



Scale-invariance of niche breadth in fleas parasitic on small mammals

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The resource specialization or niche breadth of a species is not fixed across populations, but instead varies over geographical space. A species may be a local specialist but a regional generalist, if it uses locally few resources that are substitutable across locations. In contrast, a species is a local generalist and a regional specialist if it uses locally many resources that cannot be substituted from 1 location to the next. Scale-dependence can thus be a major factor in estimation of niche breadth. Here, we test for relationships between local and global estimates of host specificity (a measure of niche breadth for parasites) in fleas (Siphonaptera) parasitic on small mammals from 49 different regions within the Holarctic. Across all fleas, we found a strong, positive relationship between the number of host species that a flea uses in 1 locality and the number of different host species that can serve as the flea's principal host (i.e. the one supporting the most fleas in a region) among all regions. Also, we observed a strong positive relationship between the taxonomic distinctness of the host species used in 1 locality and that of all known principal hosts among all localities. These relationships held after correcting for potentially confounding phylogenetic influences. We discuss the implications of scale-independent host specificity and its association with geographical range size and species-specific patterns of host use.

It is widely accepted that the niche breadth of a species is spatially variable (Fox and Morrow 1981, Brown 1984, Seagle and McCracken 1986, Gaston et al. 1997) and therefore its estimation should be scale-dependent. Indeed, classification of a species as a resource specialist or a resource generalist requires consideration of at least 2 interrelated factors, namely local resource specialization and spatial substitutability of these resources (Hughes 2000). In other words, resource specialization by a species is partitioned into local and regional components. These 2 components are linked to each other via substitution of resource use across locations. Obviously, if a species uses either a low or a high number of resources both locally and across locations, then the species is either a spatially invariant specialist or generalist, respectively. However, a species may differ in its degree of local and regional specialization. For example, a species may use few resources locally, but if these resources are substitutable across locations, then at a larger scale this species will use many resources. Such a species is a local specialist, but a regional generalist. Similarly, a species that uses many resources locally that are not substitutable over space, should be defined as a local generalist, but a regional specialist. Thus,

the scale at which niche breadth is measured needs to be considered when, for example, patterns and correlates of niche breadth are considered. Indeed, when Hughes (2000) compared specialization and distribution in lycaenid butterflies, local specialization was not associated with local distribution (measured as a proportion of sites occupied), but the continental specialization of a species was related to the area of its continental range.

Furthermore, Hughes (2000) found examples of all possible levels of specialization within the same family of butterflies (Lycaenidae). However, the level of specialization was scale-dependent in some taxa, whereas it was scale-invariant in others. Consequently, the scale at which niche breadth is measured is important for the former but not for the latter.

Recently, parasites have become popular models for studies involving estimation of niche breadth (see Poulin 2007, Poulin and Keeney 2008 for reviews). The niche breadth of a parasite can be equated to its host specificity because the latter mirrors the diversity of resources (hosts) used by the parasite (Futuyma and Moreno 1988). Consequently, the host specificity of a parasite allows one to make important predictions regarding the determinants

of that parasite's geographical distribution. For example, the likelihood that an introduced parasite species will become established and spread in a new ecosystem is related to its host specificity (Poulin et al. 2006a). Such predictions are crucial for epidemiology, veterinary medicine, and conservation. However, the host specificity of a parasite can be measured at a variety of spatial scales. Therefore, it is important to understand the effect of scale on estimation of host specificity in parasites. Furthermore, the level of host specificity shown by a parasite may also be considered in the framework of optimal foraging theory, where it can be seen as the outcome of a trade-off between food abundance and food specialization to maximise a consumer's rate of energy intake (MacArthur and Pianka 1966, Pike et al. 1977). Using this optimal foraging theory, Beckerman et al. (2006) showed that network properties emerge from the behaviour of individuals and that consumer diet breadths and food web connectance can be accurately predicted.

