

Relationships between parasite abundance and the taxonomic distance among a parasite's host species: an example with fleas parasitic on small mammals

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Abstract

Opportunistic parasite species, capable of exploiting several different host species, do not achieve the same abundance on all these hosts. Parasites achieve maximum abundance on their principal host species, and lower abundances on their auxiliary host species. Taxonomic relatedness between the principal and auxiliary host species may determine what abundance a parasite can achieve on its auxiliary hosts, as relatedness should reflect similarities among host species in ecological, physiological and/or immunological characters. We tested this hypothesis with fleas (Siphonaptera) parasitic on small Holarctic mammals. We determined whether the abundance of a flea in its auxiliary hosts decreases with increasing taxonomic distance of these hosts from the principal host. Using data on 106 flea species from 23 regions, for a total of 194 flea–locality combinations, we found consistent support for this relationship, both within and across regions, and even after controlling for the potentially confounding effect of flea phylogeny. These results are most likely explained by a decrease in the efficiency of the parasite's evasive mechanisms against the host's behavioural and immune defences with increasing taxonomic distance from the principal host. Our findings suggest that host switching over evolutionary time may be severely constrained by the coupling of parasite success with the relatedness between new hosts and the original host.

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1. Introduction

The degree of host specificity varies greatly among parasites from highly host-specific to highly host-opportunistic parasite species (Marshall, 1981; Combes, 2001). Nevertheless, even a highly host-opportunistic parasite varies in its abundance among different host species. This variation in the abundance of a parasite among multiple hosts has led to a classification that distinguishes true and accidental hosts among the entire host spectrum of

a parasite, true principal and true exceptional hosts among true hosts, and preferred and normal hosts among principal true hosts (see Marshall, 1981 and references therein).

The uneven distribution of a parasite population among different host species may have important ecological and evolutionary implications. For example, if the difference in the abundance of a parasite in different hosts stems from different fitness rewards in these hosts, then different hosts play different roles in the long-term persistence of a parasite population. In such cases the parasite population would thus depend mainly on one or a few key host species. At the evolutionary scale, differences in the probability of a parasite of landing in one host species rather than in another

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host species would allow natural selection to favour specific adaptations that would allow the parasite to exploit successfully those host species that are most likely to be encountered. This can shape the co-evolutionary process between hosts and parasites.

The reasons why parasites are distributed unevenly among different host species are sometimes quite obvious. This can be, for example, because of the different reproductive (e.g. Krasnov et al., 2002) or exploitation (e.g. Krasnov et al., 2003) performance of a parasite in different host species. However, this parasite-centred approach does not allow a full understanding of those host parameters that affect the distribution of parasite individuals among their different host species. Given that the abundance of a consumer in a habitat can be considered as a measure of its efficiency of resource exploitation (Morris 1987), abundance of a parasite in a host species can be seen as a measure of its efficiency of host exploitation. Consequently, variation in the abundance of a parasite among its different host species may also reflect parasite specialisation. Indeed, the prevalence, intensity and/or abundance of a parasite are, usually, highest in one host species, the principal host, and lower among the auxiliary host species (sensu Dogiel et al., 1961; Marshall, 1981); yet it often varies greatly among the auxiliary hosts. 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. The great difference in parasite abundance among different auxiliary hosts can be explained by different degree of similarity between the principal hosts and the various auxiliary hosts (Poulin, 2004). For example, different auxiliary hosts can be more similar or less similar to the principal host in their availability to a parasite (e.g. co-occur or not co-occur in the same habitat) or in their compatibility for a parasite (sensu Combes, 2001) (e.g. in blood biochemistry or in patterns of behavioural or immune defences).

Phylogenetic relatedness among species is generally a good reflection of their overall life-history and ecological similarity (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Silvertown et al., 1997). In other words, phylogenetically close host species are likely more similar in their ecological, physiological and/or immunological characters than phylogenetically more distant host species. Colonisation success of a new host species by a parasite would, therefore, depend on the phylogenetic proximity of the new species to the original host and this should be reflected by the abundance of the parasite in this new host relative to its abundance on the original host.

