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Interaction frequency across the geographical range as a determinant of host specialisation in generalist fleas

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Abstract

The strength of interspecific interactions varies over geographical scales, and can influence patterns of resource specialisation. Even with gene flow preventing local adaptation of a consumer to particular resources, we might expect that across its entire range, the consumer would show some specialisation for the resource types most likely to be encountered across the localities where it occurs. We tested the hypothesis that generalist fleas are more successful at exploiting small mammalian host species with which they co-occur frequently across their geographical range than host species that, though suitable, are encountered less frequently. This hypothesis was tested with data on 121 flea species compiled from field surveys across 35 regions of the Palaearctic. Using abundance (mean number of individual fleas per individual host) as a measure of flea success on a particular host species, positive correlations between flea abundance and the frequency of co-occurrence of a flea with each of its hosts amongst all regions surveyed were found in all but two of the flea species investigated, with one-fifth of these being significant. If overlap in geographical range between flea and host is used as a measure of frequency of encounters instead of the actual proportion of regions where they both occur, similar patterns are observed, though they are much weaker. In a comparative analysis across all flea species, there were significant relationships between the average abundance of fleas and average values of both measures of frequency of encounters (proportion of sites where they co-occur and range overlap), even when correcting for potential phylogenetic influences. The results suggest that for any given flea species, host species more commonly encountered throughout the spatial range of the flea are generally those on which the flea does best. Interaction frequency may be a key determinant of specialisation and abundance in host–parasite systems.

Keywords: Coevolution; Ectoparasites; Host specificity; Siphonaptera

1. Introduction

Interactions between given species are variable in both space and time. This forms the basis of the geographical mosaic theory of coevolution (Thompson, 2005). Both qualitative and quantitative aspects of interspecific interactions differ amongst the localities where two or more interacting species are found. One reason for this is that, in the vast majority of cases not involving strict specialists, interacting species such as hosts and parasites do not have identical geographical ranges. There is overlap between their geographical distributions, such that they co-occur in some localities, but the overlap is rarely perfect, such that a given host species occurs in some localities without a given parasite, and vice versa (Esch et al., 1990; Rohde, 2002; Krasnov et al., 2005b). This is a basic attribute of most interactions providing the raw material for spatially-structured coevolution (Thompson, 1999, 2005).

This spatial structure may also provide an explanation for patterns of specialisation by parasites on their hosts. Because some host species that a parasite could exploit are not present everywhere throughout the parasite's

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geographical range, we can expect selection to favour local adaptation of the parasite to the hosts that are locally available. However, when the host species involved are mobile, gene flow amongst different populations of a parasite species serves to maintain the species' integrity over large spatial scales (Blouin et al., 1995; Anderson et al., 1998; Lampo et al., 1998; McCoy et al., 2003). Thus for the parasite species as a whole, throughout its entire range, we might expect a degree of specialisation on the host species that are most likely to be encountered across all localities where the parasite occurs (Fox and Morrow, 1981). If specialisation for frequently-encountered host species has a genetic basis, then selection will favour specialisation on these hosts in many foci and result in the parasite achieving greater success on these frequent hosts than on host species that are also used but only rarely encountered throughout the geographical range.

Here, we test this hypothesis with data on fleas (Siphonaptera) parasitic on small mammals in the Palaearctic. Fleas are obligate blood-sucking ectoparasites most abundant and diverse on small to medium-sized burrowing species of mammals (Marshall, 1981). In contrast to the imago, flea larvae are usually 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 rodent fleas are not very host-specific, with particular flea species being found on two or more host genera of the same family, or on two or more host families, or even across different mammalian orders (Marshall, 1981; Poulin et al., 2006). We use two complementary methods to assess the frequency of encounter between a flea and its different host species on a geographical scale, one that measures the actual frequency of local co-occurrences, and one that estimates the potential for co-occurrences. We test for relationships between these measures and the relative abundance of a flea species on its different host species, which is used here as an estimate of its degree of resource use, i.e. its degree of specialisation on the different host species. For fleas, abundance (mean number of individuals per host) is linked to fitness: high survival and reproduction of individual fleas on one host species lead to high abundance on that host (Krasnov et al., 2004a). Thus, we test the hypothesis that spatial overlap between a flea and its different host species influences the relative fitness achieved by the flea on these hosts. Our results provide evidence that

