Host specificity and geographic range in haematophagous ectoparasites

Boris R. Krasnov, Robert Poulin, Georgy I. Shenbrot, David Mouillot and Irina S. Khokhlova

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A negative interspecific correlation between the degree of habitat specialization and the size of a species' geographic range has been documented for several free living groups of organisms, providing support for the niche breadth hypothesis. In contrast, practically nothing is known about the geographic range sizes of parasitic organisms and their determinants. In the context of the niche breadth hypothesis, parasites represent ideal study systems, because of the well documented variation in host specificity among parasite species. Here, we investigated the relationship between host specificity (a measure of niche breadth) and geographic range size among flea species parasitic on small mammals, using data from seven distinct geographical regions. Two measures of host specificity were used: the number of host species used by a flea species, and a measure of the average taxonomic distance between the host species used by a flea; the latter index provides an evolutionary perspective on host specificity. After correcting for phylogenetic influences, and using either of our two measures of host specificity, the degree of host specificity of fleas was negatively correlated with the size of their geographic range in all seven regions studied here, with only one minor exception. Overall, these results provide strong support for the niche breadth hypothesis, although other explanations cannot be ruled out.

B. R. Krasnov and G. I. Shenbrot, Ramon Science Center and Mitrani Dept of Desert Ecology, Jacob Blaustein Inst. for Desert Research, Ben-Gurion Univ. of the Negev, P.O. Box 194, IL-80600 Mizpe Ramon, Israel (krasnov@bgumail.bgu.ac.il). – R. Poulin, Dept. of Zoology, Univ.of Otago, P.O. Box 56, Dunedin, New Zealand. – D. Mouillot, UMR CNRS-UMII 5119 Ecosystemes Lagunaires, Univ. Montpellier II, CC093, FR-34095 Montpellier Cedex 5, France. – I. S. Khokhlova, Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture, Jacob Blaustein Institute for Desert Research, Ben-Gurion Univ. of the Negev, IL-84105 Beer Sheva, Israel.

Individual species vary greatly in the size of their geographic ranges. Numerous studies have searched for the correlates of geographic range size and thus attempted to explain this variation. For example, the extent of variation in the sizes of geographic ranges appears to be specific to particular taxonomic or functional groups of organisms (Brown et al. 1996). Range sizes of closely related species are, usually, more similar to each other than to those of distantly related species (Jablonski 1987, Brown 1995), suggesting that

some intrinsic characteristics of the organisms inherited from their common ancestors influence the ecological interactions that limit geographic distribution (Brown et al. 1996). Additional patterns of variation in range size as a function of characteristics of organisms include the relationships between range size and body size (Brown 1995, Gaston and Blackburn 1996a, 1996b) and between range size and abundance (Brown 1984, Gaston and Blackburn 1996c). In most cases, highly significant positive correlations between range size and both body

mass and some measure of average population density were found. Another pattern applying to geographic range size is a negative correlation between the degree of habitat specialization and a species' geographic range that has been observed for various groups (MacArthur 1972, Glazier 1980, Brown 1984, Eeley and Foley 1999). Brown (1984, 1995) proposed a niche breadth based explanation for this negative correlation. According to this explanation, a specialist is a species that can endure restricted abiotic conditions, is able to use few types of resource and is highly tolerant of a very limited set of competitors, predators, parasites and diseases. In contrast, a generalist species tolerates a wide range of physical conditions, uses a broad range of resources and survives in the presence of many natural enemies. In this niche breadth hypothesis, the same attributes that enable a species to occur in either many or a few habitats cause it to have either a broad or narrow geographic range, respectively.

Correlates of geographic range size have been studied for various, mainly free living taxa. In contrast, patterns of geographic range size of parasites are less known. For example, it is unknown whether geographic range size and the degree of habitat specialization are correlated among parasites. Habitat specialization of a parasitic species can be considered the equivalent of its host specificity, because a host represents the habitat for a parasite, providing it with a place for living, foraging and mating (Price 1990).