Assuming that taxonomy reflects phylogeny and that the taxonomic distance between species is a measure of their phylogenetic relatedness, Poulin (2004) tested recently the hypothesis that the differences in relative infection levels by a parasite among its auxiliary hosts are proportional to the taxonomic distance between the respective auxiliary hosts and the parasite's principal host in metazoan parasites of

freshwater fish. Surprisingly, it was found that taxonomic distance between the auxiliary hosts and the principal host had no real influence on infection levels in auxiliary hosts, measured as either prevalence, intensity or abundance. Negative results obtained for a limited range of parasite taxa cannot be taken as convincing evidence for the general independence of relative infection levels from taxonomic relationships among host species. Consequently, this hypothesis remains to be further tested in other environments and/or for other host-parasite systems.

In this study, we test the hypothesis that taxonomic distance between the auxiliary hosts and the principal host of a parasite influences its abundance in the auxiliary hosts using data on fleas (Siphonaptera) parasitic on small Holarctic mammals. Fleas are obligate blood-sucking ectoparasites most abundant and diverse on small to medium-sized burrowing species of mammals, with only about 6% of the almost 2000 known species parasitising birds (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, being found on two or more host genera of the same family, or on two or more host families, or even crossing between mammalian orders. The specific objective of this study was to determine whether the abundance of a flea in its auxiliary hosts decreases with increasing taxonomic distance of these hosts from the principal host.

2. Materials and methods

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora, Lagomorpha and Rodentia) in 23 different regions (Table 1). These sources provided data on the number of individuals of a particular flea species found on a number of individuals of a particular host species. 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 in a given region were included.

We used the mean number of flea individuals per individual host of a given species as a measure of flea abundance. Other measurements of infection level, such as prevalence and intensity of flea infestation, were not available for the majority of the regions considered. 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 among host species may result in confounding variation in estimates of flea abundance. In addition, hosts of different size can support different number of fleas. To ensure that variation in among-host sampling effort and body size did

Table 1
Data on small mammals and fleas in 23 regions used in the analyses

Region	Number of host species	Number of flea species	Source
Adzharia, southern Caucasus	12 (8391)	8 (1566)	Alania et al. (1964)
Akmolinsk region, northern Kazakhstan	8 (264)	6 (1490)	Mikulín (1959a)
Altai mountains	18 (1454)	8 (1944)	Sapegina et al. (1981)
California	7 (1369)	3 (1083)	Davis et al. (2002)
Central Yakutia	4 (544)	3 (169)	Elshanskaya and Popov (1972)
Dzhungarskyi Alatau, Kazakhstan	14 (5194)	11 (4680)	Burdelova (1996)
East Balkhash desert, Kazakhstan	10 (461)	7 (1129)	Mikulín (1959b)
Idaho	11 (3884)	5 (9485)	Allred (1968)
Kabarda, northern Caucasus	9 (1642)	8 (1559)	Syrvacheva (1964)
Khabarovsk region, southern Russian Far East	7 (6588)	5 (1791)	Koshkin (1966)
Kustanai region, northwestern Kazakhstan	8 (159)	6 (675)	Reshetnikova (1959)
Moyynkum desert, Kazakhstan	10 (45,433)	12 (255,866)	Popova (1967)
Mongolia	4 (1733)	3 (1731)	Vasiliev (1966)
Negev desert, Israel	9 (1053)	3 (2869)	Krasnov et al. (1997) and unpublished data
North Asian Far East	12 (1585)	6 (905)	Yudin et al. (1976)
North Kyrgyzstan	10 (4739)	4 (1342)	Shwartz et al. (1958)
North New Mexico	16 (8555)	9 (11,802)	Morlan (1955)
Novosibirsk region, southern Siberia	17 (1892)	16 (3924)	Violovich (1969)
Slovakia	12 (9921)	6 (9546)	Stanko et al. (2002)
Tarbagatai region, eastern Kazakhstan	8 (199)	4 (171)	Mikulín (1958)
Turkmenistan	14 (235,968)	25 (908,150)	Zagniborodova (1960)
Tuva	11 (2509)	16 (22,539)	Letov et al. (1966)
Volga-Kama region	20 (33,380)	20 (31,555)	Nazarova (1981)

Numbers in parentheses represent the total numbers of sampled individuals (data include mammal species in which no less than 10 individuals were examined, and flea species that were found in at least four different host species in a region).