Table 1
Number of species of small mammals and fleas from the 35 regions used in the analyses

Region	Number of species		Source
	Hosts	Fleas	
Sweden	5	9	Brinck (1966)
Slovakia	13	15	Stanko et al. (2002)
Volga-Kama region, Russia	18	27	Nazarova (1981)
Novosibirsk region, southern Siberia, Russia	18	26	Violovich (1969)
Krasnojarsk region, Russia	6	17	Ravkin and Sapegina (1990)
Tomsk and Tumen region, Russia	21	22	Sapegina et al. (1980a)
Kurgan region, Russia	15	16	Starikov and Sapegina (1987)
Altai mountains, Russia	19	9	Sapegina et al. (1981a)
Western Sayan ridge, southern Siberia, Russia	11	25	Emelyanova and Shtilmark (1967)
Tuva, Russia	12	23	Letov et al. (1966)
Selenga region, central Siberia, Russia	6	10	Pauller et al. (1966)
Central Yakutia, Russia	6	16	Elshanskaya and Popov (1972)
Taimyr Peninsula, Russia	11	10	Sapegina et al. (1980b, 1981b)
Amur river valley, Russian Far East	5	13	Koshkin (1966)
Ussury river valley, Russian Far East	4	14	Kozlovskaya (1958)
Khasan lake region, Russian Far East	5	6	Leonov (1958)
Magadan and Tchukotka regions, Russian Far East	14	12	Yudin et al. (1976)
Kamchatka peninsula, Russian Far East	3	6	Paramonov et al. (1966)
Kabarda, northern Caucasus, Russia	8	15	Syrvacheva (1964)
Adzharia, southern Caucasus, Russia	9	11	Alania et al. (1964)
Southwestern Azerbaijan	8	15	Kunitsky and Kunitskaya (1962)
Turkmenistan	17	30	Zagniborodova (1960)
Kustanai region, northwestern Kazakhstan	8	11	Reshetnikova (1959)
Akmolinsk region, northern Kazakhstan	7	14	Mikulin (1959a)
Pavlodar region, eastern Kazakhstan	6	9	Sineltschikov (1956)
Moyynkum desert, southern Kazakhstan	11	25	Popova (1968)
East Balkhash desert, Kazakhstan	10	26	Mikulin (1959b)
Dzhungarskyi Alatau ridge, Kazakhstan	14	21	Burdelova (1996)
Tarbagatai ridge, eastern Kazakhstan	12	23	Mikulin (1958)
Kyrgyz ridge, northern Kyrgyzstan	12	29	Shwartz et al. (1958)
Gissar ridge, Tajikistan	8	19	Morozkina et al. (1971)
Northwestern Khangay region, Mongolia	14	30	Labunets (1967)
Central Khangay region, Mongolia	5	18	Vasiliev (1966)

the evolution of host specialisation in fleas is driven by opportunities for interactions with their various host species across large spatial scales.

2. Materials and methods

2.1. Data set

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora, Lagomorpha and Rodentia) in 35 different regions of the Palaearctic (Table 1). These sources provided data on the average number of individuals of a particular flea species found on individuals of a particular host species. The surveys were extensive, conducted over a wide area from spring to autumn and across several years, and targeted the entire small mammal community of each region. In all surveys, most species were captured using snap-traps; shrews were also captured using pitfall traps, sciurids and lagomorphs were hunted, whereas moles were captured using mole-traps. In total, 1,394,575 individual fleas and 399,462 individual mammals were collected in the 35 surveys. Only mammal species for which at least 10 individuals have been examined per region were included, because estimates of flea abundance could be inaccurate for smaller samples. Also, only flea species occurring in at least four different mammalian host species across the entire geographical range were included. Flea species with cosmopolitan distributions (e.g., *Xenopsylla cheopis*, *Nosopsyllus fasciatus*) that were likely introduced to many regions with humans, domestic animals or synantropous rodents (e.g., *Mus musculus*, *Rattus norvegicus*) were omitted from the analysis, since their broad geographical range is of recent origin and would not have allowed much time for coevolution with hosts. 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. This resulted in 1349 flea–host associations that involved 121 (107 of which occurred in at least two regions) flea species parasitising 109 small mammalian species.

