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ORIGINAL PAPER

How are the host spectra of hematophagous parasites shaped over evolutionary time? Random choice vs selection of a phylogenetic lineage

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Abstract Among generalist parasites, some species exploit only hosts from one particular phylogenetic lineage, whereas others can use a broader phylogenetic range of hosts, often seemingly using a random subset of the locally available host species. The latter type of generalist parasites should have greater opportunities to expand their geographical range and should not be restricted to stable and predictable host species because they are less prone to extinction than generalist parasites limited to a phylogenetically narrower host spectrum. We analyzed the diversity skewness of the host spectrum of 21 flea species from South Africa and 39 flea species from northern North America. Diversity skewness measures the balance in the shape of the phylogenetic tree of a set of species: the greater the skew, the more one lineage is overrepresented in an assemblage. When compared to a null expectation, i.e., random selections from the locally available pool of host species, the host spectra of most fleas was not more or less skewed than that expected by chance, though there were a few exceptions. Across South African fleas, the diversity skewness of the host spectrum was strongly negatively correlated with the size of a flea's geographic range; this relationship was not seen among North American flea species. There was no evidence among either set of fleas that average host body mass (a surrogate measure of host life span) correlated with the diversity skewness of the host spectrum. These findings are discussed with respect to the evolution of host specificity, its measurement, and historical differences between the two geographic areas considered.

Introduction

Parasites, even among species belonging to the same taxon, vary greatly in their host specificity, ranging from being highly host-specific to host-opportunistic. The ability to extract resources from either a few or many host species and to use these resources for fitness maximization thus falls between two extreme strategies analogous to resource specialization and resource generalization in free-living organisms (Futuyma and Moreno 1988). The result of the evolutionary "choice" by a species to adopt a particular strategy will thus give it a host spectrum ranging from narrow to broad.

Frequency distributions of the values of host specificity (number of host species used) within a parasite taxon have been shown to be strongly right-skewed, suggesting that host opportunists represent a minority among parasite species (Poulin 2007). However, this is true mainly when host specificity is measured as the number of host species used by a parasite. In contrast, when measures of host specificity take into account the taxonomic relationships among hosts (Poulin and Mouillot 2003), the frequency

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distributions of host specificity lose the right skew, suggesting instead that host opportunism in terms of taxonomic diversity rather than number of hosts exploited is quite widespread (Poulin 2007). The existence of many "phylogenetic" host opportunists in a parasite taxon indicates that host switches might be an important event during the evolutionary history of this taxon (Paterson et al. 1993; Beveridge and Chilton 2001; Roy 2001; Johnson et al. 2002). However, opportunistic parasite species do not achieve the same abundance in all their hosts. Variation in the abundance of a parasite among its many host species could reflect among-host taxonomic relatedness because relatedness should reflect similarities among host species in a variety of characters. Indeed, it has been shown, for many flea species, that the abundance of a flea on its auxiliary hosts decreased with increasing taxonomic distance of these hosts from the flea's principal host (Krasnov et al. 2004a). However, no such relationship was found for metazoan parasites of freshwater fish (Poulin 2005). These results indicate two contrasting strategies for a parasite to add a new host to its host spectrum, namely, either selection of a new host as closely related to the principal host species as possible or random choice of a new host from the available species pool (availability implies some ecological constraints such as, for example, spatial coexistence of the parasite with the potential new host). An obvious outcome of the former strategy should be selection strictly from the subset of hosts that belong to a certain phylogenetic lineage. However, when this was specifically tested for fleas using randomization tests and an index of host specificity that takes host taxonomy into account, the most common scenario was that there were no differences between the taxonomic affinities of the set of host species used by a flea and random subsets drawn from the regional pool (Krasnov et al. 2004b). One reason for the apparent contradiction between the different findings of Krasnov et al. (2004a, b) may be the methodology used in their latter study. Indeed, the index of host specificity used took into account the basic taxonomic partitioning of hosts and, thus, represented a kind of a "coarse-grained" approach to host phylogeny.

