

Evolution of host specificity in fleas: Is it directional and irreversible?

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Abstract

Evolutionary trends in the evolution of host specificity have been the focus of much discussion but little rigorous empirical testing. On the one hand, specialization is often presumed to lead irreversibly into evolutionary dead ends and little diversification; this would mean that generalists might evolve into specialists, but not vice versa. On the other hand, low host specificity may limit the risk of extinction and provide more immediate fitness benefits to parasites, such that selection may favour evolution toward a generalist strategy. Here, we test for directionality in the evolution of host specificity using a large data set and phylogenetic information on 297 species of fleas parasitic on small mammals. The analyses determined whether host specificity, measured both as the number of host species exploited and their taxonomic diversity, was related to clade rank of the flea species, or the number of branching events between an extant species and the root of the phylogenetic tree (i.e., the total path length from the root of the tree to the species). Based on regression analyses, we found positive relationships between the number of host species used and clade rank across all 297 species, as well as within one (Hystrihopsyllidae) of four large families and one of seven large genera investigated separately; in addition, we found a positive relationship between the taxonomic diversity of host species used and clade rank in another of the seven genera. These results suggest a slight evolutionary trend of decreasing host specificity. Using a much more conservative likelihood ratio test, however, a random walk, or null model, of evolution could not be discarded in favour of the directional trends in all cases mentioned above. Still, these results suggest that host specificity may have tended to decrease in many flea lineages, a process that could have been driven by the benefits of exploiting a wide range of host species.

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1. Introduction

In evolutionary biology, specialization is generally presumed to be irreversible. Mayr (1963) has famously argued that specialization leads into blind alleys, and that highly specialized organisms do not give rise to new lineages. This notion is usually applied to morphological specialization, as when Noble and Noble (1976) stated that parasites, with their reduced morphological complexity well-fitted to their mode of life, were good examples of evolution's inexorable march into dead ends. Specialization can also be viewed from an

ecological perspective and measured as the diversity of resources used by an organism (Futuyma and Moreno, 1988). On the one hand, specialist taxa, capable of using only a narrow range of resources, should be less likely to colonize new habitats and therefore the potential of specialists to give rise to new lineages should be limited (Jaenike, 1990). If this is so, we might expect that generalists can evolve into specialists but that the likelihood of specialists evolving into generalists would be much lower. Thus, within a clade, the more specialized species should, on an average, be the more derived, i.e. the more recent ones. On the other hand, specialist taxa should be more prone to extinction than generalists, because of their strict dependence on a narrow resource base and thus we might expect generalist taxa to be favoured and to proliferate over evolutionary time.

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It is therefore not straightforward to predict in which direction specialization will evolve in a given clade, i.e. whether it will tend to increase or decrease over evolutionary time. Indeed, based on a review of the limited evidence available from a range of ecological systems, Thompson (1994) has concluded that there is no intrinsic direction to the evolution of ecological specialization.

Directionality and irreversibility in the evolution of ecological specialization are not easy to test, mainly because defining resource breadth for many different taxa is often problematic. Using parasitic organisms can provide a solution to this obstacle (Adamson and Caira, 1994). For parasites, ecological specialization can be defined in terms of host specificity, i.e. the number and diversity of host species used by a parasite. In a recent study, for instance, Desdèvises et al. (2002) have mapped the host specificity of 20 congeneric species of monogenean ectoparasites of fish on a molecular phylogeny of these species and found that the most highly host-specific species are not necessarily the more derived. This study is the only one to date performed within a robust phylogenetic context; because it is based on a single genus, however, the generality of its findings remains to be verified. It may not even be a common pattern among monogeneans in general. We need further tests carried out on a broader range of taxa, within a phylogenetic context.

Ideally, to test for evolutionary trends in host specificity among species of parasites, one would need to determine whether the host specificity of recent taxa is consistently different from that of ancestral taxa. Such a test is impossible because there is no information whatsoever on the host specificity of extinct parasite taxa; only extant taxa are available for analyses of evolutionary trends. Using phylogenetic information, however, it is possible to identify basal and derived taxa, i.e. taxa that have originated at different distances from the base of the tree (Pagel, 1997, 1999, 2002; Knouft and Page, 2003; Poulin, 2005a). Although this still does not provide information on the characteristics of extinct taxa, the host specificity of extant taxa gives an indication of how ancient and recent branches in the same phylogenetic tree have evolved since branching out.