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 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 ($r^2=0.0002-0.27$, $F_{1,2-1,16}=0.003-0.20$, $P>0.3$ for all). Consequently, we used non-corrected data in subsequent analyses.

We identified the principal host for each flea species in each region, i.e. the mammal species in which the flea attained its highest abundance. Other host species were considered as auxiliary hosts. Abundance of a flea in a host was in each case expressed as a relative value, i.e. expressed as a proportion of the value observed in 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 allows the comparison of abundance values that vary greatly in absolute terms among the different parasite species. The relative values were arcsine-transformed prior to analyses.

The taxonomic distance between the principal host and each auxiliary host was calculated as the path length linking the two host species in a Linnean taxonomic tree where each branch length is set equal to one unit of distance (Poulin, 2004). This type of taxonomic distance measure is commonly used in biodiversity studies that take into account the taxonomic distinctness of species in an assemblage (Izsák and Papp, 1995; Ricotta, 2004). Mammalian species were placed within a taxonomic hierarchy with five levels

above the species, i.e. genus, subfamily, family, order, and class (Mammalia), based on the taxonomic classification of Wilson and Reeder (1993). Thus, the greatest distance between an auxiliary host and the principal host was thus 10 units when they belonged to different orders, and the shortest distance between the two hosts was 2 units when they belonged to the same genus.

The influence of taxonomic distance between the auxiliary hosts and the principal host (five groups, corresponding with distances of 2, 4, 6, 8, and 10 units) on relative abundance of a flea in auxiliary hosts was analyzed using one-way analysis of variance (ANOVA). Principal hosts (taxonomic distance of zero) were excluded from the ANOVAs because including them created a false significant effect: by definition (see above) they are the hosts with the highest abundance values. The present analyses focuses on how these measures vary among auxiliary hosts only. First, we included all auxiliary hosts in the analysis. Then, we ranked auxiliary hosts from those where a flea species was most abundant to those where it was least abundant for each flea species in each region. To determine if there was any difference in the effect of the taxonomic distance between principal and auxiliary hosts on the abundance of a flea in the auxiliary host among auxiliary hosts of different rank, we sequentially removed higher ranked hosts from the data pool and ran ANOVAs until the significance of the effect disappeared. We did not use any correction of alpha-level (e.g. Bonferroni approach). This approach has been criticised by statisticians and ecologists

in recent years, because it often leads to the incorrect acceptance of the false null hypothesis when multiple comparisons are in fact independent of one another (Garcia, 2004; Moran, 2003; Perneger, 1998; Rothman, 1990) as is the case in our study.

In addition, we conducted separate regression analysis in which we treated taxonomic distance as a continuous variable and regressed the relative abundance of fleas against it.

Each host–flea–region combination was treated as an independent data point. Some host and flea species occurred in more than one region, and were used in the analyses more than once. Initially, each flea species–region combination was treated as an independent observation. A preliminary analysis in which average values for each flea species were used instead provided similar results. Nevertheless, treating values of relative abundance and taxonomic distance between hosts calculated for different flea species as independent observations can introduce a bias in the analysis. To control for the effects of flea phylogeny, we used the method of independent contrasts (Felsenstein, 1985). The phylogenetic tree of fleas was derived from the taxonomy based on morphological characters (Hopkins and Rothschild, 1953, 1962, 1966, 1971; Traub et al., 1983) and the cladistic tree of flea families (Medvedev, 1994, 1998).

