

13 Patterns of host specificity in parasites exploiting small mammals

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1 Introductory remarks

Host specificity is one of the most fundamental properties of parasitic organisms. In simple terms, host specificity can be defined as the number and identity of host species that are used by a parasite population. Parasites that are highly host-specific will occur in a single host species, whereas generalist parasites will be dispersed unequally among individual hosts from several different species. From an evolutionary perspective, host specificity reflects the parasite's historical associations with its hosts (Brooks and McLennan 1993; Page 2003). The range of host species currently used by a parasite provides strong clues about the identity of the animal that served as host to the ancestral parasite, and their number provides an indication of whether the parasite has the ability to expand its host range by colonizing new species. Host specificity also relates to other evolutionary phenomena, such as the probability of parasite extinction (Koh et al. 2004). From an ecological perspective, host specificity mirrors the diversity of resources used by a parasitic organism, or the breadth of its niche (Futuyma and Moreno 1988). Thus, it allows one to make rough predictions about the likelihood that an introduced parasite species will become established and spread in a new ecosystem.

In this chapter, we will first briefly look at some general ecological features of small mammal hosts, and discuss whether these features should favour low or high host specificity in the parasite species exploiting small mammals. We will then briefly examine patterns of host specificity among species of helminth and arthropod parasites of small mammals, using the limited evidence available at present. Then, we will review the evolutionary forces that can select for either high or low host specificity, and the processes that allow a parasite to add new host species to its range. Finally, we will take advantage of a series of recent comparative studies on the

fleas parasitic on small mammals, to address some fundamental questions about host specificity. Our aim in this chapter is not to provide an exhaustive review, but rather to highlight general patterns and the key processes that are likely to underpin those patterns.

2 Key ecological features of micromammals

Although they belong to different orders (i.e., Rodentia, Insectivora, Lagomorpha), small mammals do share several ecological traits. These traits are not possessed by every single micromammal species, but as a general rule, they do characterize the vast majority of micromammals.

First, micromammals, as their name implies, are small-bodied and they have short lifespans. In other words, compared to other mammals, they are smaller (generally less than 5 kg) and live short lives (less than 5 years). Second, again when compared with other mammals, they are characterized by high reproduction rates (i.e. high numbers of offspring per unit time) and high population densities. However, population densities of micromammals can fluctuate widely, both seasonally and from year to year. The combination of small body size, short lifespan and fluctuating population density means that as a resource base for parasites, micromammals may be unstable and unpredictable. Studies on fish parasites suggest that high host specificity is favoured only on stable, predictable resources, such as large-bodied and long-lived host species (Sasal et al. 1999; Desdevises et al. 2002). We might thus expect that, as a rule, parasites of micromammals are less host-specific than those exploiting larger, longer-lived mammalian hosts with more stable population densities.

The third main feature of micromammals concerns their habitat use and social structure. Small mammals are generally territorial, living in burrows or in nests within tree cavities. Whereas these burrows or nests represent ideal foci of parasite transmission among members of the same host species, this sort of habitat use limits opportunities for parasite transmission among different species. Unlike some other mammals, such as ungulates of different species that regularly gather around water holes on the African savannah, or bats of different species that roost together every night, most rodents and other micromammals do not come into contact with other species on a regular basis. This would constrain host-switching by parasites, and may lead to generally high levels of host specificity.

Thus, some features of micromammals seem likely to promote low levels of host specificity, relative to parasites of other mammals, whereas others appear likely to favour stricter host specificity. No comparative study

to date has attempted to untangle the potential influences of these host traits on the evolution of host specificity. Clearly, other variables will be involved. For instance, the structural complexity of the habitat can influence the dispersal, and thus the colonising abilities, of parasites. Also, features of the parasites themselves, such as their mode of transmission, determine to a large extent whether the parasite will be highly specialized or not. For instance, among parasites of primates, those transmitted by sexual or other physical contact are highly specific, with two-thirds only known to infect a single host species and none capable of infecting host species belonging to different families (Pedersen et al. 2005). In contrast, parasites using intermediate hosts and transmitted via food are much less specific, with less than half restricted to a single host species, and more than a quarter exploiting hosts belonging to different mammalian orders (Pedersen et al. 2005). Nevertheless, it remains to be seen how much the features of small mammal hosts have contributed to the evolution of host specificity in their parasites.

3 General patterns of host specificity

Assessing levels of host specificity shown by parasites in natural systems requires an account of which host species are used among those that are potentially available to a parasite. Three important issues need to be considered before we provide an illustration of patterns of host specificity among parasites of micromammals.