2.2. Abundance and co-occurrence measures

We used the mean number of flea individuals per individual host of a given species as a measure of flea abundance. Estimates of parasite abundance may be biased if some parasites or hosts are studied more intensively than others (Stanko et al., 2002). Consequently, unequal study effort amongst host species may result in confounding variation in estimates of flea abundance. In addition, hosts of different sizes can support different numbers of fleas. To ensure that interspecific variation in host sampling effort and body size did not bias estimates of flea abundance, we regressed estimates of flea abundance per host against the number of hosts examined and the body surface area of hosts (estimated from body mass; see Walsberg and Wolf, 1995) for each flea species in each region. Estimates of flea abundance per host were not affected either by sampling effort or by host body size ($r^2 = 0.002$, $F_{1,1347} = 2.57$ and $r^2 = 0.001$, $F_{1,1347} = 0.98$, both $P > 0.1$). Consequently, we used raw abundance data in subsequent analyses.

For each flea–mammal species combination, we computed the average abundance of the flea on the host across all regions in which they both occurred. We then identified the principal host for each flea species across its geographical range, i.e. the mammal species in which the flea attained its highest average abundance. Other host species were considered as auxiliary hosts. The abundance of a flea on a host species was in each case expressed as a relative value, i.e. expressed as a proportion of the value observed on the principal host. Thus, the value for the principal host is always 1, and values for auxiliary hosts are less than one. The use of relative values instead of absolute values does not affect the results of the following analyses, and allows the comparison of abundance values that vary greatly in absolute terms amongst the different parasite species (see Poulin, 2005). The relative values were arcsine-transformed prior to analyses.

The frequency of encounter between a flea and its different host species was measured in two different ways. First, for each flea–host species combination, we used the proportion of regions from which a flea species has been reported in which the host species also occurs; in other words, the number of regions in which both the flea and a particular host were found was divided by the total number of regions in which the flea was found. This serves as an estimate of the actual frequency of local co-occurrences between the parasite and each of its hosts. Second, the geographical range for each flea and host species was determined from distribution maps using the ArcView 3.2 software. The maps for fleas are based on published maps (see Krasnov et al., 2005a) and various literature sources; the maps for host species are derived from various sources (see Krasnov et al., 2004b). The standard method for estimating geographical range size when an analysis of distribution is based on presence-only point data involves the construction of a minimal convex polygon (MCP; Fortin et al., 2005). However, this method may significantly overestimate range size since an estimated geographical range might include areas from which a species is absent. For more accurate estimations of geographical ranges, the α-hull algorithm of geographical range size estimation was proposed by Burgman and Fox (2003). This algorithm also produces significant errors in range estimates because of the non-uniform distribution of data points and the low spatial accuracy unavoidable with geo-referencing of published data (Burgman and Fox, 2003). Consequently, to estimate the size of the geographical range of a species, we combined the MCP method and the GARP algorithm (Stockwell and Peters, 1999). The latter is a genetic algorithm that creates ecological niche models for each species. We constructed a MCP around the outermost record points and added around it a 25 km buffer. For species known from 4 to 5 localities only, the resulting buffer polygon was used as an estimation of geographical range. To estimate geographical ranges of species known from more than five regions, we used the modelling approach based on the GARP algorithms (DesktopGARP 1.1.3 software, University of Kansas Biodiversity Research Center). For each species, we calculated a set of 60–120 models using range and logistic regression methods and their combination. We included only areas that were located inside the original buffer polygon in the estimated geographical range, because estimation of the potential distribution of a species beyond known distributional limits has low reliability (Anderson, 2003; Anderson et al., 2003). We overlapped all models thus obtained and included areas for which 90% of models predicted a species' presence in the estimated geographical range. Finally, for each flea and host species combination, the proportion of the flea's geographical range that overlapped with the host range was used as a measure of range overlap, providing a measure of the potential for local encounters of the flea with the host.

2.3. Analyses

For each flea species, we performed regressions of each measure of frequency of encounter with a host species (i.e., actual frequency of local co-occurrences and range overlap) against average relative abundance of the flea on that host species, across all the host species used by that flea. The relationship between frequency of local co-occurrences and average relative abundance was tested only for the flea species (107 out of 121 species) that occurred in more than one region.