The recent development of analytical tools allows us to look at any species assemblage, both global and local (such as a regional fauna, a community, or the host spectrum of a parasite), from an evolutionary perspective considering, for example, phylogenetic trees as histories of the diversification of lineages (Mooers and Heard 1997). For example, the shape of a phylogenetic tree can be estimated using diversity skewness, which essentially measures the level of balance of a tree (see Mooers and Heard 1997 for details). If all lineages have similar diversification rates, then the phylogenetic tree is balanced and diversity skewness is low. In contrast, if the diversification success of some lineages is higher than that of other lineages, the resulting tree will be imbalanced and diversity skewness will be high. Recently, Heard and Cox (2007) developed a technique that allows one to elucidate the role of various processes in shaping the phylogenetic structure of a local assemblage. This technique is based on comparisons of the diversity skewness of a local assemblage with that of the "biogeographic" null (i.e., a set of species randomly drawn from a source species pool; see Heard and Cox 2007 for details) and thus allows one to determine whether an assemblage at a lower hierarchical level (e.g., a locality) is unexpectedly more or less skewed than that of a species set randomly taken from an assemblage at a higher hierarchical level (e.g., a continent). The term "biogeographic" null was coined mainly because the original aim of the application of this technique was to evaluate biogeographic patterns in the phylogenetic structure of local assemblages. However, this technique can be applied to assemblages other than spatially fragmented local assemblages. In particular, it is well-suited for the consideration of the host spectra of parasites as local assemblages compared with the entire pool of host species available in a region. Using phylogenetic trees rather than taxonomic hierarchies, this method considers the phylogeny of host species in a "fine-grained" manner and may thus capture patterns that methods based on a "coarse-grained" approach could not distinguish.

Estimating the diversity skewness of the host spectrum of a parasite in itself could be useful for further understanding of the causes and consequences of the evolution of host specificity. For instance, a parasite that can use hosts belonging to different phylogenetic lineages with equal success would presumably have greater chances of colonizing new territories, which could result in an increase of its geographic range. In addition, such parasites should be less prone to extinction and thus be less dependent on the predictability of each particular type of resource (=host species) (Ward 1992) than parasites exploiting hosts from a single phylogenetic lineage. As a result, parasites with balanced host spectra may use many short-lived hosts, whereas parasites with highly skewed host spectra should rely mainly on long-lived hosts, all else being equal.

In this study, we used published data on host occurrences of fleas (Siphonaptera) from two large, distinct geographic regions. First, we tested whether a particular phylogenetic lineage of hosts is represented in a flea's host spectrum by a disproportionately high number of species or, alternatively, the host spectrum of a flea species represents a random draw from the locally available host species pool. This was tested on a large number of different flea species to uncover general patterns in the structure of host spectra. Second, we searched for an association between the diversity skewness of a flea's host spectrum and (a) its geographic range and (b) the mean body size of its host species. Here, the body size of a host species was used as a proxy for its life span (Peters 1983).

Materials and methods

Data on the host range of fleas were obtained from published regional monographs on fleas of South Africa (Segerman 1995) and the northern part of North America (Canada, Alaska, and Greenland; Holland 1985). We focused on fleas parasitic on small mammals (Erinaceomorpha, Soricomorpha, Macroscelidea, Rodentia, and Lagomorpha) because the latter represent the main hosts for the vast majority of flea species. A few flea species only parasitize large mammals and birds (about 3% of the total number of flea species can be considered as specific bird parasites; Medvedev 1997a, b). Also, we did not consider fleas parasitic on Chiroptera because bats have a different, highly specific set of fleas (e.g., Medvedev 2005). To meet the requirement for a diverse local assemblage (see Heard and Cox 2007 for details), we used only data from fleas recorded on no less than seven host species. Flea species with cosmopolitan distributions (e.g., *Xenopsylla cheopis*, *Nosopsyllus fasciatus*) that were likely introduced to many regions with humans, domestic animals, and synanthropous rodents were omitted from the analysis. In total, our data set included 21 flea species from South Africa and 39 flea species from northern North America.