The first issue concerns the exact operational definition of host specificity, the one that tells us exactly how to measure host specificity. The simplest definition is just the number of host species used by a parasite, from the list of host species available within a given area. Because it is easy to compute, this measure of host specificity is by far the most widely employed in the literature. However, it assumes that all host species used by a parasite are equal, whereas in fact they generally differ on two fundamental levels, and the mere number of host species used fails to capture these differences. First, from an ecological perspective, some host species are used more intensely than others. The prevalence, intensity or abundance of infection by a particular parasite usually varies widely among its host species, even within the same locality. Rohde (1994) proposed an index of specificity, based on the number of parasite individuals found in each host species, that takes these ecological differences into account. Second, from a phylogenetic perspective, some of the host species used by a parasite are likely to be closely related, whereas others are only distantly related. A

parasite exploiting congeneric host species can be said to be more host-specific than one exploiting the same number of host species but from different families. Parasites with low host specificity are those capable of broad taxonomic “jumps” during their evolutionary history, regularly switching from one host species to a distantly related one. Poulin and Mouillot (2003) have proposed a useful measure of host specificity that takes host relationships into account, focusing on the average taxonomic distinctness of all host species used by a parasite species. It is even possible to combine both ecological and phylogenetic information into a single index of host specificity (Poulin and Mouillot 2005).

The second issue concerns sampling effort. High host specificity can be an artefact of inadequate sampling (Poulin 1998). Among species of parasites of freshwater fish, sampling effort explains much of the variability in host specificity: the number of known host species is strongly, positively correlated with the number of times a parasite species has been recorded in the literature (Poulin 1992). The same is true among tick species parasitic on mammals, and the distinction between highly specific and non-specific ticks may really be a distinction between rarely and frequently collected species (Klompen et al. 1996). Corrections for sampling effort are therefore necessary in any broad survey of host specificity.

The third issue is the potential impact of incorrect parasite species identification on estimates of host specificity. On the one hand, a species of parasite known to exploit several host species in a given area can in fact prove to be a complex of several species of superficially identical, highly host-specific parasites. With the recent application of molecular techniques to parasite systematics, several groups of cryptic species have been recognized where it was once thought there was a single species exploiting several host species (e.g., Hung et al. 1999; Blouin 2002; Leignel et al. 2002). On the other hand, what appears to be several related species of parasites exploiting several different host species can prove to be a single parasite species with low host specificity and whose morphology is influenced by the identity of the host species, with a resulting confusion in taxonomy. There are probably many instances in which “different” parasite species are in fact one and the same (e.g., Dallas et al. 2001), and these synonyms can also affect estimates of host specificity.

These caveats notwithstanding, a clear pattern emerges from any compilation of host specificity measures across any taxon of parasites infecting small mammals: when measured as the number of host species used, the distribution of host specificity values is typically strongly right-skewed. The majority of parasite species are highly host-specific, and there are only few true generalist species. For instance, among helminths parasitic in rodents and insectivores, between one-third and half of known parasite spe-

cies in a region are strictly host-specific and found in only one host species (Fig. 1). The majority of other helminth species use 5 or fewer host species, and only very few species use 10 or more host species (Fig. 1).