We tested for scale-dependence of host specificity in fleas (Siphonaptera). Fleas are obligate haematophagous ectoparasites. In contrast to the imago, flea larvae usually are not parasitic and feed on organic debris in the nest of the host. The adults remain as permanent satellites of their hosts, alternating periods on the host with periods in the burrow or nest. The majority of fleas are not highly host-specific, being found on 2 or more host genera within a family, or on 2 or more host families; some fleas even parasitize multiple mammalian orders.

We estimated the host specificity of 177 flea species at 2 spatial scales. At the lower (within-region) scale, we took into account the number and taxonomic diversity of all host species exploited by this flea in a geographic region. At the larger (between-region) scale, we focused on principal host species only. A principal host is defined as the host species that supports the greatest proportion of a parasite population (Krasnov et al. 2004a). Geographic replacement of a principal host species thus reflects the substitutability of host species across the geographic range of a flea. We asked a) whether the identity of the principal host species is the same across the geographic range of a flea and b) whether the ability of a flea to exploit many host species locally affects its ability to change principal host species across geographical space.

Materials and methods

We extracted data from published surveys that reported flea distribution and abundance on small mammals (Soricomorpha, Lagomorpha, and Rodentia) in 49 different regions of the Palaearctic and Nearctic (see Supplementary material for list of the regions). These taxa were selected because fleas are most abundant and diverse on small to medium-sized burrowing species of mammals. These sources provided data on the number of individuals of a particular flea species found on individuals of a particular host species. The compilation of the dataset was based on a thorough search of the primary literature (whether published in English or not) going back to the middle of the 20th century and thus beyond the range covered by most bibliographic databases. We used only those sources where sampling effort (the number of examined hosts) and

number of individuals of each flea species were reported. We developed 2 datasets corresponding to flea species that occurred in at least 2 or at least 5 regions; the resulting listings included 177 and 56 species, respectively. Two regions is the minimum necessary for the intersite comparisons, and 5 was chosen because opting for a higher number would have considerably decreased the number of species that could be included in the analyses. The first subset covered all 49 regions, whereas species from the second subset were limited to 32 regions.

For each flea species in each region, we identified its principal host species as the mammal species on which the flea attained maximal abundance (measured as the mean number of flea individuals per individual host). The principal host may or may not be the original host species, the one in which the parasite first evolved, but it is currently the one used by the majority of individuals in the parasite population. Abundance on the principal host, as defined above, was always clearly higher (on average, by 54%) than on the next most heavily-used host species (see Krasnov et al. 2004a for details), such that the principal host was clearly harbouring the majority of individuals in a flea population. For each flea species from the first subset, we evaluated the between-region change in the identity of the principal host species and genus by dividing the total number of principal host taxa (species or genera) found across all regions by the number of regions in which the flea was recorded; this yielded a mean number of principal host species or genera per region for each flea. Obviously, when a flea exploits different host species or genera in each region, this ratio equals 1.

For each of the 56 flea species from the second subset, we calculated 3 measures of host specificity: a) the number of mammalian species on which the flea species was found; b) within-region proportion of mammalian species on which the flea species was found; and c) an index of specificity, S_{TD} (Poulin and Mouillot 2003). The index S_{TD} is based on the taxonomic or phylogenetic affinities of the various host species and measures the average taxonomic distinctness of all host species used by a parasite species. Thus, this measure emphasises the phylogenetic diversity of a flea's host spectrum, providing a different perspective on host specificity (see Krasnov et al. 2004b for details of calculation). In brief, using the taxonomic classification of Wilson and Reeder (2005), mammal species were fitted into a taxonomic structure with 5 hierarchical levels above species – genus, subfamily, family, order, and class (Mammalia). Thus, the maximum value that the index S_{TD} can take (when all host species belong to different orders) is 5, 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 flea species, to reflect their strict host specificity. The greater the taxonomic distinctness between host species, the higher the value of S_{TD} : thus this index is inversely proportional to specificity. To calculate S_{TD} , DM and RP developed a computer program using Borland C++ Builder 6.0 (available at <<http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>>).