In addition, we performed a comparative analysis across all flea species, to test whether fleas that co-occur on average more frequently with their hosts achieve, on average, higher abundance on these hosts. We regressed the mean value of each measure of frequency of encounter of a flea species with hosts, averaged across all its hosts, against the average relative abundance of this flea on all its host species. These regressions were computed across all flea species ($N = 107$ flea species for frequency of local co-occurrences, $N = 121$ for range overlap). Comparisons across species performed using species values as data points may be confounded by phylogenetic relationships amongst species (Felsenstein, 1985; Harvey and Pagel, 1991). To avoid the potentially confounding effect of phylogenetic relationships and to obtain independent data points, we used the independent contrasts method (Felsenstein, 1985). The only broad molecular phylogeny of fleas is that of Whiting et al. (2008); however, it does not include the vast majority of flea species and genera that are part of our analyses. Therefore, a phylogenetic tree of our flea species was derived from flea taxonomy (see Krasnov et al., 2005a for details). The initial branch length was set to 1.0. To compute independent contrasts, we used the PDAP:PDTREE module (Garland et al., 1993; Midford, P.E., Garland, T. Jr., Maddison, W., 2005. PDAP:PDTREE package for Mesquite, Version 1.07, http://mesquiteproject.org/pdap_mesquite/index.html) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison, 2005). 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 standardised each contrast by dividing it by its standard deviation (Garland et al., 1992). To verify that contrasts were properly standardised, we plotted the absolute values of standardised 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 standardised.

3. Results

Overall, there was a total of 121 flea species included in the analysis. They parasitised 109 species of small mamma-

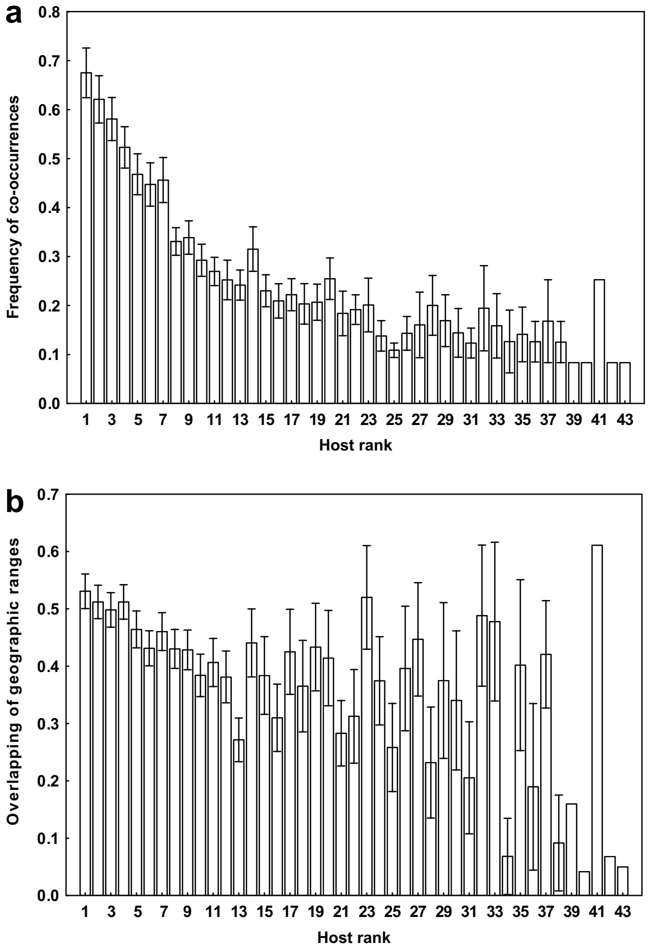

Fig. 1. Mean (±SE, arcsin-transformed) frequency of local co-occurrences (a) and geographical range overlap (b) of fleas in their mammalian hosts, as a function of host rank. Host species are ranked from the one in which flea abundance is the highest on average to the host species in which it is the lowest. Values are computed across the entire data set; sample sizes are 121 flea species for the first four ranks and then decrease rapidly for further ranks.

lian hosts and, on average, were found on 11.2 ± 0.7 host species across their geographical range. In total, there were 1349 flea–host associations that each occurred, on average, in 1.7 ± 0.04 of 35 regions (a low number because of numerous associations recorded in only one region). Fourteen flea species occurred in one region only.