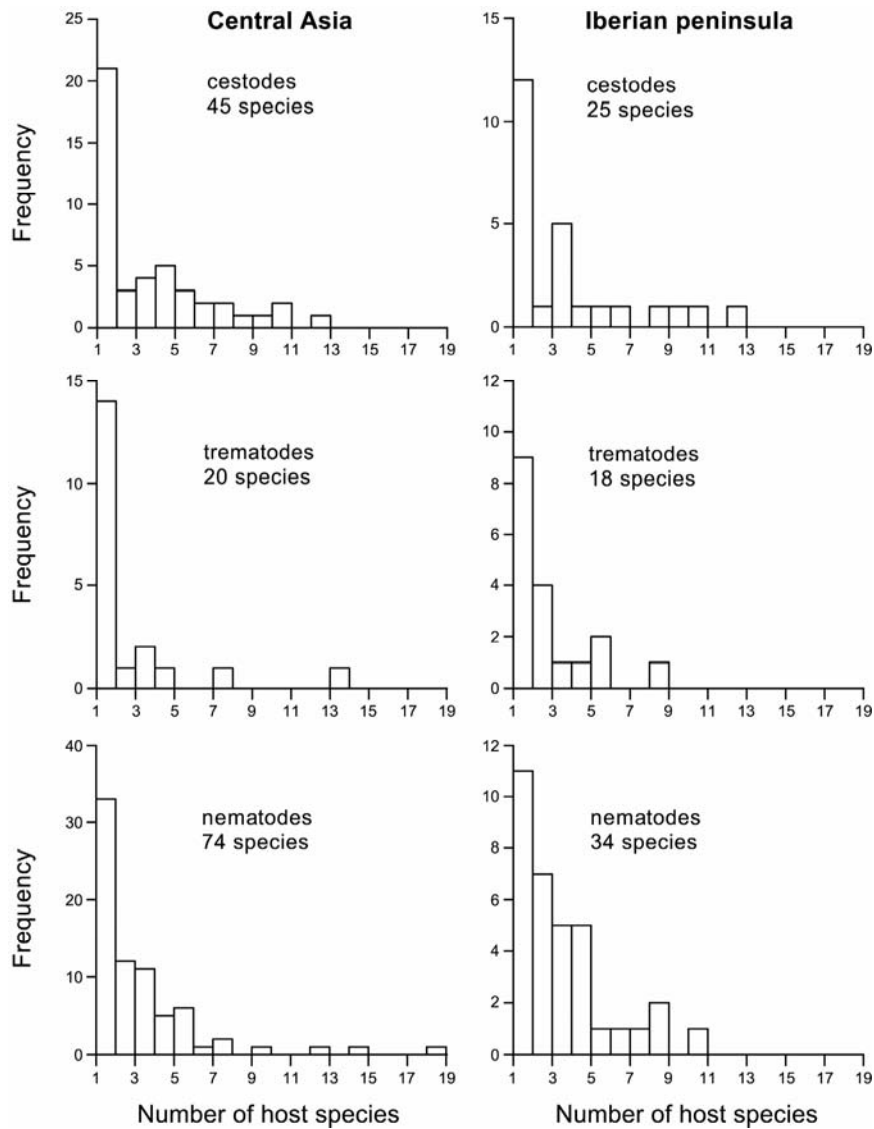


Fig. 1. Frequency distribution of host specificity (number of host species used) among species of cestodes, trematodes and nematodes parasitic in rodents and insectivores from Central Asia, and in rodents from the Iberian peninsula (data from Tokobaev 1976 and Feliu et al. 1997)

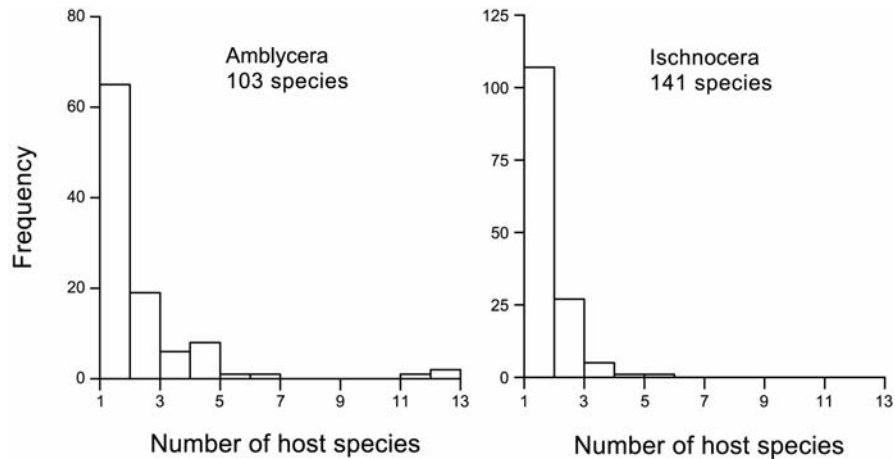


Fig. 2. Frequency distribution of host specificity (number of host species used) among all valid species of chewing lice worldwide known to parasitize rodents (the data, shown separately for the suborders Amblycera and Ischnocera, are from Price et al. 2003)

Among chewing lice ectoparasitic on rodents, the same general pattern is observed (Fig. 2). The data on chewing lice in Figure 2 come from a world checklist of host-parasite associations, as opposed from those on helminths in Figure 1, which originate from regional surveys. By considering the world fauna as the pool of potential hosts, the data on chewing lice should tend to “inflate” the numbers of host species that any given lice population could potentially use. In contrast, the data on chewing lice suggest that they might even be *more* host-specific than helminths. The vast majority of species occur on a single host species, or less frequently on two hosts (Fig. 2).

The apparently greater specificity of lice compared to helminths may be the consequence of their mode of transmission. In general, contact-transmitted parasites such as lice are expected to be more host-specific than parasites acquired via ingestion such as helminths (see Pedersen et al. 2005). This does not appear to apply to fleas, however. Among these ectoparasites of small mammals, the distribution of numbers of host species used is less right-skewed than for other parasite taxa (Fig. 3). Although many flea species are found on only one or two host species, there is a substantial number of flea species that can exploit several host species (Fig. 3). Mode of transmission is thus not necessarily constraining how many micromammal species can be used by a parasite.

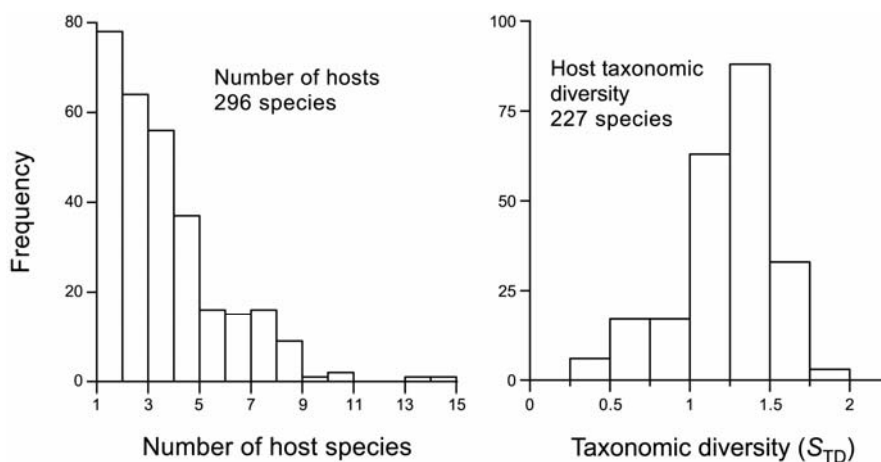


Fig. 3. Frequency distribution of host specificity among flea species parasitic on small mammals (rodents, insectivores and lagomorphs), measured as both the number of host species used and the taxonomic diversity of those host species. The latter measure is expressed as the index S_{TD} , which increases as a function of the average taxonomic distance among host species, and it is only computed for flea species with at least two host species (data from Poulin et al. 2006)