Parasites differ in their degree of host specificity from those that are strictly host specific (i.e. found on a single host species) to those using a broad range of hosts. Based on the general occurrence of a negative correlation between the degree of specialization and geographic range size in free living organisms, we hypothesized that the size of the geographic range in parasites will also conform to this pattern. In other words, the geographic distribution of highly host specific parasites should be more restricted than that of generalist parasites. We tested this hypothesis by investigating the relationship between the degree of host specificity and the size of the geographic range in fleas parasitic on small mammals (<5 kg, following the definition of the International Biological Programme Small Mammals Working Group, Bouliere 1975) from the orders Didelphimorphia, Dasyuromorphia, Paramelemorphia, Diprotodontia, Insectivora, Macroscelidea, Lagomorpha and Rodentia.

Fleas (Siphonaptera) are parasites of higher vertebrates, being most abundant and diverse on small mammals. They usually alternate between periods when they occur on the body of their hosts and periods when they occur in their hosts' burrows or nests. In most cases, preimaginal development is entirely off host. 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 a particular host species varies, with flea species ranging from highly host specific to host opportunistic (Marshall 1981).

We used published data on the geographic distribution and host occurrences of fleas from seven distinct geographic regions. Comparisons across species performed using species values as data points may be confounded by phylogenetic relationships among species (Felsenstein 1985). To avoid the potentially confounding effect of phylogenetic relationships and to obtain independent data points, we used the method of the independent contrasts (Felsenstein 1985). In addition, rather than taking the mere number of host species used by a flea as a measure of host specificity, we also applied a measure of host specificity that takes into account the taxonomic or phylogenetic affinities of the various host species (Poulin and Mouillot 2003). This measure places the emphasis on the taxonomic distance between host species used by a flea rather than on their number, providing a different perspective on host specificity, one that truly focuses on the specialization of the flea for its host habitat.

Material and methods

Data on the host range of fleas were obtained from published regional monographs on fleas of the Neotropical region (Venezuela; Tipton and Machado-Allison 1972), Nearctic region (Canada, Alaska and Greenland; Holland 1985), Australian region (Australia; Dunnet and Mardon 1974), Ethiopian region (South Africa; Segerman 1995), and Palaearctic region (Morocco, Mongolia and the northern Asian Far East; Hastriter and Tipton 1975, Kiefer et al. 1984 and Yudin et al. 1976, respectively, Table 1). We cross-checked the species lists with the catalogue of Lewis and Lewis (1990) to resolve cases of synonymy. Flea species with cosmopolitan distributions (e. g. *Xenopsylla cheopis*, *Nosopsyllus fasciatus*) that were likely introduced to many regions with humans, domestic animals and synantropous rodents (Beaucournu and Pascal 1998), were omitted from the analysis. In addition, single findings of a flea species on a host species or in a region were considered accidental and were not included in the analysis. In total, we used data on host specificity and geographic range on 341 flea species (Table 1).

The size of the geographic range for each flea species was calculated from a distribution map. A distribution range map for each species was composed as a polygon map using ArcView 3.2 software based on published maps from the original source, Traub et al. (1983), Smit (1987) and/or on the data from Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971) and Mardon (1981). We calculated both "local" (across the considered region)

Table 1. Summary of data on fleas and their hosts from different regions.

Region	Number of flea species	Number of host species	Range of host species per flea species	Median number of host species per flea species	Percentage of strictly host-specific fleas
Venezuela	25	69	2–24	8	0.0
Canada	103	118	1–27	4	12.6
Australia	35	68	1–22	4	14.3
South Africa	62	51	1–32	4	15.9
Morocco	20	10	1–18	4.5	20.0
Mongolia	76	60	1–28	8	11.8
Northern Asian Far East	19	12	1–10	3	26.3

and global (across the entire world) geographic ranges for every flea species.

For each species of flea, two measures of host specificity were used: (1) the number of mammalian species on which the flea species was found, and (2) the specificity index, S_{TD}, and its variance $VarS_{TD}$ (Poulin and Mouillot 2003). Data on either the abundance of fleas on a particular host species or on the number of examined host individuals were not available from the original sources. Consequently, correcting the data set for sampling effort (Morand and Poulin 1998) was not possible. 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 (Poulin and Mouillot 2003). 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 one 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 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 5 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 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 variance in S_{TD}, $VarS_{TD}$, 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 3 or more host species (it always equals zero with 2 host species).