We used the method of independent contrasts (Felsenstein, 1985) to evaluate the effect of taxonomic distance between the principal host and either the first ranked or the last ranked auxiliary host (see above). The measures of relative abundance and between-host taxonomic distance for flea species that occurred in more than one region were averaged across regions. To compute independent contrasts, we used the PDAP:PD TREE program (Garland et al., 1993; Midford, P.E., Garland, T. Jr, Maddison, W., 2003. PDAP:PD TREE package for Mesquite, Version 1.00. http://mesquiteproject.org/pdap_mesquite/index.html) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison, W.P., Maddison, D.R., 2004. Mesquite: a Modular System for Evolutionary Analysis. Version 1.02. <http://mesquiteproject.org>). Pairs of sister branches that diverged long ago can likely produce 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. To test for the correlation between flea relative abundance and taxonomic distance between the principal and the auxiliary host, we regressed standardised contrasts of relative abundance on standardised contrasts of taxonomic distance using major axis regression forced through the origin (Garland et al., 1992; Pagel, 1992).

3. Results

Across the 23 regions, there were a total of 194 flea species–region combinations. These associations involved 106 flea species, each present in one to eight localities. Overall, there were 1334 host–flea species associations (194 involving principal hosts and 1140 involving auxiliary hosts) for the analysis of the entire range of auxiliary hosts, and 106 host–flea species associations for analyses of both the first and the last auxiliary hosts using independent contrasts.

Abundance of fleas in their main auxiliary hosts was on average less than 50% that in the principal host (Fig. 1). In general, the highest values of relative abundance were observed in auxiliary hosts that were taxonomically close to the principal host (Fig. 2). Taxonomic distance between the auxiliary hosts and the principal host affected significantly the abundance of fleas in auxiliary hosts ($F_{4,1125}=26.12$, $P<0.0001$). Furthermore, this significant effect remained after consecutive removal of the first to seventh (ranked according to relative flea abundances) auxiliary hosts from the analysis ($F_{4,931-4,144}=18.10-4.03$, $P<0.005$ for all) and disappeared only when auxiliary hosts of ranks 1–8 were removed ($F_{4,99}=0.82$, $P=0.51$). Although these last results may be influenced by the sequential decrease in degrees of freedom left in the analysis, Figs. 1 and 2 suggest that the differences between lowly-ranked hosts are indeed small.

When the effect of taxonomic distance from the principal host on relative abundance of fleas in the auxiliary hosts was analyzed for each region separately, the significant influence was found in 14 of 23 regions (Table 2).

If, instead of being treated as a categorical variable (five groups corresponding with distances of 2, 4, 6, 8, and 10 units), taxonomic distance was treated as a continuous variable, and relative abundance of fleas was regressed

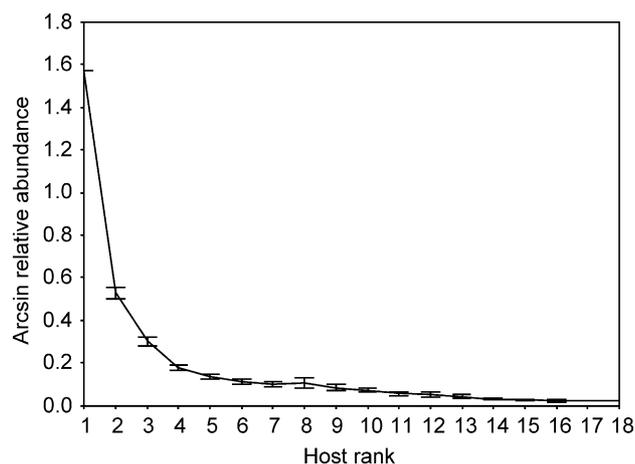


Fig. 1. Mean (\pm SEM) abundance (arcsin-transformed) of fleas in their mammalian hosts, as a function of host rank. Host species are ranked from the one in which flea abundance is highest (principal host, rank 1) to the host species in which it is lowest. Abundance values are expressed as a proportion of the value observed in the principal host. Sample sizes are 194 for the first four ranks and then decrease rapidly in further ranks.

