mean number of parasites per infected host) among helminths parasitic in birds, using data from a comprehensive field survey performed in a limited geographical area. These results suggest that parasites may be capable of adding new host species to their repertoire without sacrificing their success at infecting them and reaching relatively high average abundance in those hosts.

Previous tests of the hypothesis of a trade-off between how many hosts can be exploited and average parasite abundance have all suffered from one major weakness: they have ignored the relatedness among the host species used by individual parasite species. In studies of free-living organisms, the difficulty or cost associated with the colonization of a new locality is generally proportional to the geographical distance between the original site and the new one. For parasites, because host colonization takes place over evolutionary time scales, it is the phylogenetic distances among host species that matter. A generalist parasite species exploiting several host species may not have to invest too much in immune evasion if all its hosts are congeneric species, because their immune defences are likely to be similar; such a parasite might reach high abundances in its various hosts. In contrast, a generalist parasite exploiting hosts belonging to different families or orders would require adaptations against a wider range of defences, and these may occur at the detriment of the parasite's ability to attain high abundance in any or all of its hosts. From the perspective of adaptations against host defences, the host species barrier over which parasites must jump during host colonization is only as high as the phylogenetic distance between the original and the new hosts. Other host features (e.g. feeding habits, gastrointestinal anatomy and biochemistry, etc.) that may determine the likelihood of parasite transfers are also likely to be more similar among closely related host species. Focusing exclusively on the number of host species used by a parasite ignores their phylogenetic (or taxonomic) affinities, and this is inappropriate for tests of the trade-off hypothesis.

Here, we revisit the data on helminth parasites of birds used by Poulin (1999) using a newly developed index of host specificity that takes into account the average taxonomic relatedness of the host species used by a parasite (Poulin and Mouillot 2003). We also look at the variance of this index, which indicates whether one or a few host species used by a parasite are distinctly taxonomically distant from the rest (Poulin and Mouillot 2003). Specifically, we test the hypothesis that the average abundance achieved by helminth parasites in their bird hosts is negatively related to the average taxonomic or phylogenetic distance (or its variance) between the host species they use. The abundance of a parasite species in a host population can be seen as a measure of its infection success, since abundance accounts for both the proportion of host individuals used by the parasite and the mean number of parasites per host individual. We are therefore testing for a negative relationship between the average infection success of parasites in their various host species and the taxonomic distances that these parasites crossed to colonize new host species.

Materials and methods

Data were compiled from a survey of bird parasites in Azerbaidzhan, in which more than 6,000 individual birds from 158 different species were examined for intestinal helminths (Vaidova 1978). For the bird species included, the mean ± SE number of birds examined per species was 46 ± 12. Identifications of parasite species were all made by Vaidova (1978) and were based on morphology alone, and the possibility exists that cryptic species have been undetected; however, there is no reason to expect that lumping of cryptic species under a single name occurred systematically in a way that would bias our results one way or the other. The prevalence of a parasite species in a host species was the percentage of the birds examined that harboured the parasite. A range of intensity values (numbers of parasite individuals per infected bird) was given for each host species in which a parasite species was found; the intensity of infection by a parasite species in a host species was taken as the mid-point of this range. Intensity values are generally not normally distributed among individual hosts in a population, and thus the mid-point value may lie above the mean intensity value; however, the latter could not be estimated. The abundance of a parasite species in a host species was calculated as the product of its prevalence and intensity of infection.