Overall, arthropod and helminth parasites of micromammals show roughly similar patterns of host specificity. Most species are very host-specific, exploiting only one, or maybe two or three, host species; nevertheless, there are also some generalist parasite species capable of exploiting between 4 and 10 host species, sometimes even more (Figs. 1-3). These general patterns are based on host specificity measured as the number of host species used. Other measures of host specificity could produce different patterns. For instance, applying a measure of the average taxonomic distinctness of host species, i.e. the index S_{TD} of Poulin and Mouillot (2003), to the flea data, generates a roughly symmetrical distribution of host specificity values (Fig. 3). This index provides a measure of the average taxonomic distance between host species, computed across all pairs of host species used; in the absence of a complete phylogeny of host species, the index serves as a good surrogate measure of host phylogenetic diversity (Poulin and Mouillot 2003). The most common values, corresponding to the peak of the distribution between values of 1 and 1.5 (Fig. 3), suggest that most flea species capable of exploiting two or more host species occur on hosts belonging either to the same genus, or to different genera within the same subfamily (see Poulin et al. 2006). Estimates of S_{TD} values for

other groups of parasites of micromammals are not currently available, but are likely to be of similar magnitude.

How do these patterns of host specificity compare with those displayed by parasites of other groups of mammals? Very little information is available for other taxa of wild mammals, or it simply has not been assembled and compiled in a way that can be used for comparisons. The only group for which there are suitable data are primates. Helminths parasitic in primates show patterns of host specificity that are not too different from those shown by parasites of micromammals. Almost half of the helminth species parasitic in primates are strictly host-specific, i.e. they use a single host species (Pedersen et al. 2005). The data in Pedersen et al. (2005) do not allow the computation of the index S_{TD} , but given that only one helminth species in ten is capable of exploiting host species outside the order Primates, the taxonomic diversity of host species used is probably roughly similar for parasites of primates and parasites of micromammals.

4 Evolutionary processes shaping host specificity

The specificity of a parasite for its host species can be seen as the outcome of both historical events and current ecological conditions. We will examine how host specificity has evolved, first by looking at historical patterns of host-parasite associations, and then at smaller-scale phenomena determining whether new host species can be colonized. We illustrate these processes with examples from parasites of micromammals wherever possible.

4.1 Macroevolutionary processes

Comparisons between the phylogeny of a group of parasites and that of their hosts can shed light on the history of their association (Brooks and McLennan 1993; Page 2003). Mirror-image phylogenies would indicate strict cospeciation between parasites and their hosts. If each time a barrier to gene flow isolates two allopatric subpopulations of hosts, it also prevents gene flow between the two newly-created subpopulations of parasites, then the parasite would be forced to cospeciate with its host. Starting from an ancestral host species with one parasite species, cospeciation will result in n species of hosts and n species of parasites. This simple scenario would produce strictly-host specific parasites. Changes in host specificity occur when there are departures from a strict cospeciation pattern.

Ultimately, there are two ways in which host specificity can decrease over time, i.e. two kinds of evolutionary events through which a parasite can add new host species to its repertoire. First, the original host species can speciate without parallel speciation of the parasite, but with the parasite still capable of exploiting both daughter host species; this would result in the parasite occurring on two related host species instead of only occurring on the single ancestral host species. For example, the parasitic nematode *Longistriata caudabullata* is commonly found in short-tailed shrews of the genus *Blarina* in North America. A mitochondrial DNA phylogeny of nematode populations from different host species shows no subdivision according to host affiliation, suggesting extensive gene flow across host species boundaries (Brant and Orti 2003). In general, however, this is probably a rare situation. Second, and probably much more frequent, the addition of new host species to a parasite's repertoire can also result from host switching, or the colonization of new host species.

Host switching can be detected by comparing host and parasite phylogenies. It causes incongruence between the topologies of the two phylogenetic trees. In the classical example, the evolutionary history of several species of two related genera of chewing lice and their hosts, members of the rodent family Geomyidae (pocket gophers), was shown to be one of rather strict cospeciation with host switching playing a very minor role (Hafner and Nadler 1988, 1990; Hafner and Page 1995). Not only is there a clear congruence between the branching patterns of host and parasite phylogenies, but the timing of speciation events in both host and parasite lineages coincides remarkably well based on evidence from rates of molecular change. Not surprisingly, these lice species display strict host specificity, most being found on a single host species. This specificity is apparent at the morphological level, from the tight coupling between the width of the head groove on the head of lice used to attach to host hair, and the diameter of host hair shafts (Fig. 4). The fit between the groove on a given louse species and the hair of its particular host species resembles that between a lock and key (Morand et al. 2000). This cospeciation pattern may be the outcome of the social structure of pocket gophers and the transmission mode of the lice, both combining to greatly limit opportunities for host switching. In contrast, host switching appears to have been very common and cospeciation almost non-existent in lice parasitic on several species of one genus of rock wallabies in Australia (Barker 1991), and, on a larger scale, across all mammalian taxa (Taylor and Purvis 2003). Thus, the hosts' social structure may be a stronger barrier to host switching than the parasites' mode of transmission in the case of pocket gophers, since lice can switch hosts readily in other mammals.