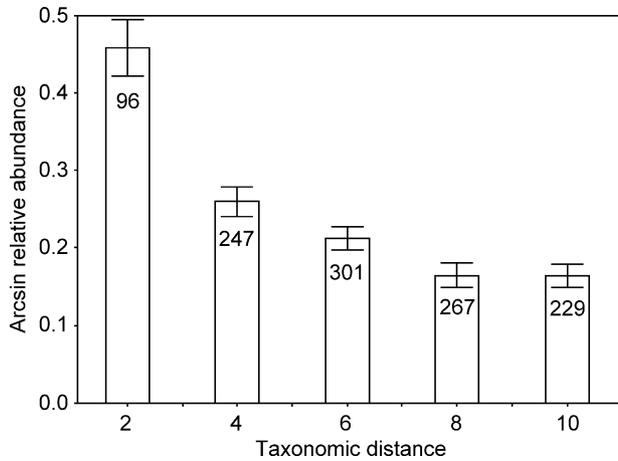


Fig. 2. Mean (\pm SEM) abundance (arcsin-transformed) of fleas in their auxiliary host species, as a function of the taxonomic distance between the auxiliary hosts and the principal host. Abundance values are relative, i.e. expressed as a proportion of the value observed in the principal host. Numbers on the bars indicate sample sizes.

against it, the resulting negative relationship was significant ($F_{11,128}=74.28$, $P<0.001$), although taxonomic distance between the principal host and an auxiliary host was a weak predictor of the relative abundance of a flea in the latter host ($r^2=6.2\%$).

Regression analyses using independent contrasts of flea relative abundance in the first auxiliary host and taxonomic distance between the principal host and this auxiliary host demonstrated that these two parameters were negatively correlated ($r=-0.42$, $P<0.0001$; Fig. 3). The same was

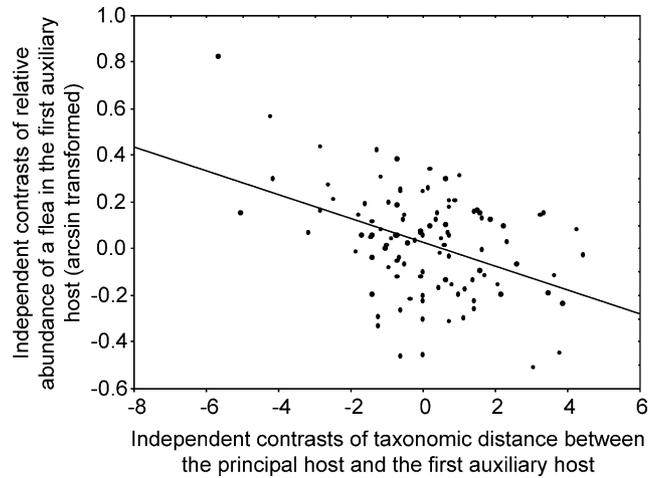


Fig. 3. Relationship between flea relative abundance in the first auxiliary host and taxonomic distance between the principal host and this auxiliary host using independent contrasts.

true for the last auxiliary host, although taxonomic distance between the principal host and the last auxiliary host explained much less variance than that between the principal host and the first auxiliary host ($r=-0.24$, $P<0.01$; Fig. 4).

4. Discussion

The results of this study demonstrate that the abundance of a flea in its auxiliary hosts decreases with increasing taxonomic distance of these hosts from the principal host. This means that every time a flea adds a new host to its host spectrum, the taxonomic affinity of this new host matters. This appeared to be true for, at least, auxiliary hosts of rank 2–7. It thus appears advantageous for a flea species to exploit taxonomically close host species. If, for example, taxonomically close host species possess similar

Table 2
Summary of ANOVAs of the effect of taxonomic distance from the principal host on relative abundance of fleas in auxiliary hosts for each region separately