For each species of trematode, cestode and nematode parasites, the following variables were recorded: (1) the mean number of birds examined per host species, with the few parasite species for which this number was lower than 15 being excluded from further analyses (this arbitrary cutoff number was used to eliminate estimates of prevalence and intensity based on small numbers of sampled birds); (2) mean prevalence, computed as the average of prevalences in the parasite's different host species; (3) mean intensity of infection, taken as the average, weighted for host sample size, of the mid-points of ranges reported for each host species; (4) mean abundance, computed across all of a parasite's host species; (5) the number of bird species in which the parasite was found; and (6) the specificity index, S_{TD} and its variance $VarS_{\mathrm{TD}}$ (Poulin and Mouillot 2003). This index measures the average taxonomic distinctness of all host species used by a parasite species. When these host species are placed within a taxonomic hierarchical tree, the average taxonomic distinctness is simply the mean number of steps up the tree that must be taken to reach a taxon common to two host species, computed across all possible pairs of host species (see Poulin and Mouillot 2003 for details). For any given host species pair, the number of steps corresponds to half the path length connecting two species in the taxonomic tree, with equal step lengths of 1 being postulated between each level in the taxonomic hierarchy. The greater the taxonomic distinctness between host species, the higher the number of steps needed, and the higher the value of the index S_{TD}; thus it is actually inversely proportional to specificity. A high index value means that on average the hosts of a parasite species are not closely related. Using the taxonomic classification of Sibley and Monroe (1990), which is based on phylogenetic relationships among bird taxa (Sibley and Ahlquist 1991), all bird species included here are in the infraclass Neoaves, and there are 12 taxonomic levels above species, i.e. genus, tribe, subfamily, family, superfamily, parvorder, infraorder, suborder, order, superorder, parvclass, and infraclass. The maximum value that the index S_{TD} can take (when all host species belong to different parvclasses) is thus 12, and its lowest value (when all host species are congeners) is 1. However, since the index cannot be computed for parasites exploiting a single host species, we assigned a S_{TD} value of 0 to these parasite species, to reflect their strict host specificity and distinguish them from parasites exploiting more than one congeneric host species (which would have a S_{TD} value of 1). The variance in S_{TD}, $VarS_{\mathrm{TD}}$, provides information on any asymmetries in the taxonomic distribution of host species (Poulin and Mouillot 2003); it can only be computed when a parasite exploits three or more host species (it always equals zero with two host species).

All analyses were carried out on log-transformed [log(x+1) if there were zero values] data. Comparative analyses were performed using the phylogenetically independent contrasts method (Felsenstein 1985; Harvey and Pagel 1991), implemented with the program CAIC version 2.0 (Purvis and Rambaut 1994). Detailed procedures follow those recommended by Garland et al. (1992). All regressions and correlations among sets of contrasts were forced through the origin. Estimates of parasite prevalence and intensity may be influenced by host sample size (Gregory and Blackburn 1991; Gregory and Woolhouse 1993). To correct for the potential confounding effect of host sample size (mean number of birds examined), the mean number of birds examined was entered as a second independent variable in a multiple regression, with a measure of host specificity (number of host species used, S_{TD} or $VarS_{\mathrm{TD}}$) as the main independent variable.

Separate analyses were performed for trematodes, cestodes and nematodes. Phylogenies of the helminth species in the analyses were constructed using published information. For trematodes, we used the phylogenetic framework of Olson et al. (2003) supplemented with taxonomic information from Gibson et al. (2002) and Kostadinova (2004). For cestodes, we used the phylogenetic information in Mariaux (1998), Hoberg et al. (1999), von Nickisch-Rosenegk et al. (1999) and Olson et al. (2001), and the taxonomy of Khalil et al. (1994). For nematodes, we followed the phylogeny of higher taxa proposed by Blaxter et al. (1998) and the classification of lower taxa presented in Anderson (2000).

Results

Our analyses included data on 197 species of trematodes, 95 species of cestodes and 101 species of nematodes; the full dataset is available from R.P. or as Electronic Supplementary Material from the journal's website. There were no differences among these three groups of helminth parasites with respect to either the number of bird species in which parasite species are found (ANOVA on log-transformed values: $F_{2,390}=0.566$, $P=0.568$), S_{TD} ($F_{2,390}=0.135$, $P=0.874$), or $VarS_{\mathrm{TD}}$ ($F_{2,158}=0.303$, $P=0.739$); thus trematodes, cestodes and nematodes display roughly similar patterns of host specificity (Table 1). The number of host species per parasite species ranged from 1 to 22, and values of S_{TD} ranged across the full spectrum, from 0 to 12. Based on the numbers in Table 1, we can say that the parasite species in our dataset are found on average in just over two host species, and these hosts typically belong to different tribes or subfamilies.