Calculation of host specificity measures was done at a smaller spatial scale within each region (all 3 measures; hereafter referred to as local host specificity) and at a larger

spatial scale across all regions where a flea species was recorded (the number of host species and taxonomic distinctness; hereafter global host specificity). To calculate local host specificity, we used all host species on which a flea species was found in a region, and the number of hosts, proportion of hosts used, and S_{TD} were averaged for each flea species across all regions. To calculate global host specificity, we used only principal host species for each region. All measures of host specificity were $\log(x+1)$ -transformed prior to further analyses, except for the proportion of hosts used which was arcsin-transformed.

We handled the potentially confounding effect of sampling effort in the following way. Across flea species, neither the number of host species nor the proportion of host species on which a flea species was found in a region was correlated with the number of host individuals examined in this region ($r^2=0.03$, $F_{1,54}=1.4$ and $r^2=0.004$, $F_{1,54}=0.02$; $p>0.2$ for both). However, the number of host species used by flea species within a region was positively correlated with S_{TD} ($r^2=0.56$, $F_{1,54}=68.6$, $p<0.001$), indicating that this measure was influenced by the number of host species in a flea's repertoire. Across all flea species, the number of principal host species used was positively correlated with the number of regions analyzed ($r^2=0.30$, $F_{1,54}=22.8$, $p<0.001$), whereas global S_{TD} correlated positively with the number of principal host species across all regions ($r^2=0.34$, $F_{1,54}=27.3$, $p<0.001$), but not with the number of regions where a flea was recorded ($r^2=0.02$, $F_{1,54}=1.3$, $p>0.2$). Therefore, in subsequent analyses, the number of principal host species was corrected for the number of regions where a flea species was recorded, whereas local and global S_{TD} were corrected for the number of host species in a region or the number of principal host species across all regions where a flea was recorded, respectively. These corrections were done using residual deviations from the respective regressions.

To test for relationships between measures of host specificity calculated at the 2 scales, we regressed global measures against their respective local measures. More specifically, we regressed global host specificity measured as number of principal hosts across regions against either local number of host species exploited or local proportion of host species used, whereas the global taxonomic distinctness of principal hosts was regressed against the local taxonomic distinctness of all hosts used. This was done using original data as well as after controlling for the confounding effect of phylogeny using the method of independent contrasts (Felsenstein 1985). A phylogenetic tree of flea species was derived from flea morphological characters and taxonomy (Krasnov et al. 2005). The initial branch length was set to 1.0. To compute independent contrasts, we used the PDAP:PDTree module (Midford et al. 2007) implemented in Mesquite modular system for evolutionary analysis (Maddison and Maddison 2007). Pairs of sister branches that diverged long ago can likely yield greater contrasts than pairs of sister branches that diverged recently. To avoid this, we standardized each contrast by dividing it by its standard deviation (Garland et al. 1992). To verify that contrasts were properly standardized, we plotted the absolute values of standardized contrasts against their standard deviation (Garland et al. 1992). No significant linear or non-linear trend was found in these plots, suggesting that the contrasts

were adequately standardized. Then, we regressed standardized contrasts in a dependent variable against standardized contrasts in an independent variable using major axis regressions forced through the origin (Pagel 1992, Garland et al. 1993).

Results

Flea species included in our dataset (177 species that occurred in at least 2 of 49 different geographic regions) belonged to 57 genera of 5 families. On average, a flea species exploited 9.8 ± 0.6 host species across the entire range of regions (from a minimum of 1 to a maximum of 44, with a coefficient of variation of 83.4%). These hosts represented 175 species belonging to 62 genera from 23 subfamilies and 12 families.

Among these 177 flea species, only 28 exploited the same host species in all regions they inhabited. The frequency distribution of the mean number of principal host species per region was strongly left-skewed ($\gamma = -0.28\pm 0.18$) among flea species, but frequency of the mean number of principal host genera per region was strongly right-skewed ($\gamma = 0.27\pm 0.18$).