For each flea species, we measured the diversity skewness of its host spectrum using Colless' index I_c (Colless 1982). This index is readily understandable and statistically powerful (Agapow and Purvis 2002; Blum and François 2005). Its value ranges from 0 to 1, with 0 representing a perfectly balanced phylogeny and 1 representing a fully imbalanced phylogeny (i.e., maximum skew in diversification rates of the different lineages). Tests for significance against the null host spectrum were carried out similarly to those against the "biogeographic" null of Heard and Cox (2007), namely, by comparing the I_c value calculated for the host spectrum of a flea consisting of a given number of species, with distributions of random I_c values. To obtain the latter, I_c was calculated for each of 10,000 assemblages of the same number of host species taken at random from the phylogeny of the entire host species pool of a region. The phylogenetic tree for mammals was based on various sources (see details in Morand and Poulin 1998; Grenyer and Purvis 2003; Krasnov et al. 2004c). The South African tree was fully resolved, whereas the North American tree contained only one polytomy (*Sorex cinereus*, *Sorex fumeus*, *Sorex hoyi*). The occurrence of this polytomy did not affect our calculations because no flea species included all three shrews in its host spectrum. The reported p values are one-tailed tests in each direction, namely, p_h is the probability that diversity skewness is as high as or higher than the expected value, whereas p_l is the probability that it is as low as or lower than the expected value. Host spectra for which significance tests of I_c values against null expectations produced $p<0.05$ were considered as having significantly higher or lower than expected skewness, whereas spectra for which significance tests produced $0.05<p<0.1$ were considered as tending toward higher or lower than expected skewness. Calculations were done using the software SkewMatic 2.01 developed by S. B. Heard (see Appendix in Heard and Cox 2007).

The size of the geographic range for each flea species was calculated from a distribution map (see details in Krasnov et al. 2005). Data on mean mammalian body mass were obtained from Silva and Downing (1995). To test for the correlations between diversity skewness of flea host spectra and flea geographic range or host body mass, we regressed log+1-transformed indices of diversity skewness against log-transformed values of either flea geographic ranges or host body mass (either body mass of the principal host or host body mass averaged across all host species). These regressions were made across flea species, but separately for South Africa and North America. The regressions were done both using the conventional approach and the method of independent contrasts (Felsenstein 1985; Harvey and Pagel 1991). The latter allowed us to control for potential effects of flea phylogeny. The phylogenetic tree for fleas was based on a detailed morphological taxonomy (see details in Krasnov et al. 2004a). The initial branch length was set to 1.0. To compute independent contrasts, we used the PDAP:PDTREE module (Garland et al. 1993; Midford et al. 2007) implemented in the Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2007). Procedures for the analyses followed Garland et al. (1992, 1993) and Pagel (1992).

Results

Values of the diversity skewness of host spectra for fleas from South Africa and northern North America are presented in Tables 1 and 2, respectively. The diversity skewness of the host spectra of the majority of fleas did not differ significantly from that of the assemblages of host species drawn randomly from the available host pool. Nevertheless, among South African fleas, although in one species (*Dinopsyllus lypusus*) diversity skewness tended to be marginally higher than the null expectations, it was not

Table 1 Diversity skewness (I_c) of host spectra of fleas from South Africa and the probability that it is higher (p_h) or lower (p_l) than that of the null host spectrum (see text for explanations)