Region	d.f.	F	P
Adzharia	4.33	2.99	0.04
Akmolinsk	2.28	0.002	0.99
Altai mountains	4.85	1.36	0.25
California	3.5	563.9	0.0001
Yakutia	2.5	92.9	0.04
Dzhungarskyi Alatau	4.64	3.44	0.01
East Balkhash	3.22	3.8	0.02
Idaho	4.17	4.99	0.007
Kabarda	3.37	1.06	0.37
Khabarovsk	3.13	15.71	0.0001
Kustanai	3.26	0.57	0.63
Moyynkum	3.51	5.62	0.002
Mongolia	2.5	58.76	0.04
Negev	2.11	0.38	0.70
North Asian Far East	3.26	6.67	0.001
North Kyrgyzstan	3.12	1.23	0.34
New Mexico	4.36	3.63	0.01
Novosibirsk	4.107	2.81	0.02
Slovakia	3.38	0.84	0.47
Tarbagatai	2.11	1.64	0.2
Turkmenistan	3.161	1.10	0.34
Tuva	4.79	5.98	0.001
Volga-Kama	4.173	6.43	0.0001

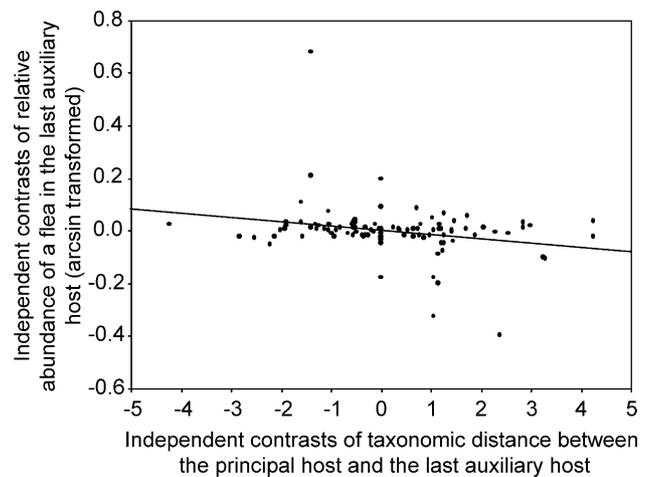


Fig. 4. Relationship between flea relative abundance in the last auxiliary host and taxonomic distance between the principal host and this auxiliary host using independent contrasts.

behavioural or immune defences, a flea could invest less by adapting to a restricted set of host immune defences than it would if its hosts were distantly related and the parasite would be forced to develop multiple adaptations to cope with the array of immune defences of its several hosts (Combes, 1997; Poulin, 1998; Poulin and Mouillot, 2004). Another explanation of our results might be the greater spatial overlap among related hosts because these hosts often have similar ecological preferences (Brooks and McLennan, 1991). Consequently, their habitat distribution can be similar, so a new host encountered by a flea in the habitat of an original host is possibly a close relative of this original host and, thus, the fact that taxonomically related hosts offer fleas similar immunological and feeding conditions is, perhaps, not the main factor involved. Nevertheless, these two explanations associated with the causes of exploitation of closely related hosts are not mutually exclusive. In other words, our results can be explained in the framework of the host-encounter and host-compatibility filter concept of Euzet and Combes (1980) and Combes (1991, 2001). The host-encounter filter excludes all potential host species which a parasite cannot encounter because of ecological or geographic reasons, whereas the host-compatibility filter excludes all potential host species in which a parasite cannot survive and develop for morphological, physiological or immunological reasons. The degree of opening of both filters seems to be higher for closely related than for distant host species. However, the host-compatibility filter probably plays a more important role in the selection by a flea of auxiliary hosts closely related to its principal host than does the host-encounter filter, because taxonomic relatedness between host species does not always determine their similarity in habitat distribution and ecological preferences (Losos et al., 2003; Price et al., 2000).

Nevertheless, successful colonisation of new hosts by fleas and other ectoparasites is not necessarily restricted to taxonomically related host species. Indeed, most studies of cophylogeny of host–parasite associations have demonstrated that association by descent (which is indicated by congruence of host and parasite phylogenies) is not necessarily the norm and that the common history of hosts and parasites is complicated by evolutionary events other than cospeciation, such as host switching (Beveridge and Chilton, 2001; Johnson et al., 2002; Paterson et al., 1993; Roy, 2001). Furthermore, the evolutionary history of mammal–flea associations has been shown to involve mainly association by colonisation with frequent host switching rather than association by descent (Krasnov and Shenbrot, 2002; Lu and Wu, 2003). This is also true for other host–ectoparasite systems (e.g. Barker, 1991; Johnson et al., 2002). However, the results of this study suggest that host switching may be constrained by host taxonomy in the coevolutionary history of mammal–flea associations.