Across all parasite species, none of the above three measures of host specificity correlated with the mean number of birds examined per host species (all $P\geq0.203$). However, the three measures were inter-related. Across all parasite species, both the index S_{TD} (correlation using log-transformed data: $r=0.796$, $n=393$, $P=0.0001$) and to a lesser extent its variance $VarS_{\mathrm{TD}}$ ($r=0.187$, $n=161$,

Table 1 Mean (± standard error) values of three measures of host specificity, for trematodes, cestodes and nematodes parasitic in birds. Means are geometric means, i.e. the anti-logarithm of the means of log-transformed data (numbers of parasite species in each helminth group shown in parentheses)

Parasite taxa	No. host species	S_{TD}	$VarS_{\mathrm{TD}}$
Trematodes	2.19±1.06 (197)	2.82±0.23 (197)	7.32±0.90 (75)
Cestodes	2.14±1.08 (95)	2.99±0.36 (95)	7.35±1.38 (39)
Nematodes	2.38±1.09 (101)	3.02±0.33 (101)	8.28±1.18 (47)

P=0.017) tended to covary with the number of bird species in which a parasite was found. In addition, S_{TD} and $VarS_{TD}$ are also positively related to one another (r=0.818, n=161, P=0.0001). Although they measure different aspects of host specificity, the three measures are therefore not entirely independent of each other.

In the main comparative analyses based on phylogenetically independent contrasts, the mean number of birds examined per host species was often found to correlate negatively with mean prevalence, mean intensity, and/or mean abundance (Table 2). Including the mean number of birds examined as an independent variable in multiple regressions was thus justified. Using phylogenetic contrasts, S_{TD} correlated with the number of bird species in which a parasite is found for each of the three helminth groups (all P<0.0001), but $VarS_{TD}$ did not; the former index was thus corrected for the number of host species in all subsequent analyses, by using the residuals of S_{TD} values regressed against the number of host species.

Relationships between measures of infection success and measures of host specificity for trematodes, cestodes and nematodes are summarized in Table 3. In both trematodes and nematodes, but not in cestodes, as the number of host species exploited by a parasite increased, so did the parasite's mean prevalence, intensity and/or abundance of infection (Table 3). Thus in trematodes and nematodes, infection success covaries with the number of host species used by a parasite (see also Poulin 1999).

Using the index S_{TD} to quantify host specificity, we found that as the value of the index increased, both the mean prevalence and abundance of trematode species increased significantly (Table 3; Fig. 1). In other words, average infection success is positively related with the mean taxonomic distinctness of the host species used by a parasite. The pattern was more or less the opposite for cestodes and nematodes (Table 3). In cestodes, mean intensity and mean abundance were negatively related to $VarS_{TD}$ (Table 3; Fig. 2). If the outlier in both relationships corresponding to a large contrast in $VarS_{TD}$ (see Fig. 2) is removed, the negative relationship between $VarS_{TD}$ and mean intensity remains significant (P=0.028), because the majority of contrasts in mean intensity are negative whereas those in $VarS_{TD}$ were computed to be positive; the relationship between $VarS_{TD}$ and mean abundance loses its statistical significance if the outlier is excluded. In nematodes, mean abundance was negatively related to S_{TD} (Table 3; Fig. 3). Thus, greater taxonomic distances between the host species used by a parasite tended to be associated with higher infection success in trematodes, and with lower infection success in both cestodes and nematodes.

Table 2 Correlations between the mean number of birds examined per host species and three measures of infection success, computed using phylogenetically independent contrasts (numbers of sets of contrasts shown in parentheses)

Parasite taxa	Mean prevalence	Mean intensity	Mean abundance
Trematodes	−0.485 (88)***	−0.251 (88)*	−0.458 (88)***
Cestodes	−0.415 (41)**	0.134 (41)	−0.252 (41)
Nematodes	−0.572 (44)***	0.213 (44)	−0.332 (44)*

*P<0.05; **P<0.01; ***P< 0.001

Discussion

The evolution of ecological specialization in general, and host specificity in parasites in particular, has been the subject of much research over the past two decades (Futuyma and Moreno 1988; Ward 1992; Adamson and Caira 1994; Thompson 1994). For a parasite species, specializing on a single host species, or on very few closely related host species, has important advantages. For instance, local adaptation to a limited set of host immune defences can allow specialist parasites to allocate more resources to reproduction or other functions than if they needed to develop an array of counter-adaptations to combat the immune systems of several potential hosts. Nevertheless, not all parasites are specialists: many taxa have the ability to successfully infect a range of host species. Within clades of parasite species, there exist both