Flea species	I_c	p_h	p_l
Chiastopsylla godfrei	0.491	0.814	0.227
Chiastopsylla mulleri	1.000	0.306	1.000
Chiastopsylla octavii	0.333	0.994	0.076
Chiastopsylla rossi	0.428	0.230	0.786
Ctenophthalmus calceatus	0.483	0.640	0.395
Dinopsyllus ellobius	0.327	0.646	0.372
Dinopsyllus lypusus	0.627	0.057	0.951
Listropsylla agrippinae	0.442	0.588	0.444
Listropsylla dorippae	0.321	0.989	0.015
Listropsylla prominens	0.564	0.644	0.410
Xenopsylla brasiliensis	0.341	0.717	0.299
Xenopsylla eridos	0.524	0.845	0.260
Xenopsylla erilli	0.583	0.696	0.362
Xenopsylla hipponax	0.533	0.759	0.291
Xenopsylla nubica	0.214	1.000	0.004
Xenopsylla philoxera	0.582	0.141	0.875
Xenopsylla phyllomae	0.667	0.700	0.419
Xenopsylla piriei	0.444	0.687	0.339
Xenopsylla scopulifer	0.385	0.948	0.068
Xenopsylla trifaria	0.600	0.829	0.297
Xenopsylla versuta	0.364	0.972	0.042

significantly higher than expected in any flea species. In five species, however, the diversity skewness of the host spectrum was either significantly lower (in three species) or tended to be lower (in two species) than expected. North American fleas demonstrated the opposite trend. In eight flea species, the diversity skewness of the host spectrum was either significantly higher (in five species) or tended to be higher (in three species) than expected, whereas it was either significantly lower (in two species) or tended to be lower (in one species) than expected in only three species.

Across South African fleas, the diversity skewness of the host spectra was strongly negatively correlated with the size of geographic ranges ($r^2=0.40$, $F_{1,19}=12.8$, $p<0.001$; Fig. 1a). This relationship held when the confounding effect of flea phylogeny was controlled for ($r=-0.57$, $p<0.01$; Fig. 2a). In contrast, no significant relationship between the diversity skewness of the host spectrum and flea geographic range was found for North American fleas. This was true both when conventional statistics ($r^2=0.04$, $F_{1,37}=1.4$, $p<0.24$; Fig. 1b) and the method of independent contrasts were used ($r=0.21$, $p=0.18$; Fig. 2b).

Diversity skewness values did not correlate with body mass of either the principal host or host body mass averaged across all host species of a flea ($r^2=0.03$, $F_{1,19}=0.1$, and $r^2=0.02$, $F_{1,19}=0.4$, for South African fleas, respectively; $r^2=0.05$, $F_{1,37}=2.2$, and $r^2=0.06$, $F_{1,37}=2.4$, respectively, for North American fleas; $p>0.1$ for all). The method of independent contrasts produced essentially the same results ($r=0.05$ and $r=0.17$ for South African fleas, respectively; $r=0.22$ and $r=0.21$, respectively, for North American fleas; $p>0.1$ for all).

Discussion

The results of this study demonstrate that, in general, the phylogenetic structure of a flea's host spectrum does not differ from that of the available host species pool. In other words, the likelihood of a flea exploiting hosts belonging to a particular lineage simply depends on the availability of these hosts in a region. This supports findings of our earlier

Table 2 Diversity skewness (I_c) of host spectra of fleas from northern North America and the probability that it is higher (p_h) or lower (p_l) than that of the null host spectrum (see text for explanations)