To control for the effects of flea phylogeny, we used the method of independent contrasts (Felsenstein 1985). The phylogenetic tree for fleas was based on the taxonomy used in Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971), Mardon (1981), Traub et al. (1983) and Smit (1987) and the cladistic tree of flea families of Medvedev (1994, 1998). 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. 2003) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2004). Pairs of sister branches that diverged long ago can likely return 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.

To test for the correlation between flea host specificity and geographic range, we regressed standardized contrasts in log-transformed measures of host specificity against standardized contrasts in log-transformed values of geographic ranges using major axis regression forced through the origin (Pagel 1992, Garland et al. 1993). We avoided an inflated type I error by performing Bonferroni adjustments of α that resulted in a level of 0.007.

Results

The frequency distribution of local and global geographic ranges of fleas (pooled across the entire data set) was highly right skewed ($\gamma_1 = 5.53$ and $\gamma_1 = 3.05$, respectively, Fig. 1 for global geographic ranges). The same was true for distributions of local and global geographic ranges within regions ($\gamma_1 = 0.43–3.07$ and $\gamma_1 = 1.22–6.81$, respectively). The most right skewed distribution of local geographic ranges was shown by fleas of Canada, whereas the distribution of local geographic ranges was least right skewed in the North Asian Far East. The distribution of global geographic
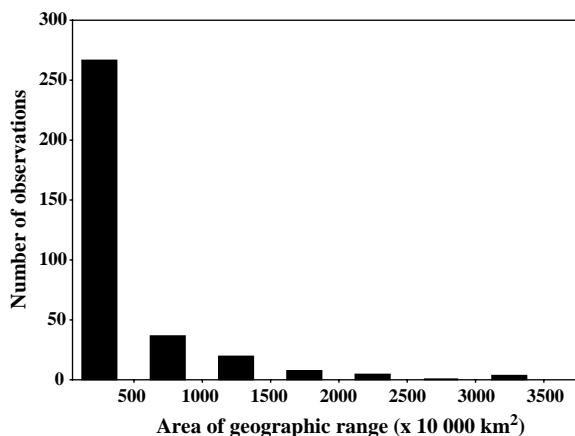
Fig. 1. Frequency distribution of global geographic range sizes of 341 flea species.

ranges of fleas was the most rightly skewed in South Africa and the least rightly skewed in Venezuela.

Flea species from different regions differed in the degree of their host specificity measured by the number of host species they use (Kruskal–Wallis ANOVA, $H = 21.6$, $p = 0.001$). The number of host species exploited by a particular flea species ranged from 1 to 32 with median values being highest in Venezuela and Mongolia and lowest in the north Asian Far East (Table 1). The percentage of strictly host specific fleas (those that parasitize one host species only) was highest in the north Asian Far East and lowest in Canada and Venezuela (in Venezuela no strictly host specific fleas were found, Table 1). Comparisons of S_{TD} and $VarS_{TD}$ values among fleas from different regions revealed that, in general, the average value of the specificity index and its variance differed among regions (ANOVA, $F = 2.1$, $p = 0.05$ and $F = 9.00$, $p < 0.01$, respectively). S_{TD} was the highest in Venezuela and the lowest in Morocco, South Africa and the North Asian Far East, whereas its variance was the highest in the north Asian Far East and the lowest in South Africa. Comparisons of average values of the specificity index between regions of similar longitude but not necessarily similar latitudes showed that the specificity index (S_{TD}) of fleas from Canada was significantly lower than that of Venezuelan fleas (2.80 versus 3.42, respectively, $t = 2.7$, $p < 0.01$), whereas no difference in specificity index existed between Moroccan and South African fleas (2.55 versus 2.53, respectively, $t = 0.04$, $p = 0.9$).

In general, the degree of host specificity of fleas was negatively correlated with the size of their geographic range in all studied regions (Table 2). This was true for both measures of host specificity, namely the number of host species used and the specificity index, S_{TD}, and whether local or global geographic ranges were used. The only exception was demonstrated by fleas of Morocco, for which no significant correlation was found

between the specificity index S_{TD} and "global" geographic range. An example of the relationship between the two measures of host specificity and global geographic range (for fleas of Australia) is represented in Fig. 2.