Across the 56 flea species that occurred in at least 5 regions, local host specificity, measured either as the averaged number of host species or as the proportion of host species used within a region, correlated positively with the number of principal hosts across regions ($r^2=0.30$, $F_{1,54}=23.6$ and $r^2=0.24$, $F_{1,54}=17.4$, respectively; $p<0.0001$ for both) (Fig. 1a). The same was true for host specificity measured as the taxonomic distinctness of the host spectrum ($r^2=0.23$, $F_{1,54}=16.4$, $p<0.001$) (Fig. 1b). All these relationships held when we controlled for phylogeny ($r=0.51$ for host specificity measured as the number of host species used within a region, $r=0.81$ for host specificity measured as the proportion of host species used within a region, and $r=0.42$ for host specificity measured as the taxonomic distinctness of the host spectrum, respectively, $p<0.001$ for all) (Fig. 2a for host specificity measured as the number of host species used and Fig. 2b for host specificity measured as the taxonomic distinctness of the host spectrum).

Discussion

Our study demonstrates that although many, albeit not all, fleas are able to switch principal hosts across locations, the degree of host specificity in fleas generally is scale-invariant whatever measure is used. This is manifested in that a flea exploiting a narrow host spectrum in a particular location also exploits a narrow spectrum of principal hosts across its geographic range, and appears unable to change its principal host species across regions. In contrast, a locally host-opportunistic flea appears also to be host-opportunistic on a larger spatial scale and may change its principal host across regions. Furthermore, host opportunism may be expressed as the ability to exploit many hosts and/or hosts from a wide range of taxa, since the local-versus-global patterns hold for both measures of host specificity.

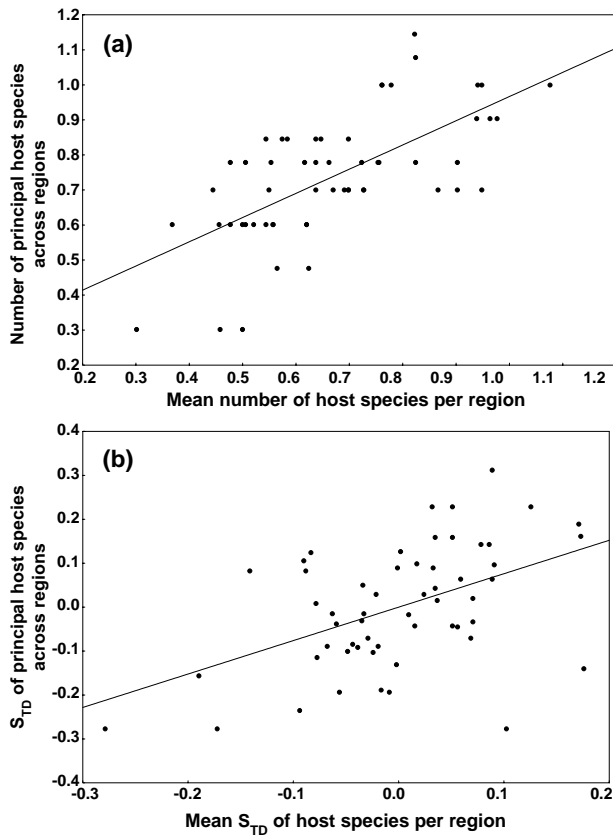


Figure 1. Relationship between the mean number of host species exploited per region and the number of principal hosts across all regions where a flea was recorded (a) and the mean taxonomic distinctness (S_{TD}) of a flea's host spectrum in a region and the taxonomic distinctness of principal hosts across all regions where a flea was recorded (b), across 56 flea species using conventional statistics.