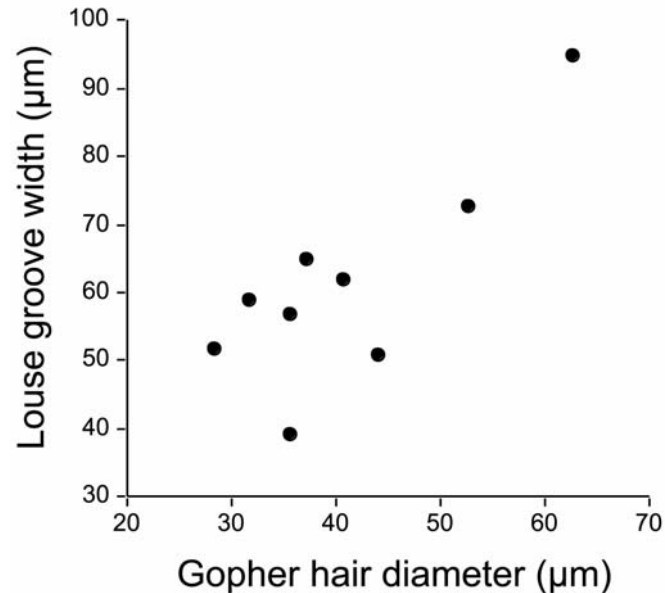


Fig. 4. Relationship between the width of the groove on the head of chewing lice and the average diameter of body hairs from their pocket gopher host species. Each point represents a different louse-gopher species combination (modified from Morand et al. 2000)

There have been few other comparisons of host and parasite phylogenies involving micromammals and their parasites. Krasnov and Shenbrot (2002) tried to reconcile the phylogenies of jerboas and their flea parasites, and concluded that host switching had been common in these host-parasite associations. They proposed that ecological and geographical factors can allow host-switching and override any tendency toward strict cospeciation expected from the transmission mode of these parasites. Brant and Gardner (2000) also concluded that rampant host switching is a better hypothesis to explain the coevolutionary history of filarioid nematodes of the genus *Litomosoides* with their hosts, which include mainly rodents but also bats and marsupials. This is not too surprising, since these nematodes are transmitted by mobile vectors, i.e. blood-sucking dipterans. Phylogeographic studies, although focused on shorter time scales, can also provide information on the evolutionary “fidelity” of parasites to their hosts. For instance, populations of the cestode *Paranoplocephala arctica* form distinct clades across their Holarctic range, showing significant congruence with similar subdivisions existing among the populations and species of their rodent hosts, lemmings of the genus *Dicrostonyx* (Wickström

et al. 2003). Similarly, populations of the nematode *Heligmosomoides polygyrus* form three genetic and geographical lineages across their European range, which are congruent with those found among the populations of their rodent host, the field mouse *Apodemus sylvaticus* (Nieberding et al. 2004). In both the nematode and the mouse, postglacial recolonization of northwest Europe came from the Iberian populations, and not from other southern populations (Nieberding et al. 2005). These results suggest that helminth parasites acquired by ingestion, like *P. arctica* and *H. polygyrus*, can evolve with micromammal hosts following a pattern consistent with cospeciation rather than rampant host switching.

To date, the few available studies on the evolutionary history of micromammals and their parasites tend to suggest that strict cospeciation is perhaps a more common pattern than rampant host switching. This may have something to do with the ecological features of small mammals, and could serve to constrain host specificity in these parasites. However, parasites with modes of transmission that can overcome these host features (such as the vector-transmitted nematodes *Litomosoides* spp.; Brant and Gardner 2000) can also evolve following different scenarios. Clearly, we need many more cophylogenetic and phylogeographic studies before any robust conclusion.

4.2 Microevolutionary processes

The above discussion focused on the macroevolutionary history of host-parasite associations and host specificity. On a microevolutionary scale, many phenomena can facilitate host switching and subsequent decreases in host specificity, or, conversely, promote greater specialization on fewer host species. We now discuss the processes by which natural selection may favour changes in host specificity.

The central question concerns the direction of selection: should we expect natural selection to generally favour increases or decreases in host specificity? There are no easy answers. Just as parasites may be selected to increase the range of hosts in which they can successfully develop, they may also sometimes face selection for greater specialization through a narrowing of their range of suitable hosts. The growth and fecundity of any given parasite vary among host species. If selection can fine-tune the mechanisms of host infection to ensure that fewer host species are encountered, then one would predict that host species in which development is suboptimal will eventually be excluded. This would result in a narrow host range comprising only host species on which parasite fitness is high. Although greater specialization on fewer host species can be advantageous, it

also links the fate of parasites to that of their hosts and can make highly host-specific parasites more prone to local extinction. There are thus pros and cons associated with both high and low host specificity. We might expect a trade-off between the ability to use many host species and the average fitness achieved in these hosts (Ward 1992). Close adaptation to one host species may only be achieved at the expense of adaptations to other host species. Given that different host species have different defense systems, investing in many counter-adaptations should have a fitness cost for the parasite: a jack-of-all-trades may be a master of none. Different parasite species may achieve greater overall fitness at different points along the continuum of strategies between the high-specificity-low-mean-abundance and low-specificity-high-mean-abundance extremes. This kind of trade-off is often used to explain the host specificity of phytophagous arthropods (Fry 1990). We will further address the trade-off issue using a study on fleas in the next section.