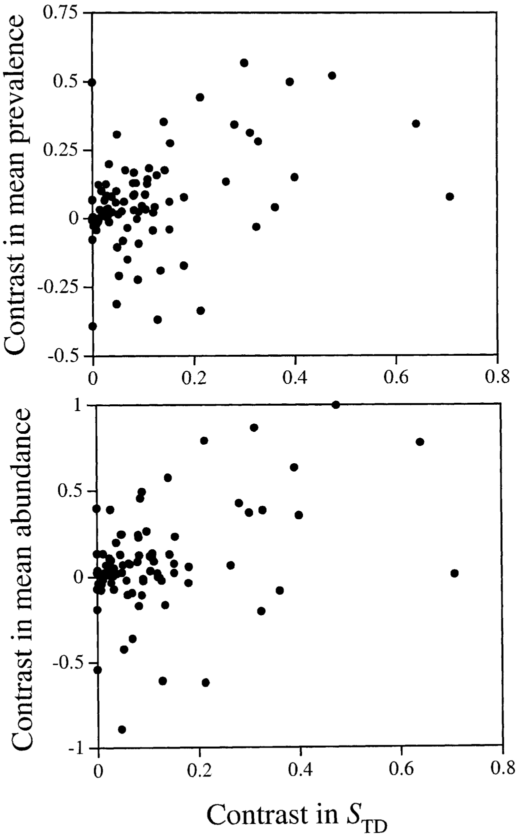

Fig. 1 Relationships between mean prevalence and abundance, and the value of the index S_{TD} (corrected for the number of host species used by a parasite), across species of trematodes parasitic in birds (see Table 2). Data are phylogenetically independent contrasts (n=88). For illustrative purposes, values of prevalence and abundance are residuals of linear regressions against the number of host individuals examined, to exclude the influence of the latter variable

Table 3 Correlations between three measures of host specificity and three measures of infection success, computed using phylogenetically independent contrasts (numbers of sets of contrasts shown in parentheses). The numbers are partial regression coefficients from multiple regressions also including the number of birds examined as an independent variable

Measure of host specificity	Mean prevalence	Mean intensity	Mean abundance
Trematodes			
Number of host species	0.191 (88)*	0.349 (88)**	0.339 (88)**
S_{TD}[a]	0.287 (88)**	−0.097 (88)	0.213 (88)*
$VarS_{TD}$	−0.165 (47)	0.002 (47)	−0.113 (47)
Cestodes			
Number of host species	0.155 (41)	−0.030 (41)	0.111 (41)
S_{TD}[a]	−0.113 (41)	−0.127 (41)	−0.157 (41)
$VarS_{TD}$	−0.348 (22)	−0.763 (22)**	−0.730 (22)**
Nematodes			
Number of host species	0.508 (43)**	−0.089 (43)	0.434 (43)**
S_{TD}[a]	−0.232 (43)	−0.223 (43)	−0.324 (43)*
$VarS_{TD}$	0.247 (26)	−0.244 (26)	0.054 (26)

*$P<0.05$; **$P<0.001$

[a] Corrected for the number of host species exploited by a parasite

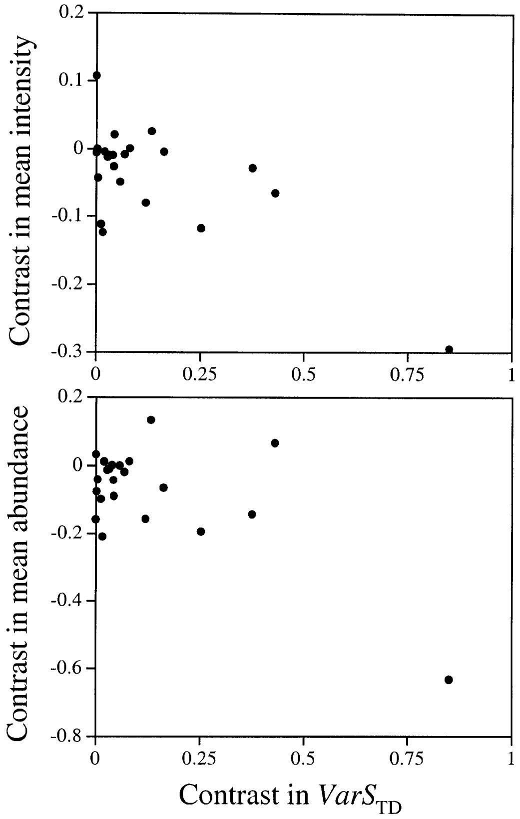

Fig. 2 Relationships between mean intensity and abundance, and the variance in the taxonomic distinctness of the host species used, $VarS_{TD}$, across species of cestodes parasitic in birds (see Table 2). Data are phylogenetically independent contrasts (n=22). For illustrative purposes, values of intensity and abundance are residuals of linear regressions against the number of host individuals examined, to exclude the influence of the latter variable