The scale-invariance of high levels of host-specificity suggests that the colonization abilities of specialist taxa, capable of using only a narrow range of resources, are low. Consequently, host-specific fleas have more restricted geographic ranges than host-opportunistic fleas (Krasnov et al. 2005). A small geographic range, in turn, plays the role of the encounter filter (sensu Combes 2001) ruling out opportunities for a flea to colonize host species that could be potentially suitable but are absent from its geographic range. As a result, although host specificity in many flea lineages tends to decrease on a macroevolutionary scale (Poulin et al. 2006b), high host specificity appears to be a rather conservative trait within flea species (Krasnov et al. 2004c). For example, in each region where the strictly host-specific *Tarsopsylla octodicedentata* was recorded, it exploited almost exclusively the red squirrel *Sciurus vulgaris*. It is not surprising therefore that this flea did not change its principal host across its geographic range and has not been found in any region from which this rodent was absent.

In contrast, the scale-invariance of low levels of host specificity suggests that the same features that allow a flea to use many hosts locally, also allow it to switch readily from 1 principal host in 1 region to another principal host in another region and thus to invade new geographic areas. Another reason for this is the spatial substitutability of hosts

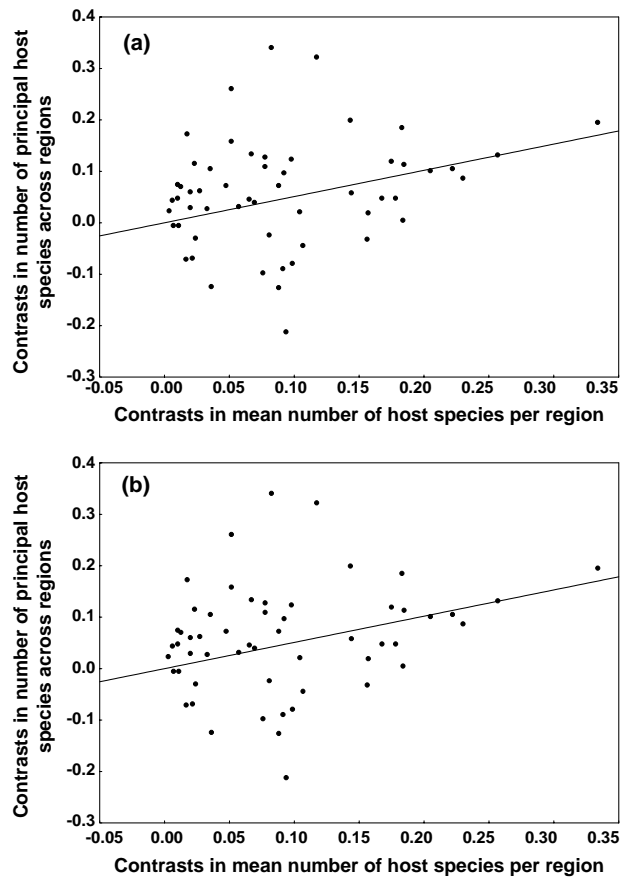


Figure 2. Relationship between the mean number of host species exploited per region and the number of principal hosts across all regions where a flea was recorded (a) and the mean taxonomic distinctness (S_{TD}) of a flea's host spectrum in a region and the taxonomic distinctness of principal hosts across all regions where a flea was recorded (b), across 56 flea species using the method of independent contrasts.

and their phylogenetic relatedness. Indeed, if several hosts display mutually exclusive distributions but they are similar in their availability to a flea (e.g. have the same habitat preferences) or in their compatibility for the parasite (sensu Combes 2001) (e.g. in blood biochemistry or in patterns of behavioural or immune defenses), the flea can change its hosts across its geographic range. A comparison of frequency distributions of principal host species per region and principal host genera per region suggests that when fleas use different mammals as their principal host, these different host species often belong to the same genus. For example, within each of 6 regions where *Peromyscopsylla hesperomys* was recorded, it attained maximal local abundance on different host species (*Peromyscus nasutus* in New Mexico (Morlan 1955); *Peromyscus truei* in central California (Linsdale and Davis 1956); *Onychomys leucogaster* in Idaho (Allred 1968); *Peromyscus leucopus* in Connecticut (Main 1983); *Neotoma mexicana* in Colorado (Campos et al. 1985); and *Peromyscus boylii* in southern California (Davis et al. 2002)). All of these hosts belong to the same subfamily (Neotominae) and 4 of them are congeners.