Across all fleas, when host species are ranked from the one in which flea abundance is the highest on average to the host species in which it is the lowest, there is initially a clear decrease in frequency of local co-occurrences with the host across hosts ranked from 1 to about 14, after which the decrease weakens considerably (Fig. 1a). However, when the frequency of encounter between flea and host was estimated using the overlap between the geographical ranges of fleas and hosts, the decrease in the frequency of encounters as a function of host rank is weaker and becomes much more erratic beyond rank 12 (Fig. 1b).

In 21 of the 107 flea species investigated that occurred in more than one region, there was a positive relationship between relative abundance on a host species and the frequency of local co-occurrences between the flea and the host (Table 2; see example in Fig. 2a). Although non-significant because of low power, positive relationships dominated the rest of the analyses: negative (albeit non-significant) correlation coefficients between relative abundance on a host species and the frequency of local co-occurrences between the flea and the host were found in only two cases out of 107 tests. This pattern also emerged from the comparative analysis. The average frequency of co-occurrences correlated positively with the average relative abundance across the 107 flea species ($r^2 = 0.10$, $F_{1,105} = 11.0$, $P < 0.001$; Fig. 3a). The same was true when independent contrasts were used instead of the species values ($r = 0.39$, $P < 0.001$; Fig. 3b).

A positive relationship between relative abundance on a host species and the range overlap between the flea and the host was found in only six of the 121 flea species (Table 2; see example in Fig. 2b). In four of these six species, relative abundance also correlated positively with the frequency of local co-occurrences between the flea and the host. Among the 121 flea species, positive relationships again dominated, although not as clearly as when using the frequency of local co-occurrences: negative correlation coefficients between relative abundance on a host species and overlap between flea and host geographical ranges were found in 51 of 121 flea species, though none of these coefficients differed significantly from zero. In the comparative analysis, the average overlap between flea and host geographical ranges correlated positively with the average relative abundance of fleas on hosts, across the 121 flea species ($r^2 = 0.06$, $F_{1,119} = 7.4$, $P < 0.01$; Fig. 4a). The significant positive correlation also holds when the two outliers that can be seen in the right side of Fig. 4a (*Leptopsylla nana* and *Stenoponia conspecta*) are omitted from the analysis ($r^2 = 0.04$,

Table 2
Summary of significant regressions of flea relative abundance on mammal hosts versus the frequency of encounter between a flea and its different host species, measured either as the proportion of regions from which a flea species has been reported in which the host species also occurs (frequency of local co-occurrences; FLO) or as the proportion of the flea's geographical range that overlapped with the host range (range overlap; RO)

Flea species	Number of host species	Measure of frequency of encounter	r^2	F	p
Amphipsylla anceps	5	FLO	0.93	46.3	0.005
		RO	0.94	51.4	0.001
Amphipsylla kuznetzovi	8	FLO	0.95	175.6	0.0001
Amphipsylla schelkovnikovi	4	FLO	0.99	217.0	0.0001
Citellophilus lebedewi	4	FLO	0.99	116.0	0.0001
Citellophilus tesquorum	24	FLO	0.51	22.4	0.0001
		RO	0.22	5.6	0.02
Ctenophthalmus arvalis	15	FLO	0.47	11.5	0.04
Ctenophthalmus assimilis	37	FLO	0.15	6.6	0.01
		RO	0.14	5.9	0.02
Ctenophthalmus pisticus	6	FLO	0.81	16.7	0.01
Frontopsylla ambigua	4	RO	0.99	207.5	0.004
Frontopsylla macrophthalma	5	FLO	0.91	26.2	0.01
Megabothris advenarius	13	FLO	0.64	19.8	0.001
Monopsyllus indages	11	FLO	0.61	14.1	0.01
Monopsyllus sciurorum	10	FLO	0.77	27.2	0.001
Neopsylla teratura	8	FLO	0.89	50.3	0.001
		RO	0.71	14.6	0.01
Nosopsyllus turkmenicus	11	FLO	0.38	5.4	0.04
Oropsylla alaskensis	5	RO	0.87	19	0.02
Palaeopsylla soricis	29	FLO	0.16	5.3	0.02
Paradoxopsyllus repandus	5	FLO	0.99	301.8	0.001
Rhadinopsylla altaica	5	FLO	0.99	6665.2	0.00001
Rhadinopsylla dahurica	6	FLO	0.94	63.6	0.001
Xenopsylla gerbilli	13	FLO	0.37	6.4	0.02
Xenopsylla hirtipes	7	FLO	0.78	18.2	0.01

Slopes of all regressions are positive.