Flea species	I_c	p_h	p_l
Amalaraeus dissimilis	0.368	0.079	0.929
Aetheca wagneri	0.474	0.198	0.833
Amphipsylla sibirica	0.762	0.130	0.937
Catallagia charlottensis	0.383	0.311	0.725
Catallagia dacenkoi	0.909	0.001	1.000
Catallagia decipiens	0.364	0.61	0.428
Ceratophyllus ciliatus	0.422	0.532	0.519
Ceratophyllus vison	0.333	0.808	0.288
Corrodopsylla curvata	0.289	0.875	0.178
Ctenophthalmus pseudagyrtes	0.181	0.981	0.024
Delotelis hollandi	0.467	0.647	0.497
Epitedia scapani	0.333	0.958	0.293
Epitedia wenmanni	0.484	0.124	0.893
Eumolpianus eumolpi	0.308	0.762	0.277
Foxella ignota	0.467	0.647	0.497
Hystrichopsylla dippiei	0.364	0.610	0.428
Hystrichopsylla occidentalis	0.462	0.232	0.802
Megabothris abantis	0.486	0.002	0.999
Megabothris asio	0.324	0.626	0.416
Megabothris calcarifer	0.867	0.003	0.998
Megabothris groenlandicus	0.844	0.004	0.998
Megabothris lucifer	0.286	0.916	0.219
Megabothris quirini	0.303	0.386	0.643
Nearctopsylla genalis	0.429	0.748	0.391
Opisodasys keeni	0.472	0.490	0.605
Orchopeas caedens	0.467	0.418	0.667
Orchopeas leucopus	0.462	0.165	0.855
Orchopeas nepos	0.524	0.525	0.656
Orchopeas sexdentatus	0.214	0.988	0.073
Oropsylla arctomys	1.000	0.091	1.000
Oropsylla idahoensis	0.571	0.335	0.761
Oropsylla tuberculata	0.600	0.503	0.622
Peromyscopsylla catatina	0.556	0.281	0.775
Peromyscopsylla hesperomys	0.333	0.958	0.293
Peromyscopsylla ostsibirica	0.722	0.058	0.957
Peromyscopsylla selenis	0.577	0.043	0.965
Rhadinopsylla fraterna	0.378	0.701	0.438
Rhadinopsylla sectilis	0.162	0.994	0.009
Thrassis petiolatus	0.467	0.647	0.497