Here, we examine evolutionary trends in host specificity of basal and derived species of fleas (Siphonaptera) parasitic on small mammals. Fleas usually alternate between periods when they occur on the body of their hosts and periods when they occur in their hosts' burrows or nests. The larvae are usually not parasitic and feed on organic debris in the burrow and/or nest of the host. The degree of association between a particular flea species and various host species varies, with flea species ranging from highly host-specific to host-opportunistic (Marshall, 1981). Our analyses allow both an assessment of general directional trends in the evolution of host specificity, as well as an evaluation of whether it is irreversible or not. We also test for consistent patterns among different genera and families of fleas, to assess the generality of any trend. The study makes use of a large data set on the host specificity of fleas, combined with phylogenetic information and robust analytical tools, to uncover phylogenetically correct statistical

trends in the evolution of host specificity in parasitic organisms.

2. Methods

2.1. Host specificity data

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Didelphimorphia, Insectivora, Lagomorpha and Rodentia) in 35 different geographical regions, mostly in the Northern Hemisphere (for further details and all original sources, see Krasnov et al., *in press*). Among other information, these sources provided data on which flea species were found on each particular host species in each region. Based on the abundance data provided in the surveys, we excluded cases where a single individual of a flea species occurred on a host species or in a region, as these were considered accidental occurrences. In total, we used data on 297 flea species found on 197 mammalian species, representing 838 different flea species-region combinations. The complete list of flea species used and the entire dataset are available upon request from either RP or BRK.

For each species of flea, two measures of host specificity were used: (i) the number of mammalian species on which the flea species was found; and (ii) the specificity index, S_{TD} (Poulin and Mouillot, 2003). The index S_{TD} measures the average taxonomic distinctness of all host species used by a parasite species. When these host species are placed within a taxonomic hierarchy, the average taxonomic distinctness is simply the mean number of steps up the hierarchy 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). The greater the taxonomic distinctness between host species, 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 flea species are not closely related. Using the taxonomic classification of Wilson and Reeder (1993), all mammal species included here were fitted into a taxonomic structure with five hierarchical levels above species, i.e. genus, subfamily, family, order, and class (Mammalia). The maximum value that the index S_{TD} can take (when all host species belong to different orders) is thus five and its lowest value (when all host species are congeners) is one. However, since the index cannot be computed for parasites exploiting a single host species, we assigned a S_{TD} value of zero to these flea species, to reflect their strict host specificity. Clearly, host taxonomy is only a crude substitute for true host phylogeny; nevertheless, the index does capture real information about the relationships existing among host species (Poulin and Mouillot, 2003). To calculate S_{TD} , a computer program using Borland C++ Builder 6.0 is freely available (at <http://www.otago.ac.nz/zology/downloads/poulin/TaxoBiodiv1.2>).

Measures of host specificity were averaged across regions for each flea species that occurred in more than one region. In addition, the total number of host individuals examined was weakly, albeit significantly correlated with the number of host

species on which a flea species has been recorded ($r^2=0.03$, $F_{1,295}=8.2$, $P<0.005$), but not with S_{TD} ($r^2=0.01$, $F_{1,295}=3.6$; $P>0.05$). To avoid the potential confounding effects of host sampling effort, the residuals of the regression of the log-transformed number of host species on which the flea species was found against the log-transformed number of host individuals sampled were used in subsequent analyses. In addition, S_{TD} was $\ln(x+1)$ -transformed prior to all analyses. The above logarithmic transformations were necessary to normalise the distributions of these variables.

2.2. Data analysis

Evolutionary trends in host specificity were examined at different levels: (i) across all 297 flea species in the data set; (ii) separately in each of four large families: Ceratophyllidae, Leptopsyllidae, Hystrichopsyllidae, and Pulicidae; and (iii) separately in the seven most-speciose genera: three leptopsyllid genera (*Amphipsylla*, *Frontopsylla* and *Paradoxopsyllus*), three hystrichopsyllid genera (*Ctenophthalmus*, *Neopsylla* and *Rhadinopsylla*) and one pulicid genus (*Xenopsylla*). The phylogenetic trees for fleas used here were based on the morphologically derived taxonomy used in Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971), Smit (1987); Traub et al. (1983) and the cladistic tree of flea families of Medvedev (1998). The complete phylogenetic tree used here, coded in Newick format, is available upon request from either RP or BRK.