$F_{1,117} = 7.4$, $P < 0.05$). When the confounding effect of phylogeny was accounted for by using the method of independent contrasts, the positive relationship between average overlap of geographical ranges and average relative abundance again proved to be true ($r = 0.23$, $P < 0.01$; Fig. 4b).

4. Discussion

On a geographical scale, interactions between given species are not homogeneous, with many species often existing in some areas in the absence of some of their interaction partners. This geographical variation provides the essential raw material for spatially structured coevolution (Thompson, 1999, 2005). Local adaptation to different interaction partners in different localities is unlikely if there is sufficient gene flow amongst populations. However, on a larger scale, if some interaction partners are more common than others, specialisation on the more frequently encountered interaction partners is possible, with selection in one locality being reinforced by similar selection elsewhere. Here, we looked for evidence that interaction frequency can influence patterns of specialisation in parasites. Our findings are based on correlations, therefore causal relationships must be inferred with caution. Still, overall our results suggest that for any given flea species, host species more commonly encountered throughout the spatial range of the flea are generally those species on which the flea does best. In addition, in comparisons amongst species, flea species exploiting mainly hosts that are frequently encountered tend to achieve higher mean abundance than flea species also exploiting rarely encountered hosts. These patterns support a role for interaction frequency in the evolution of specialisation in host-parasite systems.

Two potential caveats require some discussion. First, we had to exclude ‘specialist’ flea species from the analyses, since the intra-specific regressions we performed require at least four host species to yield meaningful results. We therefore do not know whether the trends observed here would also apply to fleas exploiting only two or three host species, though there is no reason to expect that they would not. Second, host density may be a confounding factor influencing flea abundance. It could be that commonly encountered host species are also the ones achieving higher local density, and that host density per se influences flea abundance. Indeed, positive relationships between parasite abundance and host density are a central assumption of epidemiological models (e.g., Anderson and May, 1978). The surveys from which we compiled our datasets do not provide reliable data on density of the different host species. However, the link between host density and flea abundance is far from universal. Although the abundance of some fleas has been shown to increase with host density (Kotti and Kovalevsky, 1995; Krasnov et al., 2002), abundance of other fleas either declines with increasing host density (Zhovty and Kopylova, 1957; Haitlinger, 1981; Stanko et al., 2006) or is completely unaffected by host density (Stanko et al., 2006). Therefore, variation in density amongst host species is unlikely to have systematically biased our findings.

The patterns obtained using the frequency of co-occurrences between a flea and its hosts amongst the regions surveyed, as a measure of the likelihood of encounters with particular hosts, were much clearer and stronger than those obtained using the overlap between their geographical ranges. The reason for this may be that the former measures the actual or realised frequency of co-occurrences, whereas the latter only provides an estimate of the potential for such co-occurrences. Range overlap is a coarser measure that ignores finer-scale variation in habitat types; it is possible for two species to have similar geographical ranges without actually coming into real proximity because of different microhabitat preferences (Rosenzweig, 1995; MacDonald, 2001). Thus, results based on the actual proportion of localities where a flea co-occurs with a host species most likely provide a more representative picture of the importance of interaction frequency.