In contrast, no correlation was found between $VarS_{TD}$, i.e. the variance in the taxonomic distinctness of host species, and either measure of geographic range size, for any of the seven regions ($r = 0.0001 – 0.30$, $p > 0.07$ for all).

Discussion

Our results provide very strong support for the niche breadth hypothesis. In general, host specific fleas have more restricted geographic ranges than host opportunistic fleas. Flea species with a broad geographic range are not only capable of exploiting more host species, but they also exploit host species from a wider range of taxa. The patterns highlighted by the two measures of host specificity (number of host species and S_{TD}) represent two independent trends: as the geographic range of fleas expands, not only are additional hosts being used, but these come from increasingly phylogenetically distant mammalian taxa.

There can be several, not necessarily mutually exclusive, explanations for this pattern. First, the negative correlation between the degree of flea host specificity and geographic range can be explained via Brown's (1984, 1995) niche breadth based model and its parasitological equivalent, the host compatibility filter concept of Euzet and Combes (1980) and Combes (1991, 2001, 2002). The host compatibility filter excludes all potential host species in which a parasite cannot survive and develop for morphological, physiological or immunological reasons. Highly host specific parasites are adapted to a restricted range of conditions, such as the physical and chemical properties of host blood for the imago (Marshall 1981, Krasnov et al. 2003) and the microclimate of the host burrow/nest for pre imaginal stages (Krasnov et al. 2001). In other words, very few host species will be compatible with the strict requirements of host specific parasites. In contrast, a host opportunistic flea can feed on blood from a wide range of hosts and its pre-imaginal stages can survive under variable microclimatic conditions. For example, the cosmopolitan *Xenopsylla cheopis* can successfully digest blood from laboratory hamsters, mice, rats, guinea pigs and pigeons (Vatschenok et al. 1976). The broadly distributed *Xenopsylla brasiliensis* can complete its life cycle at a wide range of relative humidities, i.e. 51–95% (Bahmanyar and Cavanaugh 1976 cited by Marshall 1981); furthermore, Bruce (1948) reported that the survival of larvae of the cosmopolitan flea *Ctenocephalides felis* can occur at range of 45–95% relative

Table 2. Summary of major axis regressions (forced through the origin) of independent contrasts in number of host species and independent contrasts in specificity index (S_{TD}) against independent contrasts in geographic range size, for fleas from different regions. All r, except those marked by *, are significant (p < 0.007).

Region	Number of host species		S_{TD}	
	"Local" geographic range	"Global" geographic range	"Local" geographic range	"Global" geographic range
Venezuela	0.64	0.56	0.36	0.34
Canada	0.58	0.60	0.37	0.45
Australia	0.73	0.58	0.41	0.58
South Africa	0.81	0.77	0.46	0.47
Morocco	0.59	0.21	0.49	0.12*
Mongolia	0.72	0.26	0.40	0.33
Asian Far East	0.75	0.61	0.76	0.61

humidity. In other words, numerous host species will offer conditions compatible with the requirements of host opportunistic parasites. The same mechanisms that enable a flea to exploit either few or many host species can be the reason why it has either a small or a large geographic range.

Second, the negative relationship between the degree of host specificity and geographic range size can stem from the pattern of frequency distribution of geographic ranges. Indeed, the geographic range of a host specific parasite can be either equal to or smaller than the combined range of its hosts. The distributions of within-taxon species-geographic range sizes tend to be unimodal with a strong positive skew, i. e. most species have relatively small range sizes, whereas a few have relatively large ranges (Gaston 2003). In particular, this is true for different mammalian taxa (Letcher and Harvey 1994, Eeley and Foley 1999). A host specific flea is, therefore, expected to have, on average, a small geographic range simply due to the high probability of its mammalian host also having a small geographic range. This mechanistic approach cannot, though, clearly explain the large geographic ranges of host opportunistic fleas, except if the geographic range of a host opportunistic flea is simply the summation of the geographic ranges of its multiple hosts (if the degree of overlap among the geographic ranges of these hosts is relatively small).