Assuming that lower average fitness is not constraining parasites from expanding to new host species, then what is? On microevolutionary time scales, host specificity is mainly determined by opportunities for colonization and availability of suitable host species. Opportunities can arise in many ways. Hybridisation between host species, for example, can create a genetic and ecological bridge between host species and allow the colonization of one host by parasites from the other (Floate and Whitham 1993). The intermediate ecological and physiological characteristics of hybrids may provide stepping stones facilitating host-switching between two different host species that would otherwise be too distinct to allow parasite colonization. Indeed, two studies have shown that the resistance of rodents to infections by nematodes and cestodes breaks down in hybrid zones (Sage et al. 1986; Moulia et al. 1991). In European areas where the mice *Mus musculus* and *Mus domesticus* hybridise, hybrids acquire higher parasite loads than either parent species (Fig. 5). However, hybridisation between closely related species of micromammals is probably not widespread, and this mechanism may rarely provide opportunities for host switching.

A range of immunological or physiological mechanisms serving to maintain host specificity can be identified by experimental studies. For instance, the nematode *Strongyloides ratti*, a gastrointestinal parasite of rats, has only a limited attachment success and achieves reduced fecundity in mice, even in immunosuppressed mice (Gemmill et al. 2000). Experimental selection, achieved by serial passage in mice for 18 generations, failed to improve the performance of *S. ratti* in this novel host, suggesting that factors stemming from the different physiologies of rats and mice are responsible for maintaining host specificity (Gemmill et al. 2000).

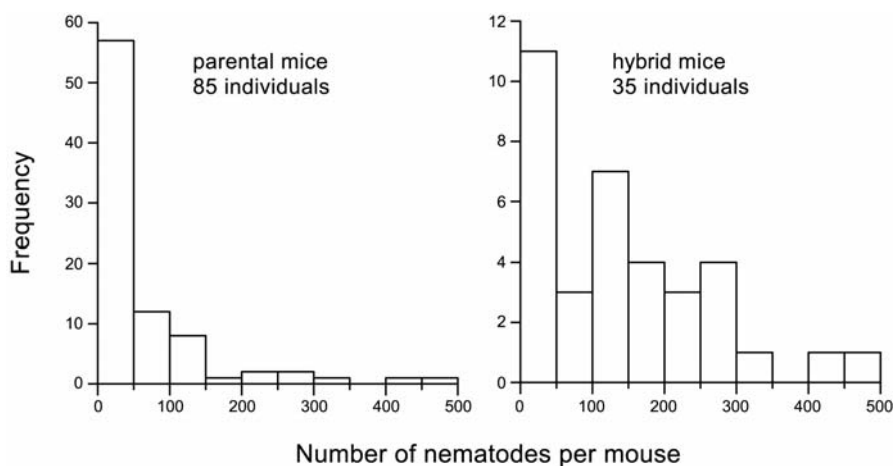


Fig. 5. Frequency distribution of numbers of parasitic nematodes per mouse, among mice belonging to either of two parental species (*Mus musculus* and *M. domesticus*), or among hybrids of these two species. All mice were collected in a Danish hybrid zone. Worms of two nematode species, *Aspicularis tetraptera* and *Syphacia obvelata*, are combined (data from Moullia et al. 1991)

Strict host specificity is therefore not always easily overcome. Recent models offer reasons for this observation. In these models, adaptation to a particular host species occurs via the fixation of alleles whose beneficial effects are host-specific; this is more rapid and more likely to occur in parasite populations restricted to that host species than in parasite populations spread among several host species (Kawecki 1997, 1998). These models predict that parasite species that begin as generalists gradually lose the ability to exploit seldom-encountered host species and eventually exclude them altogether from their range of suitable alternatives.

Kawecki's (1997,1998) models suggest that local adaptation could maintain host specificity. The selection of greater host specificity in parasites on a local scale would be apparent when comparing the specificity of different populations of the same parasite species exploiting different populations of the same host species. In a review of the literature on local adaptation by parasites, Lajeunesse and Forbes (2002) found that local adaptation is more likely to be observed in parasite species that already show some host specificity, i.e. parasites that only exploit few host species. This makes sense because generalist parasites exploiting many host species would have difficulty simultaneously tracking the changes in genotype frequencies in different local populations of their different host species. In general, though, after generations of isolation from other host genotypes,

parasites may lose the ability to infect allopatric hosts in favour of a greater specialization for the local host genotypes. Alternatively, parasites can retain the ability to infect allopatric genotypes but achieve lower fitness when exploiting them.