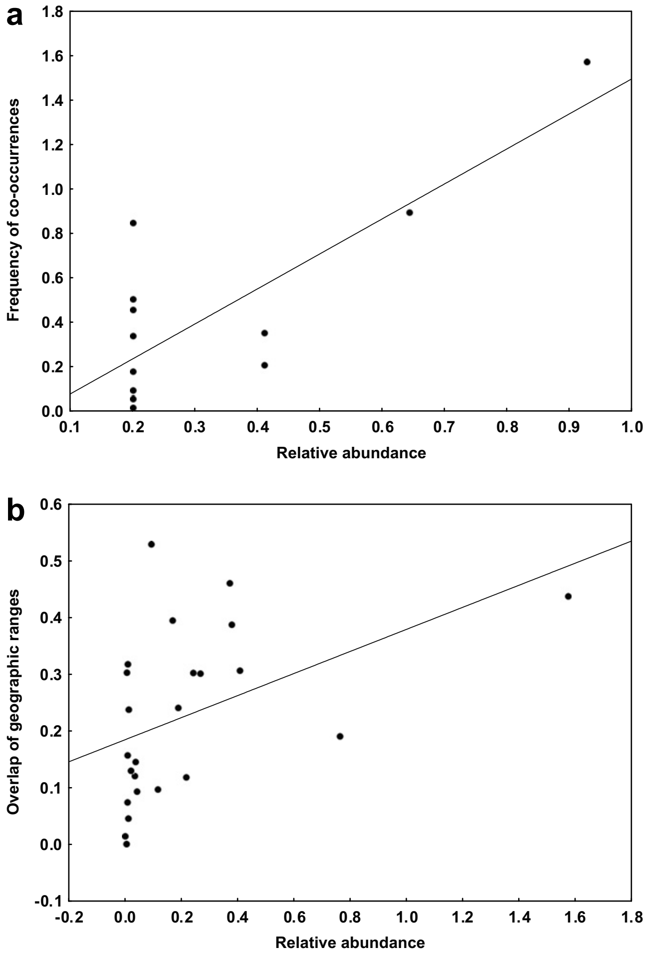

Fig. 2. Relationship between (a) relative abundance of the flea, *Megabothris advenarius*, on its 13 host species and the frequency of local co-occurrences between flea and host, and (b) relative abundance of the flea, *Citellophilus tesquorum*, on its 24 host species and range overlap between flea and host. All variables are arcsin-transformed.

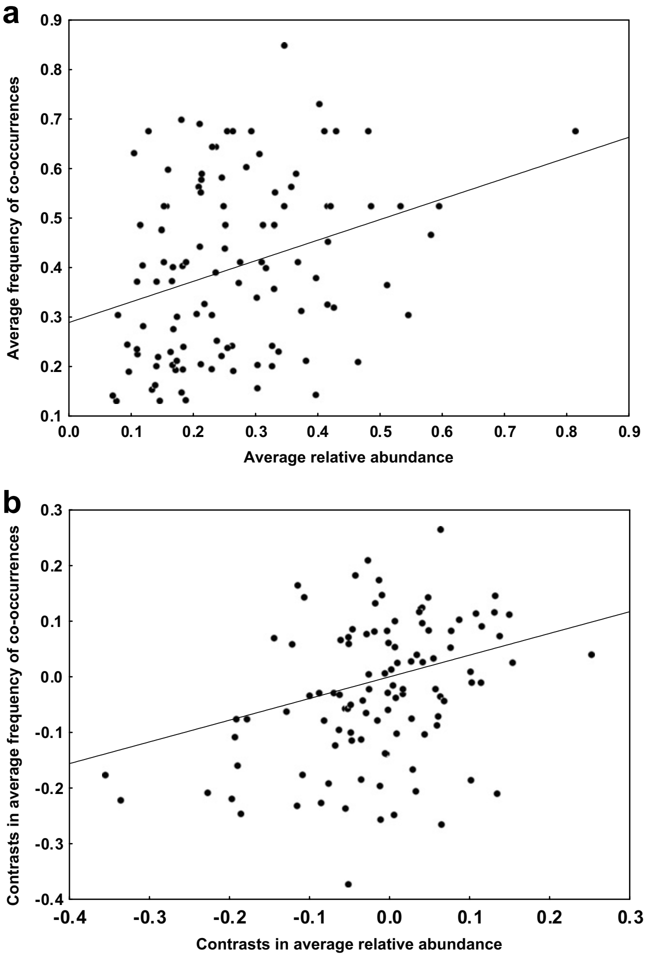

Fig. 3. Interspecific relationship between mean relative abundance of a flea and the average frequency of local co-occurrences between the flea and its hosts across 107 flea species using conventional statistics (a) and independent contrasts (b).