Two approaches were used to assess evolutionary trends in host specificity. First, we used generalised least squares (GLS) regressions. This allows one to determine whether host specificity correlates with clade rank among extant species (Pagel, 1997, 1999, 2002; Knouft and Page, 2003). Clade rank is not equivalent to taxonomic rank; instead, it is the number of branching or speciation events between an extant flea species and the root of a phylogenetic tree, the root being the bifurcation from which all taxa in the group have descended (Norell and Novacek, 1992; Knouft and Page, 2003; Poulin, 2005a). Clade rank quantifies the evolutionary position of a species within a clade, or the total path length from the root of the tree to a given species: basal species are taxa with the lowest rank and derived species have the highest rank. Host specificity for each flea species is predicted from the GLS regression of host specificity on clade rank, i.e. on the distance from the root of the phylogeny to the species (Pagel, 1997, 1999, 2002; Knouft and Page, 2003; Poulin, 2005a). In this directional model of evolution, the slope defines the phylogenetically correct slope of the line relating clade rank to log-transformed host specificity (Pagel, 1997, 1999, 2002; Knouft and Page, 2003). The value and significance of the slope indicate whether host specificity evolved in a general direction and if so in what direction, whereas the amount of variance explained (r^2 value) indicates how strictly host specificity has adhered to this trend, i.e. whether reversals have been common or not. Information on branch length was not available and all branches within a clade were set equal; this places a constraint on the evolutionary model, where most of the divergence in host specificity between sister taxa must

be assumed to take place at, and not between, speciation events. This is a reasonable assumption since, when it occurs, parasite speciation is thought to generally coincide with host colonization and thus with a possible change in host specificity.

The second approach we used was to apply a likelihood-ratio (LR) test statistic to assess the probability that a directional model based on a GLS regression was a better predictor of host specificity evolution within a clade than a null, or random walk, model in which the slope equals zero. In the test, $LR = -2 \log(H_0/H_1)$, where H_0 is the likelihood associated with the null hypothesis and H_1 is the likelihood associated with the directional hypothesis (Pagel, 1997, 1999). The significance of the test is determined by comparing LR to a χ^2 statistic with d.f. = 1 ($\alpha = 0.05$). The test was implemented using Pagel's computer program Continuous (available at <http://sapc34.rdg.ac.uk/meade/Mark/>). The likelihood-ratio approach essentially allows one to determine whether the degree of evidential support for the directional model is stronger than that for the null model; it is a more conservative test than a simple regression but it is increasingly seen as a better option to weight scientific evidence (see Taper and Lele, 2004).

3. Results

Measures of host specificity (untransformed and not corrected for sampling effort) varied widely across the 297 flea species in the dataset: the average number of host species exploited was 3.3, and ranged from 1 to 22, whereas S_{TD} values covered the full range possible, from 0 to 5, with an average of 1.95. There is thus much variability in host specificity among the fleas in the dataset.

3.1. Whole dataset and family-level analyses

Based on the regressions, we found a significant positive relationship between the number of host species used by a flea and clade rank, across all 297 flea species ($r^2=0.02$, $F_{1,295}=5.39$, $P=0.0209$). The positive trend means that the more derived flea species tend to exploit more host species than basal species. The relationship was weak, however, with much scatter (Fig. 1) and clade rank explaining only about 2% of the variance in the number of host species used. This result using all flea species appears to be caused mainly by a similar and slightly stronger relationship between the number of species used and clade rank within the flea family Hystrichopsyllidae ($r^2=0.06$, $F_{1,113}=7.73$, $P=0.0064$). This is the best-represented family in our dataset (115 species), and there was no significant relationship between the number of host species used and clade rank for any of the three other families investigated here (all $P>0.16$).