The decrease in the abundance of a flea on its auxiliary hosts with increasing taxonomic distance of these hosts

from the principal host found in this study is in sharp contrast to the findings of Poulin (2004) for metazoan parasites of fish. Taxonomic distance between host species appears to be important for fleas parasitic on mammals but not for several taxa of fish parasites. There could be several factors contributing to this discrepancy.

First, it could simply be due to a lack of statistical power in the analysis of fish parasites where the number of parasite species–locality combinations was much lower (29 parasite species, 47 parasite species–locality combinations, 285 host–parasite species associations versus 106 flea species, 194 flea species–region combinations, 1334 host–flea species associations). Second, if the greater spatial overlap between related hosts is the main explanation of why fleas encounter taxonomically related hosts more often than they encounter other hosts, then perhaps the reason that the fish parasites show a different pattern is that they are more likely to encounter an unrelated host than are the parasites of burrowing hosts.

Third, the difference might arise from differences in the way these parasites infect their host. Helminths of fish are acquired mainly via ingestion of an infected prey item, whereas fleas attach actively to the external surfaces of their host. Fleas use various cues to find their hosts including vibration, increased concentration of CO₂, increased temperature, light (Benton and Lee, 1965; Cox et al., 1999; Humphries, 1968) as well as host odour (Crum et al., 1974; Vaughan and Mead-Briggs, 1970). Moreover, fleas appeared to be able to distinguish between different host species using an odour cue (Krasnov et al., 2002). In contrast to fleas, natural selection in fish helminths may favour tolerance to a broader set of living conditions because they have little choice in what host species they will end up parasitising, and this could manifest itself in reduced differences in abundance among different host species.

Fourth, the patterns of immune responses mounted by the hosts against these parasites may also explain the difference between fish helminths and fleas of mammals. Fleas are perhaps exposed to stronger or more specific immune attacks because of their intimate association with host blood, the site of major immune defence systems, and skin associated lymphoid tissues (SALT), the complex of cells responsible for immune response at the cutaneous interface (Streilein, 1990; Wikel, 1996). Their adaptations to evade the attacks of the immune system of their principal host may not be efficient against the immune responses of taxonomically distant hosts, and therefore, they cannot achieve high abundances on these hosts. Indeed, Studdert and Arundel (1988) reported a severe allergic reaction in cats which hunted rabbits infested with the rabbit flea *Spilopsyllus cuniculi*. The severity of these symptoms indicated that cats had a much higher response to rabbit fleas than rabbits did and than cats had to the cat flea *Ctenocephalides felis* with which they were normally infested. However, the immune responses of different mammals against different fleas are poorly known and remain to be studied (Jones, 1996).

Immune responses against intestinal helminths in fish are probably weaker and less specific, perhaps not differing as much among hosts, even taxonomically distant ones. In addition, many fish helminths have been shown to evade fish immune surveillance by migration inside the host body to subvert and lessen the toxic effects of the immune response to invasion (see review in Secombes and Chappel, 1996), whereas fleas apparently lack such evasion strategies.

Finally, behavioural defence against fleas is well developed among mammalian species, whereas behavioural defence in fish is much more limited. Indeed, mammalian autogrooming is an effective tool against ectoparasites (Hinkle et al., 1998; Mooring et al., 2004). As a response, fleas develop specific anatomical features such as sclerotinised helmets, ctenidia, spines and setae which anchor the flea within the host fur to resist the host's grooming effort (Traub, 1985). Furthermore, the development of these anatomical features is correlated with particular characteristics of the host's fur and grooming pattern (Traub, 1985). Fur structure and grooming pattern are similar among taxonomically close mammalian species (Berridge, 1990; Sokolov, 1973). Consequently, the patterns of sclerotinised features and grooming-evasion behaviour of a flea species are likely more effective against the behavioural defences of taxonomically close than taxonomically distant host species.

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