These ideas have not yet been tested using micromammals and their parasites. The limited evidence available, however, suggests that local adaptation of this nature, serving to promote high levels of host specificity, may not be common in nature. In the trematode *Schistosoma mansoni* parasitic in rats, although some genetic differentiation exists among populations inhabiting fragmented marshy habitats on the island of Guadeloupe, there is also evidence of much gene flow (Sire et al. 2001). This parasite uses two hosts, snail first intermediate hosts and rat definitive hosts. Rats are clearly more vagile than snails, and there is good evidence showing that exchanges of parasites among populations are indeed mediated almost entirely by rat movements (Prugnolle et al. 2005). Whether or not the parasite could infect other hosts, gene flow maintained by one host would prevent local adaptation. Studies of geographical population structure in nematodes parasitic in mammals indicate that, overall, there is only very little genetic structure, a pattern consistent with high levels of gene flow among populations (Anderson et al. 1998). This is true even in situations where genetic structure is expected a priori, such as in the nematode *Strongyloides ratti*, parasitic in wild rats, that reproduces mainly by parthenogenesis (Fisher and Viney 1998). Here again, gene flow prevents local adaptation. Paterson (2005) has tested whether the infectivity of particular genotypes of *S. ratti* depends on the particular host (rat) genotype in which it occurs, and found no evidence of specificity between host and parasite at the genotype level. Therefore, studies to date on micromammals and their parasites do not support the possibility that fine-tuned, local adaptation is promoting tight host specificity.

5 Fleas on micromammals: a case study

There have been rather few studies of host specificity in parasites of micromammals, not nearly enough to allow any general conclusion. Recently, one group of parasites of small mammals has been the focus of several investigations. Fleas (Siphonaptera) are common haematophagous ectoparasites of rodents, insectivores, lagomorphs and other 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, pre-imaginal development is entirely off-host; the larvae are

usually not parasitic and feed on organic debris in the burrow or nest of the host. Fleas range from highly host-specific to host opportunistic (Marshall 1981). Here, we use recent comparative studies of fleas parasitic on small mammals to address three fundamental questions about the ecology and evolution of host specificity.

5.1 Is host specificity a species character?

In this chapter, we have treated host specificity as a species character, i.e. a trait that is as characteristic of a species as its morphological features. In fact, host specificity varies among populations of the same parasite species. Whereas the size and shape of a parasite will be more-or-less constant among different populations, host specificity is influenced by the local availability of host species. If variation in host specificity among populations of the same parasite species is less pronounced than variation in host specificity among different parasite species, however, host specificity would still represent a species trait. It would be a variable trait, but one that remains constrained within a range of values.

Krasnov et al. (2004a) investigated geographic variation in host specificity of fleas using data from 21 regional surveys, mainly from the Palearctic. They performed a repeatability analysis using 118 flea species that were recorded in at least two of the regions, to determine whether host specificity showed some constancy across populations of the same flea species. Whether measured as the number of host species used or as the taxonomic distinctness (index S_{TD}) of these hosts, host specificity estimates from the same flea species were more similar to each other than expected by chance, but they varied significantly among flea species (Fig. 6). Although statistically significant, the similarity among host specificity values from different populations of the same flea species is still subject to wide variations (Fig. 6). To some extent, this reflects geographic differences in host availability. Within a given region, the subset of host species used by a flea species tends to be taxonomically constrained, i.e. the host species used by a flea are more closely related to each other than if they were subsets of species drawn at random from the regional pool of available host species (Krasnov et al. 2004a). The absence of one or a few host species from a region can affect the realised host specificity of a flea in that region, and thus contribute to variability in host specificity across regions. In addition, local environment factors, such as mean temperature and precipitation levels, can also affect realised host specificity (Krasnov et al. 2004a). Nevertheless, one can see a certain predictability superimposed over this geo-

graphical variation, such that host specificity in fleas, though far from constant, can still be considered as a species character.

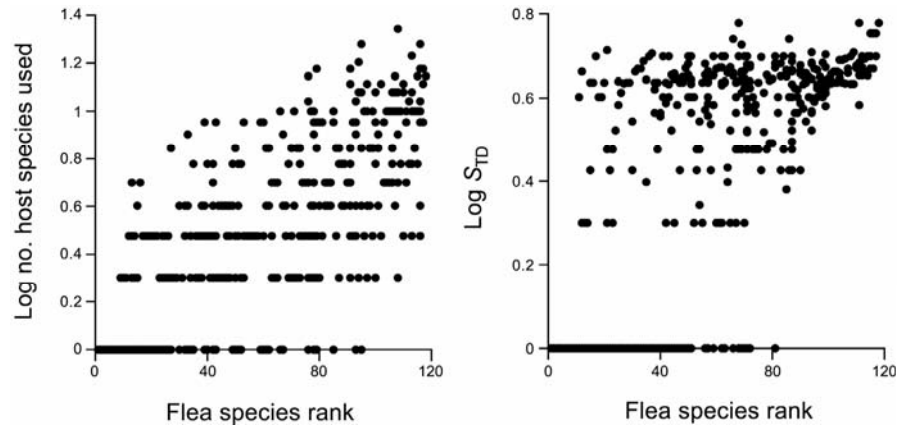


Fig. 6. Rank plots of number of host species used and average taxonomic distinctness, S_{TD} , of these hosts across 118 flea species ranked from lowest to highest mean host specificity. All population estimates are plotted for each species; the number of host species has been corrected for sampling effort, whereas S_{TD} has been corrected for the number of host species used. If geographic variation were small within compared to between flea species, we would expect the points to fall in an area of the plot stretching from the lower left to the upper right corner, with few points in either the upper left or lower right corner (data from Krasnov et al. 2004a)

5.2 Is there a trade-off between number of hosts used and the average fitness achieved in these hosts?

As discussed in the previous section, we might expect a trade-off between the ability to use many host species and the average fitness achieved in these hosts. The rationale behind the trade-off is that close adaptation to one host species may only be achieved at the expense of adaptations to other host species. Given that different host species have different defense systems, investing in many counter-adaptations should have a fitness cost for the parasite: a jack-of-all-trades may be a master of none.