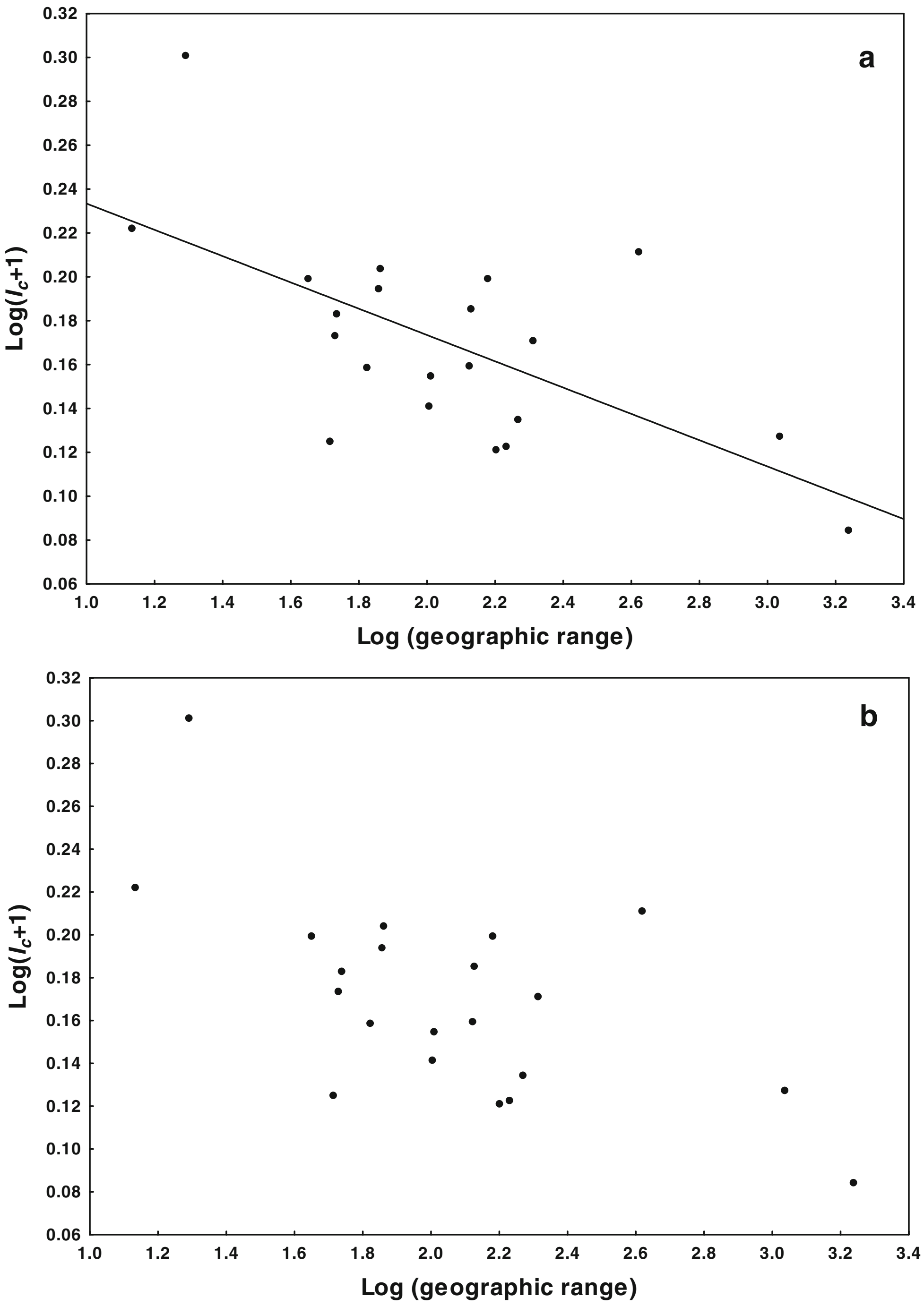
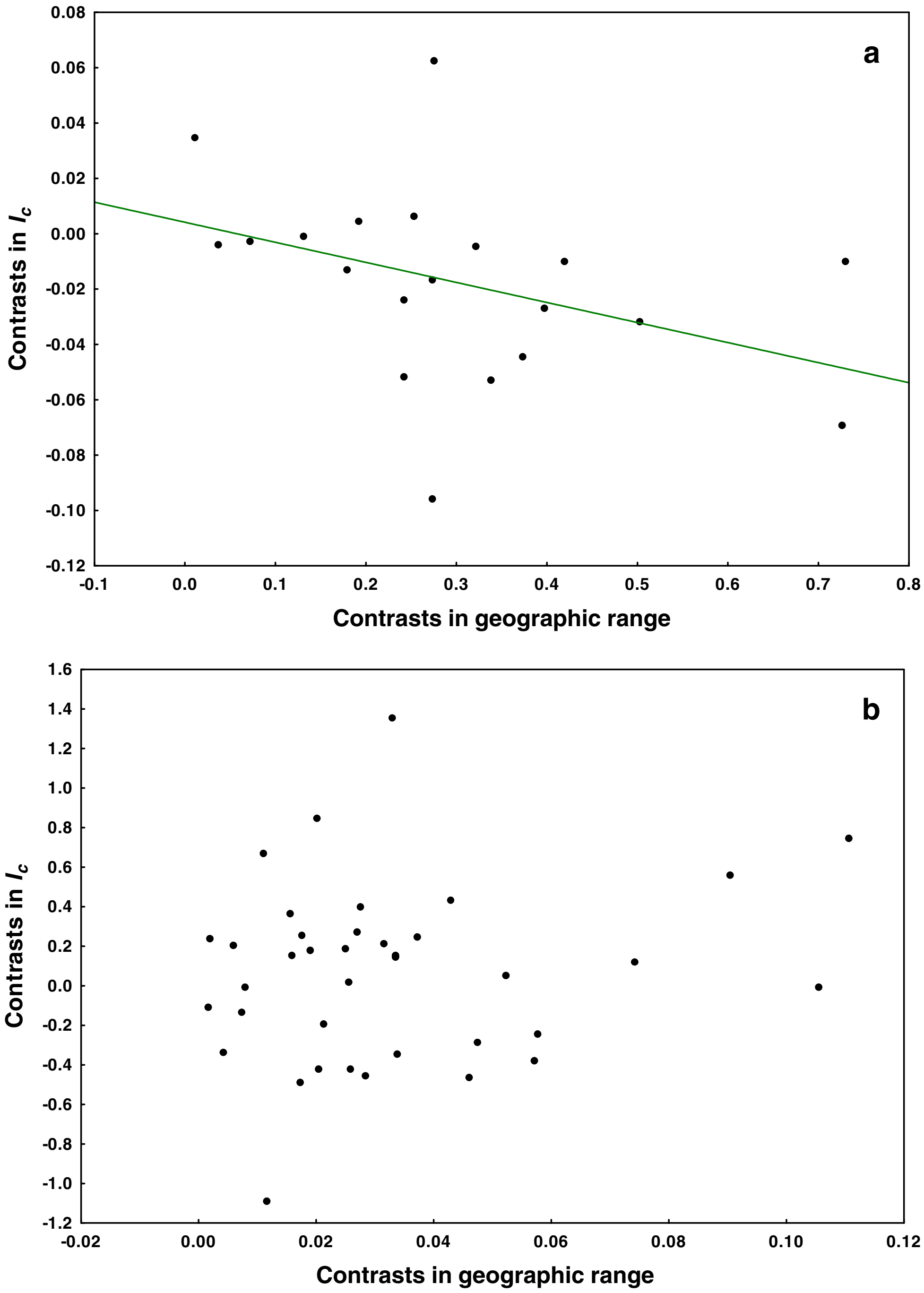