Third, the negative correlation between the degree of flea specificity and geographic range size can be related to latitudinal gradients in species richness, niche breadth and geographic ranges. Indeed, in general, the inventory of species declines as one moves away from the equator, as has been repeatedly shown for free living animals (Rohde 1992, Rosenzweig 1992, 1995) although the generality of this rule has been much debated (Rohde 1999, Gaston 2003). Studies of this pattern in relation to parasite assemblages have provided contrasting results. For example, Rohde and Heap (1998) showed this pattern for ectoparasitic monogeneans but not for endoparasites of marine fish, whereas Poulin (1995) did not find any relationships between latitude and the diversity of gastrointestinal parasites of birds and mammals. The absence of a latitudinal gradient pattern

for endoparasites can be explained by the relative stability of their environment (inside the host body, Rohde and Heap 1998). Ectoparasites, in contrast, are exposed to environmental conditions that change with
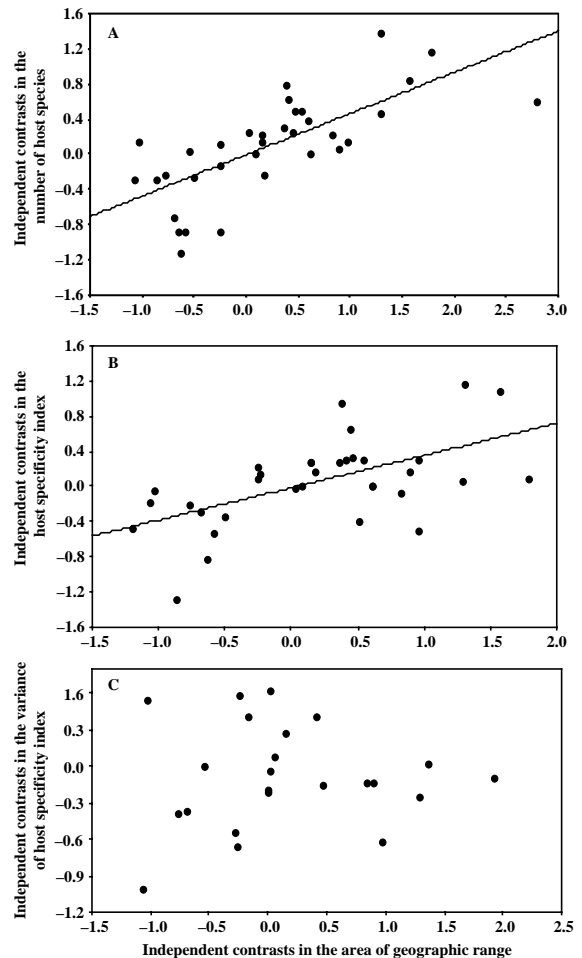

Fig. 2. Relationship between either the number of host species (A), the specificity index (S_{TD}, B) or its variance (VarS_{TD}, C), and global geographic range in fleas from Australia using independent contrasts. The lines are linear regressions using independent contrasts.

latitude and, thus, their species richness is expected to decrease with increasing latitude. Another latitudinal pattern is the positive correlation between niche breadth and latitude (Pagel et al. 1991). The reason for niche breadth being narrower at low latitudes can be either increased interspecific competition due to higher number of co-occurring species (Brown 1975) or the relative stability of environmental conditions that allows the persistence of specialized species (Chesson and Huntly 1997) or both. Indeed, in our data set, the average values of the specificity index (S_{TD}) differed significantly between fleas from regions of similar longitude but different latitude, being higher in the region closest to the equator (fleas of Canada versus fleas of Venezuela). However, this index did not differ between fleas from regions of similar longitude and latitude but situated on different sides of the equator (Morocco versus South Africa). Finally, there is a positive correlation between species range size and latitude (Rapoport 1982, Stevens 1989). This pattern was identified as "Rapoport's rule" by Stevens (1989). While the validity and generality of Rapoport's rule has been much debated (Rhode et al. 1993, Brown 1995, Gaston et al. 1998, Rhode 1999, Gaston 2003), coincident latitudinal patterns in species richness and average species range size have been demonstrated for a variety of taxa and across different geographical regions (Stevens 1989, Pagel et al. 1991, Letcher and Harvey 1994, Gaston 2003). Taken together, these three latitudinal gradients could result in the pattern observed in this study, i.e. the increase of geographic range size with decreasing host specificity.