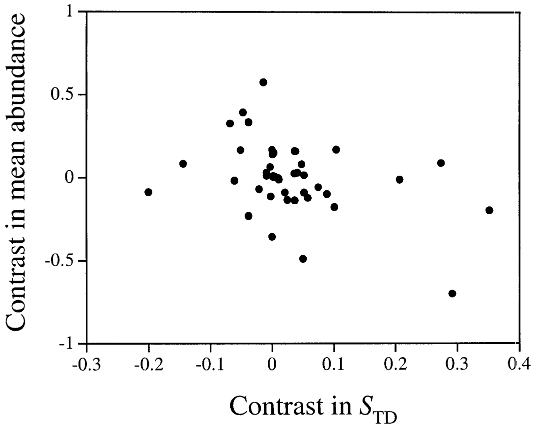

Fig. 3 Relationship between mean abundance and the value of the index S_{TD} (corrected for the number of host species used by a parasite), across species of nematodes parasitic in birds (see Table 2). Data are phylogenetically independent contrasts (n=43). For illustrative purposes, values of abundance are residuals of a linear regression against the number of host individuals examined, to exclude the influence of the latter variable

specialist and generalist species. Host specificity is a plastic trait that can evolve in both directions. Some factors, such as the temporal predictability of the host resource (see Sasal et al. 1999; Desdevises et al. 2002), may promote greater specialization. Here, we show that there may be a trade-off between average infection success across all host species and how taxonomically distant these host species are from each other, in at least two large groups of helminth parasites. This trade-off may also be an important force shaping the evolution of parasite specialization.

It is interesting to note that, for cestodes and nematodes, the pattern obtained when using the number of host species exploited as a measure of host specificity was the opposite of that seen when using either S_{TD} or $VarS_{TD}$, i.e. specificity indices that take taxonomic distances among host species into account. All three measures of host specificity tend to covary positively, but it is not rare for a parasite species with many host species to have a low value of S_{TD} or vice versa. This happens, for instance, when all the host species are congeners or species belonging to the same subfamily. Parasites that exploit hosts belonging to species-rich genera may be more likely to colonize close relatives of their original host, eventually building up a large repertoire of potential host species (see Poulin 1992). Using the number of known host species as a measure of host specificity for such parasites, one might conclude that they show low host specificity. Using S_{TD} instead, these parasites would appear to be quite host-specific, being restricted to a single genus of hosts. The number of host species used by a parasite and S_{TD} (and its variance $VarS_{TD}$) thus capture different aspects of parasite specialization, and they should be used in combination in investigations of host specificity.

In the present study, S_{TD} and $VarS_{TD}$ are more relevant because they measure, respectively, the average taxonomic distance and asymmetries in those distances between the host species exploited by a parasite, and we thus assume that they serve as a surrogate measure of the range of immune defences that the parasite must be capable of coping with during its adult life inside a bird host. In nematodes, an increase in S_{TD} was associated with a decrease in mean abundance. Thus, there appears to be a trade-off between the average taxonomic distances crossed by nematodes as they colonized new hosts and the average infection success they achieve in these hosts. In cestodes, the pattern is slightly different. An increase in $VarS_{TD}$ was associated with a decrease in one of the components of cestode abundance (prevalence and intensity of infection). In this group of helminths, species that exploit one or a few hosts markedly distant (from a taxonomic or phylogenetic perspective) from the rest of their hosts tend to achieve lower average infection success across all their hosts. Cestodes occasionally crossing large taxonomic distances to colonize hosts in families or orders other than those to which their initial hosts belong may do so at the expense of their average infection success. Although the patterns differ between nematodes and cestodes, they both show evidence of a trade-off: nematodes with host species that are on average distantly related, and cestodes with one or a few host species very distantly related to the rest of their hosts, all tend to achieve low mean abundance in these hosts. In sharp contrast, the relationship between S_{TD} and mean abundance was positive among trematode species. There is no hint of a trade-off in trematodes; instead, trematode species capable of infecting several host species achieve higher mean abundances than trematodes restricted to few host species. Why is there such a sharp difference between nematodes and cestodes on the one hand, and trematodes on the other hand?