Fig. 1 Relationships between the diversity skewness of the host spectrum and the size of the geographic range across 21 South African (**a**) and 39 North American (**b**) flea species

study carried out on a smaller geographic scale (see Krasnov et al. 2004b), suggesting that this pattern of host species selection from an available pool is scale-invariant.

Parasites of the same taxon often display a broad continuum of host specificity ranging from oixeny (parasitic on a single host species) via stenoxeny (parasitic on a group of related host species) to euryxeny (parasitic on unrelated host species) (Euzet and Combes 1980). In this study, we dealt only with the latter category of fleas due to the limitations of the method used (Heard and Cox 2007). Although fleas vary in their level of host specificity, euryxenous species represent a relatively large proportion, albeit not the majority, of species of fleas in a region. Indeed, species considered in this study (i.e., species with at least seven known hosts) represented 33% and 37% of all fleas parasitic on small mammals in South Africa and Canada, respectively. The high number of euryxenous species among fleas is likely a consequence of the life style of these insects. A female flea oviposits either on or off the host, but even in the former case, the eggs drop off

Fig. 2 Relationships between the diversity skewness of the host spectrum and the size of the geographic range across 21 South African (**a**) and 39 North American (**b**) flea species using phylogenetically independent contrasts



typically into the host' nest, lair, or burrow. The larvae usually are not parasitic and feed on debris and materials found in the nest of the host. On completion of feeding, a larva spins a silken cocoon and pupates. In nearly all cases, larval and pupal development is entirely off-host. After emergence from the pupa and cocoon, adult fleas must locate a vertebrate host to complete their life cycle. A host may not always return in a regular or predictable manner to its nest or resting area where the immature fleas develop. Survival of fleas is thus dependent on a variety of factors, one of the most important being the ephemeral nature of the host. Consequently, species that are able exploit alternative resources (e.g., any available host species) may have an advantage compared with species that rely on a limited set of resources (host species belonging to a particular lineage).