Asymmetries in the taxonomic structure of the host species used by a parasite, as measured by the variance in the index S_{TD} (VarS_{TD}, Poulin and Mouillot 2003), was not correlated with geographic range. This means that the level of taxonomic heterogeneity among a group of host species did not differ between narrow and broadly distributed flea species and seems to depend on other still unknown factors. Relationships between geographic range and VarS_{TD} were surprisingly very consistent across scales (local and global) and all regions considered. This result suggests that the irregularity of the taxonomic tree of the hosts is an invariant parameter, i.e. that when the geographic range increases, new host species add more diversity but not more complexity to the host taxonomic tree. This trend certainly requires further investigation, and might be related to the findings of Enquist et al. (2002) showing taxonomic regularities across scales in the composition of natural communities.

The pattern of a negative relationship between the degree of host specificity and geographic range size persists despite sharp exceptions to this trend, such as highly host specific fleas that demonstrate broad geographic distributions due to the broad distribution of their hosts. For example, the principal host of the flea

Tarsopsylla octodicemdentata is a squirrel *Sciurus vulgaris* that is distributed across most of Eurasia. In the New World, *T. octodicemdentata* occurs on the closely related *Tamiasciurus hudsonicus* that is distributed across most of North America. As a result, both the "local" (within Canada and north Far East regions) and "global" geographic ranges of this flea are large. Alternatively, the apparently large range of a species can be merely an artifact of poor taxonomy concealing the existence of cryptic species (i.e. several flea species erroneously considered as one) as it was suggested in studies of geographic ranges in other taxa (Murray and Dickman 2000).

Another type of exception from the observed pattern consists of host opportunistic fleas with restricted geographic distributions. For example, the South African fleas *Dinopsyllus ellobius* and *D. lypusus* were found on a wide range of rodent hosts (32 and 20, respectively). However, their geographic distributions are restricted mainly to the higher rainfall areas of the eastern part of the southern African subcontinent (Segerman 1995). The reasons for the absence of these fleas from the other parts of the geographic ranges of their numerous hosts might be some as yet unknown abiotic preferences of the pre imaginal and/or adult insects. The important effect of abiotic factors on flea distribution has been shown, for example, in southern Israel. A flea *Xenopsylla conformis mycerini* was found to be replaced with *Xenopsylla ramesis* on the same rodent host *Meriones crassus* between two different habitats situated at the opposite ends of a steep precipitation gradient (Krasnov et al. 1998). These two flea species appeared to have different microclimatic and substrate preferences that conformed to their between-habitat distribution (Krasnov et al. 2001, 2002).

High numbers of such species in the flea fauna can cause deviations from the reported trend. Indeed, the negative host specificity-geographic range size correlation was consistent across all studied regions, except for Morocco where no correlation between the degree of host specificity and "global" geographic range was found. The absence of this correlation can be explained, at least partly, by the composition of the Moroccan flea fauna which is characterized by a relatively high percentage of highly host specific fleas with relatively broad geographic distributions (*Xenopsylla nubica*, *Spilopsyllus cuniculi*, *Leptopsylla taschenbergi*, *Leptopsylla algira*) and host opportunistic fleas with restricted geographic distributions (*Xenopsylla blanci*, *Nosopsyllus oranus*, *Nosopsyllus barbarus*, *Ctenophthalmus andorrensis*). These seven flea species represent 35% of the species poor Moroccan flea fauna. It should be noted that highly host specific fleas include not only species exploiting a small number of hosts, but also species that parasitize multiple closely related hosts. Similarly, highly host opportunistic fleas include not only species

exploiting a large number of hosts, but also species that parasitize a few distantly related host species. Nevertheless, the one exception to the rule found among the many independent data sets used here is not enough to weaken the overall trend: among flea species, the size of the geographic range is strongly associated with the degree of host specificity. This is the first demonstration for a parasite taxon of a relationship between geographic distribution and ecological specialization.

It should be noted, however, that flea taxonomy is based mainly on morphological characters. Therefore, in some cases, the existence of cryptic flea species can either mask the true patterns of host specificity and/or lead to overestimation of a flea geographic range. For example, the large geographic range of a flea species can arise when dealing with several geographically vicariate flea species erroneously considered as a single valid species. However, for the vast majority of flea species, molecular data are not yet available.

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