The difference is not merely due to the fact that these three groups of helminths occupy different parts of the host-specificity spectrum: there were no differences among the three groups with respect to the number of host species used, S_{TD} or $VarS_{TD}$. Instead, there may be differences in the strength of the immune responses of birds against these helminths. For instance, the spleen is a major lymphoid organ in birds, playing a more prominent role in systemic immunity than it does in mammals (Toivanen and Toivanen 1987; John 1994). There is evidence that within a bird population, individuals with a relatively small spleen are more susceptible to nematode infections, but not to infections by other types of helminths (Shutler et al. 1999). In comparative analyses across bird species, positive relationships have been observed between the relative spleen mass of birds and either the prevalence of nematode infections (John 1995) or the species richness of nematode parasites infecting a bird species (Morand and Poulin 2000); no such patterns have been observed for cestodes or trematodes. This all suggests that the immune system of birds has evolved more closely with nematodes than other helminths, possibly because nematodes are on average more virulent to birds than cestodes or trematodes. Colonizing new host species may therefore require greater investments in evasive mechanisms for nematodes than for other helminths. This would not explain why the abundance-specificity trade-off was also observed for cestodes, however.

Perhaps one distinctive feature of trematodes allows them to overcome the cost of adapting to the immune systems of many different host species and still attain high abundances. The trematodes, cestodes and nematodes in this study, with only rare exceptions, are acquired by birds when the latter feed on infected intermediate hosts. However, prior to encysting in their final intermediate host, trematodes multiply asexually in their first intermediate host, something that cestodes and nematodes do not do (some taeniid cestodes parasitic in mammals have asexual multiplication, but not the avian parasites in this study) (Kearn 1998). If asexual multiplication in the first host leads to higher proportions of second intermediate hosts being infected, with higher numbers of infective trematode stages (metacercariae) per individual host than are possible for cestodes and nematodes, then asexual proliferation may allow trematodes to occur at high abundance in their avian definitive hosts while permitting frequent colonization of new host species. There exist no comprehensive data on the infection rates of intermediate hosts of trematode, cestode and nematode parasites of birds, and thus no easy way to test this possibility. Similarly, other general differences between trematodes and the other two helminth groups, such as the generally smaller body sizes of trematodes compared to cestodes and nematodes, may account for the different patterns we observed, but their importance cannot yet be evaluated.

Among free-living animals, the ubiquitous positive relationship between the local abundance of a species and its frequency of occurrence over a larger area (Brown 1984; Hanski et al. 1993; Gaston et al. 1997; Gaston and Blackburn 2000) suggests that whatever gives a species the ability to achieve high abundance locally does not reduce its potential for dispersal and colonization of new localities. Our analyses did not examine the exact same patterns for parasites, because different host species are different kinds of habitats, rather than different localities offering the same general living conditions. Still, we searched for a parallel relationship, i.e. a general positive relationship between local abundance and the ability to exploit slightly different kinds of living conditions. Our results show that this relationship does not hold for at least certain groups of parasites, namely cestodes and nematodes parasitic in birds. The living habitat of parasites, and its resistance to parasite invasion, creates a trade-off between the phylogenetic distances among the host species used by a parasite, and how well it does on average in those hosts. This situation parallels that between herbivorous insects and their host plants: there is evidence for a continuum between specialist herbivores well-adapted to cope with the chemical defences of their single host plant and generalists feeding on many plants but with a lower average feeding success (Berenbaum 1983; Cornell and Hawkins 2003). The extent of host specificity varies widely among parasites and other obligate symbionts (see Futuyma and Moreno 1988; Poulin 1992; Ward 1992; Adamson and Caira 1994; Thompson 1994). Our results provide one of the first empirical demonstrations that parasite specialization allows greater local adaptation and therefore greater local population abundance, and thus support some of the key predictions regarding the evolution of ecological specialization.

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