We found no relationship between host specificity measured by the index S_{TD} and clade rank, either across the entire data set ($r^2=0.005$, $F_{1,295}=1.58$, $P=0.2099$) or within each of

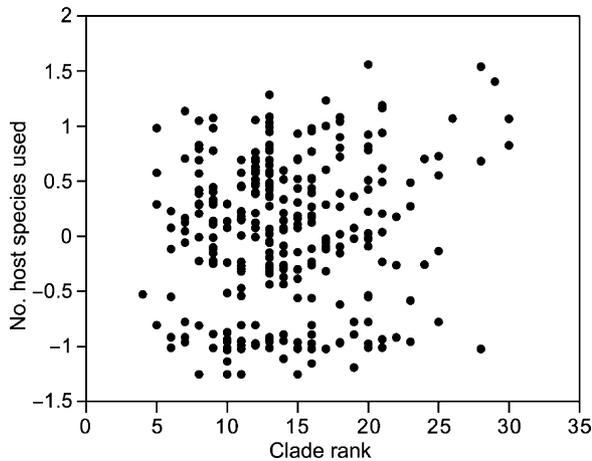


Fig. 1. Relationship between the number of host species used by a parasite species and clade rank, among 297 species of fleas parasitic on small mammals. The number of host species used is corrected for sampling effort: data shown are residuals of the regression of the log-transformed number of host species on which the flea species was found against the log-transformed number of host individuals sampled.

the four large flea families (all $P > 0.22$). In other words, the taxonomic diversity of host species used by a flea did not differ between basal or derived flea species and thus showed no evolutionary trend (Fig. 2). From Fig. 2, it is clear that there is a slight discontinuity in the distribution of S_{TD} values, because of the many null values assigned to strictly host-specific flea species (see Section 2). If we exclude these null values, the positive relationship between host specificity measured by the index S_{TD} and clade rank across the entire dataset becomes clearer but still does not reach significance ($r^2 = 0.012$, $F_{1,225} = 2.77$, $P = 0.0973$). Excluding null S_{TD} values, there was also no significant relationship within each of the four large flea families (all $P > 0.26$).

Using the likelihood-ratio test, the trend across all species between the number of host species used and clade rank

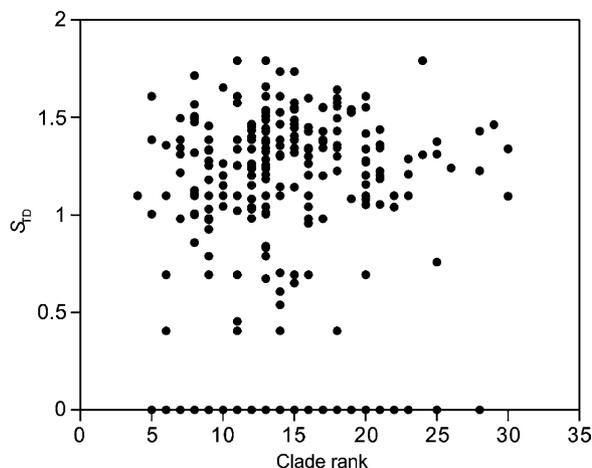


Fig. 2. Relationship between the taxonomic distinctness of host species used, measured by the index S_{TD} ($\ln(x+1)$ -transformed), and clade rank, among 297 species of fleas parasitic on small mammals.

Table 1

Results of the tests of the relationship between host specificity and clade rank in fleas, across the entire dataset and within selected families

Host specificity measure (data set)	No. flea species	α^a (SE)	β^a (SE)	P^a
Number of host species				
All flea species	297	-0.309 (0.517)	0.056 (0.038)	0.1374
Ceratophyllidae	76	-0.840 (0.583)	0.104 (0.105)	0.3235
Leptopsyllidae	73	-0.278 (0.567)	0.036 (0.074)	0.6385
Hystrichopsyllidae	115	0.141 (0.396)	0.047 (0.053)	0.3699
Pulicidae	19	-0.057 (0.503)	0.067 (0.118)	0.6018
S_{TD} index				
All flea species	297	0.734 (0.461)	0.047 (0.034)	0.1651
Ceratophyllidae	76	0.199 (0.516)	0.104 (0.093)	0.2628
Leptopsyllidae	73	0.687 (0.524)	0.037 (0.068)	0.5931
Hystrichopsyllidae	115	1.061 (0.357)	0.032 (0.047)	0.5058
Pulicidae	19	1.208 (0.386)	0.025 (0.090)	0.9387

^a α is the Y-axis intercept and β the phylogenetically correct slope of the regression of host specificity on clade rank from the directional model of evolution; P is from the likelihood ratio test based on the difference between the likelihoods of the directional and random walk models.

disappeared ($P = 0.137$; see Table 1). In fact, the non-directional random walk model of evolution cannot be rejected for either measure of host specificity, whether the analyses are performed across all 297 flea species or limited only to species in one of the four large families (Table 1). In all cases, the slopes are positive, but the directional model of evolution does not explain sufficiently more of the variance in host specificity among extant species than the null model.