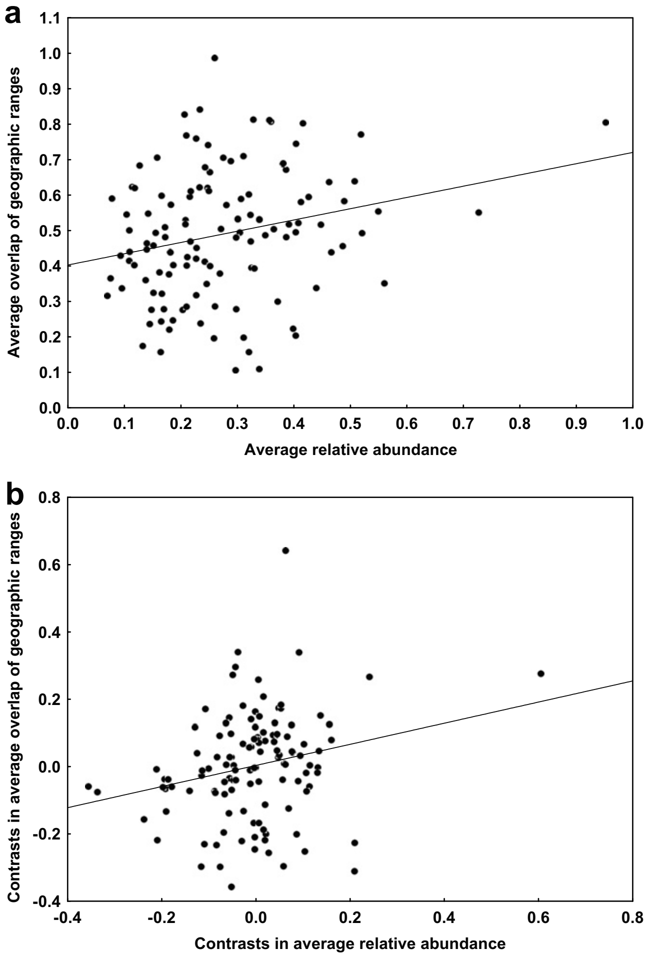

Fig. 4. Interspecific relationship between mean relative abundance of a flea and the average overlap between flea and host geographical ranges across 121 flea species using conventional statistics (a) and independent contrasts (b).

The determinants of flea abundance in a particular region or on a particular host species include more than the suitability of the host for the flea. Because fleas spend a significant portion of their life off the host, i.e. in its nest or burrow, physical factors such as temperature and humidity also play major roles in flea reproduction and survival (see Silverman and Rust, 1983; Metzger and Rust, 1997; Krasnov et al., 2001a,b). There is substantial visiting and sometimes even sharing of burrows between different mammal species (Kucheruk, 1983), and local climatic conditions will likely be similar for all host burrows present in one region. We might thus expect that these local factors, which are independent of the frequency of co-occurrences between a flea and its many hosts, would override any influence of interaction frequency. The fact that a general effect of interaction frequency on flea abundance nevertheless emerges from our analysis suggests that it is an important driver of specialisation patterns in fleas.

Fleas parasitic on small mammals are often capable of exploiting several host species (Marshall, 1981; Poulin et al., 2006). Despite being generalists, they still demonstrate a certain degree of specialisation, since there is usually a clear distinction between the relative abundance they achieve on their principal host versus what they achieve on their auxiliary hosts. In other words, a large proportion of the flea population is concentrated on only one or a few of its many potential host species. Earlier, it has been shown that host taxonomy is in part responsible for this common pattern of host use by fleas (Krasnov et al., 2004c). The abundance achieved by a flea on an auxiliary host species tends to decrease as a function of the taxonomic or phylogenetic distance between that auxiliary host and the flea's principal host. This influence of host taxonomy appears independent of that of interaction frequency, however. This is because the geographical ranges of closely related host species, which determine how likely they are to co-occur with particular fleas, do not overlap more than those of more distantly related species, for most major taxa of small mammals (Fitzpatrick and Turelli, 2006). Therefore, two host species with similar frequencies of co-occurrences with a flea, are not necessarily also closely related; both the phylogenetic history of a host species and its current spatial co-occurrence with a parasite will independently influence patterns of host use and specialisation.

The influence of interaction frequency with hosts across the whole geographical range of a parasite not only provides evidence of the importance of the spatial component of coevolution. It also means that the local structure of parasite populations and communities is determined by extrinsic processes. In other words, the unequal way in which parasites use their many host species, i.e. the uneven distribution of parasite individuals within a flea population amongst the suitable host species that are locally available, might simply be the local manifestation of large-scale evolutionary phenomena. This contrasts with the localised patterns observed amongst phytophagous insects (Fox and Morrow, 1981), in which inter-population gene flow may be less extensive than in parasites of mobile vertebrates. The generality of this conclusion will need to be evaluated with other host-parasite associations.

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