Phylogenetic relatedness among species generally reflects similarity in overall life-history and ecological similarity (Harvey and Pagel 1991). Consequently, close-relatedness

between hosts facilitates host substitutions from 1 region to the next because a flea would not be forced to develop multiple adaptations to cope with a diverse array of defences (Combes 1997, Poulin and Mouillot 2004, Poulin 2007) but rather would invest less by adapting to a restricted set of host defenses than it would if its hosts were distantly related. For example, the repertoire of grooming behaviour is quite similar within host taxa (Kalueff and Tuohimaa 2004 for rodents, Mooring et al. 2004 for ungulates). Similarly, related hosts often have similar ecological preferences (Brooks and McLennan 1991). Furthermore, some fleas may use distantly-related principal hosts in different localities. However, in such cases, these hosts usually are ecologically similar and may thus be considered as substitutable. For example, *Hoplopsyllus anomalus* is a flea normally associated with ground squirrels (Sciuridae). However, in the San Joaquin Valley of California where the giant kangaroo rat *Dipodomys ingens* replaces the niche ordinarily filled by ground squirrels, this flea is found mainly on *D. ingens* (Tabor et al. 1993).

The results of this study suggest that the majority of flea species are either scale-invariant specialists or scale-invariant generalists. Nevertheless, the relatively low coefficients of determination of the regressions of global against local host specificity suggest that a substantial part of the variance in the former could not be explained by the latter. One reason for this is the occurrence of local generalist/global specialist and local specialist/global generalist species. An example of a local generalist/global specialist is *Xenopsylla gerbilli*. This flea exploited 3–13 host species in different regions. However, wherever this species was recorded, its principal host was the great gerbil *Rhombomys opimus*. Local specialists/global generalists are exemplified by *Rhadinopsylla rothschildi* that uses from 1 to 3 host species in each of 5 regions where it was recorded. However, in each of these regions it attains its maximum abundance on different host species belonging to 2 different families (Cricetidae and Muridae) with 2 different subfamilies within Cricetidae (Arvicolinae and Cricetinae).

The above examples concern host specificity measured as the number of hosts exploited. If, instead, host specificity is measured as the taxonomic diversity of the host spectrum, local generalists/global specialists can also be easily discerned. For example, *Nosopsyllus laeviceps* is locally able to exploit hosts belonging to distantly-related taxa. For example, in Turkmenistan it was found on rodents belonging to 5 different families (Zagniborodova 1960). However, the principal host of this flea in each of the 6 regions where it was recorded was always a species of *Meriones*. In contrast, local specialists/global generalists could not be easily distinguished. This supports the idea that geographic substitutability of resources is an important mechanism behind colonization success. This also suggests that the number of hosts exploited and the taxonomic diversity of the host spectrum capture different aspects of host specificity (Poulin and Mouillot 2003).

Finally, the general scale-invariance of host specificity in fleas supports earlier findings that the degree of host specificity represents a true attribute of a flea species (Krasnov et al. 2004c) and may only vary within some species-specific limits. These limits likely reflect a flea's responses to host-related traits such as the structure of skin,

hair density, physical and chemical properties of the blood, behavioural and immunological defences, and the environmental conditions of the host burrow/nest. For example, the morphometrics of mouthparts differ among flea species (Suter 1964). Species with relatively short mouthparts are able to exploit only a restricted range of host species, namely those in which the skin is thin or blood vessels are close to the skin surface (Vashchenok 1988). The species-specific limits of host specificity reported earlier (Krasnov et al. 2004c) and the scale-invariance of host specificity found in this study suggest that the ability of a flea species to use a certain set of hosts is phylogenetically constrained.

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