3.2. Genus-level analyses

Based on regression analyses, there was a marginally significant positive relationship between the number of host species used and clade rank among species of the genus *Neopsylla* ($r^2 = 0.39$, $F_{1,8} = 5.15$, $P = 0.0529$), as well as a significant positive relationship between the specificity index S_{TD} and clade rank among *Xenopsylla* species ($r^2 = 0.44$, $F_{1,8} = 6.21$, $P = 0.0375$). No other significant regression results were obtained for other genera (all $P > 0.16$).

Using the more conservative likelihood-ratio test, the two above trends disappeared (Table 2). In fact, the non-directional random walk model of evolution cannot be rejected in favour of the directional model for either measure of host specificity, in any of the flea genera (Table 2).

4. Discussion

The evolution of ecological specialization in general, and host specificity in parasites in particular, has generated much discussion, but rather little in terms of empirical evidence (Futuyma and Moreno, 1988; Jaenike, 1990; Ward, 1992; Adamson and Caira, 1994; Poulin, 1998). Our study on the evolution of host specificity in fleas parasitic on small mammals has produced some interesting findings. First, trends in the evolution of host specificity in fleas, if any, tend to show an increase in the number of host species used over time,

Table 2

Results of the tests of the relationship between host specificity and clade rank in fleas within seven genera

Host specificity measure (Genus)	No. flea species	α^a (SE)	β^a (SE)	P^a
Number of host species				
<i>Amphipsylla</i>	18	-0.246 (0.498)	0.034 (0.122)	0.9995
<i>Frontopsylla</i>	11	-0.616 (0.862)	0.166 (0.262)	0.5713
<i>Paradoxopsyllus</i>	9	0.830 (0.717)	-0.109 (0.285)	0.9918
<i>Ctenophthalmus</i>	26	-0.183 (0.592)	0.054 (0.133)	0.7355
<i>Neopsylla</i>	10	-0.834 (0.349)	0.179 (0.132)	0.1715
<i>Rhadinopsylla</i>	22	-0.045 (0.197)	-0.020 (0.101)	0.9944
<i>Xenopsylla</i>	10	-0.881 (0.506)	0.174 (0.195)	0.3792
S_{TD} index				
<i>Amphipsylla</i>	18	0.612 (0.576)	0.031 (0.142)	0.9963
<i>Frontopsylla</i>	11	0.573 (0.683)	0.126 (0.208)	0.5971
<i>Paradoxopsyllus</i>	9	1.428 (0.601)	-0.056 (0.239)	0.9895
<i>Ctenophthalmus</i>	26	0.938 (0.476)	-0.001 (0.107)	0.9990
<i>Neopsylla</i>	10	0.344 (0.295)	0.119 (0.112)	0.2827
<i>Rhadinopsylla</i>	22	1.263 (0.489)	-0.072 (0.111)	0.5354
<i>Xenopsylla</i>	10	0.168 (0.293)	0.154 (0.113)	0.1664

^a α is the Y-axis intercept and β the phylogenetically correct slope of the regression of host specificity on clade rank from the directional model of evolution; P is from the likelihood ratio test based on the difference between the likelihoods of the directional and random walk models.

i.e. a decrease in host specificity rather than an increase. Second, the trends vary among taxa. For instance, there is a relatively clear trend in the family Hystrichopsyllidae but no pattern whatsoever in the other three families investigated here. Third, except for weak trends in a couple of genera, relationships among families or across all species in the dataset are characterised by low r^2 values, suggesting that clade rank is not a good predictor of host specificity, and that evolutionary changes in host specificity are not constrained in a single direction. Thus, evolutionary changes in host specificity are clearly reversible. Fourth, and perhaps most important of all, the evolutionary trends observed in this study are not strong enough to allow us to reject a null, random walk model of evolution, in which host specificity does not change in any particular direction. This is true whether we consider all species together, or only subsets representing given families or genera.