From an evolutionary perspective, this advantage may be manifested by an expansion of the geographic range with decreasing diversity skewness of a flea's host spectrum. The exact mechanism underlying this pattern remains unknown. On the one hand, fleas with a large geographical range may come into contact with a higher number of phylogenetic lineages of host species, and can thus "sample" a more representative subset of the available pool, whereas fleas with a small range are more likely to be limited to colonize few hosts that belong to a single phylogenetic lineage. On the other hand, fleas that exploit with equal success hosts belonging to different lineages are more likely to disperse over large distances and persist in a variety of localities compared with fleas that mainly exploit related hosts and thus persist only in localities where these hosts are present. Obviously, if a "preferable" host lineage is broadly distributed, then fleas selectively exploiting this lineage would also be broadly distributed. Nevertheless, the relationship between the size of a flea's geographic range and the diversity skewness of its host spectrum was found only for South African, but not for North American, fleas. One of the reasons for this may be the low variability in the size of the geographic ranges of North American fleas (i.e., most fleas have similar ranges). Indeed, the coefficient of variation of geographic range sizes was 1.71 for South African fleas and only 1.01 for North American fleas.

From an ecological perspective, the advantage to fleas of exploiting substitutable resources (i.e., fleas in which the value diversity skewness of the host spectra is low) may likely be reflected in their higher average abundance, as seen in some analyses using other measures of host specificity (Krasnov et al. 2004d). However, the relationship between the diversity skewness of host spectra and abundance achieved on these hosts remains to be tested. The data set used in this study does not allow this because information regarding flea abundance was not available.

Interestingly, in cases where the diversity skewness of host spectra differed significantly or tended to differ from the null expectations, South African and North American fleas demonstrated opposite trends. In the former, the trend was to have host spectra with greater "phylogenetic" balance compared with the available host pool, whereas the latter tended to select disproportionately more hosts of certain lineages from the available pool. This difference between regions can be related, for instance, to glaciation events during the Cenozoic, i.e., the period covering the main evolutionary development of flea–mammal associations (Medvedev 2005). In particular, frequent glaciation–interglaciation events have been characteristic of North America, whereas this was not the case for South Africa (see Ehlers and Gibbard 2007 for review). As a result, the temporal stability of flea–host associations has likely been higher in South Africa, a fact which could have led to the observed pattern.

Following Combes' (2001) concept of host-encounter and host-compatibility filters as determinants of a parasite's host spectrum, the results of our study suggest that the evolution of host spectra in host-opportunistic parasites is mainly governed by the host-encounter filter, whereas in host-specific parasites, it is mainly governed by the host-compatibility filter. However, the host-compatibility filter also plays an important role in shaping host spectra in generalist parasites because even a highly host-opportunistic parasite varies in its abundance among different host species (Krasnov et al. 2004a; Poulin 2005). Although the measurement of the diversity skewness of the host spectra of parasites represents a more sophisticated method than earlier methods developed for the estimation of host specificity that take into account taxonomic relationships among hosts (see Caira et al. 2003; Poulin and Mouillot 2003), the diversity skewness has one important limitation. It is based on presence–absence data and, thus, cannot take into account differences in parasite abundance among host species. In other words, it does not consider the relative performance of a parasite when exploiting different host species as an ideal method of host specificity measurement should do. Unfortunately, no modern measure of host specificity is ideal, although recently, an index that takes into account both taxonomic relationships between host species and differences in a parasite's prevalence among these hosts has been introduced (Poulin and Mouillot 2005). Furthermore, the results of this study validate earlier findings obtained using a method with lower "resolution" of host phylogeny, i.e., using basic taxonomic hierarchical categories instead of phylogenetic trees. This suggests that parasites such as fleas differentiate phylogenetic partitioning of their hosts in a relatively rough manner, and thus, methods based on the main taxonomic categories (e.g., index of taxonomic distinctness of the host assemblage; Poulin and Mouillot 2003), as opposed to methods based on distinguishing phylogenetic lineages and clades (e.g., phylogenetic diversity and diversity skewness; Mooers and Heard 1997), are sensitive enough to be reliable tools for comparative studies of host specificity. One of the reasons for this might be the almost complete lack of congruence between phylogenies of fleas and their hosts (Krasnov and Shenbrot 2002; Lu and Wu 2005) and strong evidence that the major events during their common history were host switches rather than cospeciations.

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