One issue that arises concerns the suitability of host specificity as a trait for evolutionary study. Is host specificity a true species character? Does its evolution show some degree of phylogenetic constraints? The answer to both questions is yes. Host specificity, measured either as the number of host species used or their taxonomic diversity, varies among populations of the same flea species. This is to be expected, because the pool of host species available to a parasite species is not the same everywhere. However, this variation within flea species is significantly much lower than the variation observed among different flea species (Krasnov et al., 2004a). Values of both the number of host species used and S_{TD} from the same flea species but from different populations, are significantly more similar to each other, and significantly more different from those of other species, than expected by

chance (Krasnov et al., 2004a). Host specificity can thus be considered as a real species character. It shows a degree of heritability from ancestral to daughter flea species, making it a suitable character to track in a phylogenetic context.

Although none of the trends found here using regression analyses were strong enough to outperform a random walk model, based on the strict and rigorous likelihood-ratio test, they were nevertheless all positive. This suggests a slight expansion of the number of host species used by flea species within certain clades over evolutionary time. This trend is most clearly visible in ancient flea species belonging to the ancient families Hystrichopsyllidae and Pulicidae (*Neopsylla* and *Xenopsylla*, respectively) than in representatives of younger families such as Ceratophyllidae and Leptopsyllidae (Traub, 1980; Traub et al., 1983; Medvedev, 1996). Indeed, Hystrichopsyllidae and Pulicidae are thought to date back to the Lower Cretaceous or Upper Jurassic (Jellison, 1959; Traub et al., 1983), whereas Ceratophyllidae appeared no earlier than the Middle Eocene (Traub et al., 1983). There are at least two reasons why such a decrease in host specificity could be favoured. First, because fleas have an intimate dependence on their host's survival, flea species with a larger diversity of hosts would have a lower risk of extinction during host extinctions (Koh et al., 2004). Parasites adding more host species to their repertoire coincidentally hedge their bets against extinction, by reducing their dependence on any given resource base (Futuyma and Moreno, 1988; Bush and Kennedy, 1994). Second, there may be more immediate fitness benefits associated with the exploitation of many host species. Among flea species, generalists exploiting many host species consistently achieve higher abundance (mean number of fleas per individual host) than specialists using only one or very few host species (Krasnov et al., 2004b). For a range of reasons, generalist fleas occur at higher abundance; assuming that this reflects individual fitness, then selection should favour fleas that expand the number of host species that they can exploit. Furthermore, adding host species taxonomically close to those already used might also be advantageous. The reason for this is that in fleas, as in other parasites, the abundance achieved on new or secondary hosts is lower than that on the main host, and the difference is proportional to the taxonomic or phylogenetic distance between the secondary hosts and the main host (Krasnov et al., 2004c; Poulin, 2005b). This may explain why there were fewer indications of an increase in specificity measured as S_{TD} over evolutionary time. Thus, to maximise fitness benefits and minimize the risk of extinction, fleas may be selected to infect more host species, as well as taxonomically related hosts, possibly accounting for the weak trends identified in our analyses.

Recent studies on other animal groups also challenge the paradigm that specialization is both directional and irreversible. In his re-evaluation of 15 studies on evolutionary transitions between specialized and generalized host-plant use, Nosil (2002) found that generalist-to-specialist transitions were more frequent overall among phytophagous insects, but that in some groups of butterflies and bark beetles, the opposite was true. Furthermore, Stireman (2005) reported that transitions

from specialist to generalist strategies have occurred more frequently than the reverse during the evolutionary history of tachinid flies, a group of endoparasitoids of insect hosts. The result is that generalist tachinid species tend to be the most derived, i.e. they tend to occupy branch tips in the phylogeny of the group (Stireman, 2005).

The present analysis is the first to investigate the evolution of host specificity in parasites on such a large scale. Based on the available evidence, it is impossible to reject the random walk model for the evolution of host specificity in fleas and therefore there may be reversibility and no consistent directional trend in the evolution of this trait. Still, given the handful of significant positive relationships suggested by simple regressions and the highly conservative nature of the likelihood-ratio test, it is possible that slight increases in the number of host species used by fleas have outnumbered decreases over evolutionary time. Searching for similar patterns in other parasite taxa would allow us to see whether this is a general tendency among parasitic organisms, or, as suggested for ecological specialization in general (Thompson, 1994), whether there is no consistent directionality in the evolution of host specificity.

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