Looking at flea species parasitic on small mammals, it is clear that any given flea species does not do equally well on all its potential host species. Fleas typically achieve much higher abundance (average number of individual parasites per host) on one host species (Krasnov et al. 2004b). If we take this to be the principal host species, then it is also clear that the abundance of a flea on its auxiliary host species decreases with increasing taxo-

onomic distance between an auxiliary host and the principal host species (Krasnov et al. 2004b). The success of a flea following a host switch is thus lower if the newly colonized host is not a close relative of the original host. However, most host species used by a flea tend to fall within the same taxon (e.g., same rodent subfamily), with only rarely one or two host species belonging to other taxa (e.g. another order, like insectivores).

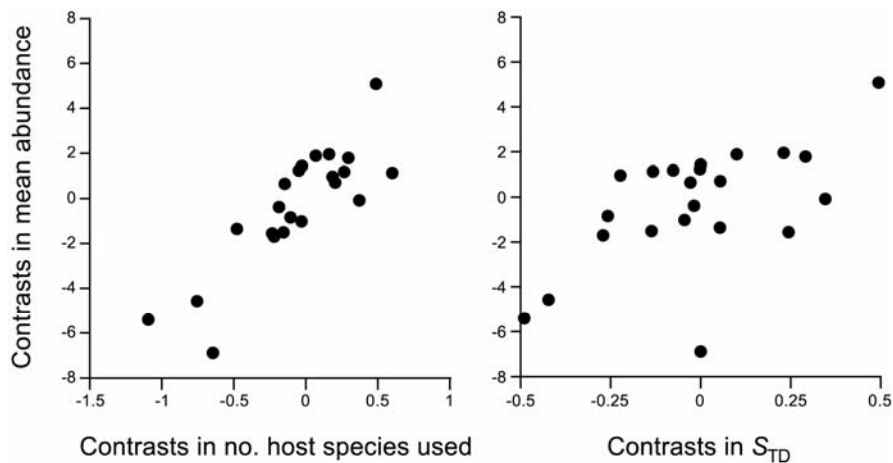


Fig. 7. Relationship between the mean abundance achieved by a flea across all its host species, and either the number of host species used or their taxonomic distinctness, measured by the index S_{TD} . The data are for flea species parasitising rodents in Mongolia; each point represents a phylogenetically independent contrast, with abundance corrected for both sampling effort and host body surface area (data from Krasnov et al. 2004c)

So, is there a trade-off between *average* abundance, i.e. overall fitness, and host specificity among fleas parasitic on small mammals? Using data from 20 regional surveys of fleas on micromammals, Krasnov et al. (2004c) found that there are generally strong *positive* relationships between parasite abundance and either the number of host species used or the index S_{TD} . These relationships were significant in three-quarters of the regions investigated (see Fig. 7 for an example). This finding indicates that there is no general trade-off between how many host species a parasite can use and how well it does on them. In fleas, the opposite happens: whatever features of fleas make them successful on a host also allows them to colonize other host species. In fact, it also appears that fleas using either many host species or taxonomically diverse host species achieve not only greater average abundance, but also a broader geographical range than the more

host-specific fleas (Krasnov et al. 2005). Perhaps the epidemiological advantages of having many host species outweigh the physiological costs of adaptations against their immune defences. Mathematical models predict that for parasites with direct, one-host life cycles in which transmission is strongly dependent on host density, such as fleas, the more host species are exploited in a locality, the greater the probability that the parasite population will persist and spread (Dobson 2004). For indirectly transmitted parasites, however, the models predict the exact opposite (Dobson 2004). These different dynamical features of parasite populations with different modes of transmission may explain the complete absence of any trade-off in parasitic fleas. The next step would now be to perform similar analyses for other taxa parasitic on small mammals.

5.3 Is the evolution of host specificity directional and irreversible?

Parasite specialization is generally presumed to be irreversible, leading into evolutionary dead ends that do not give rise to new lineages. On the one hand, specialist taxa, capable of using only a narrow range of host species, should be less likely to colonize new hosts, and therefore the potential of specialists to give rise to new lineages should be limited (Jaenike 1990). If this is so, we might expect that generalists can evolve into specialists, but that the likelihood of specialists evolving into generalists would be much lower. Thus, within a clade, the more specialized species should on average be the more derived, i.e. the more recent ones. On the other hand, specialist taxa should be more prone to extinction than generalists, because of their strict dependence on a narrow range of host species, and thus we might expect generalist taxa to be favoured and to proliferate over evolutionary time. It is therefore not straightforward to predict in which direction host specificity will evolve in a given clade, i.e. whether it will tend to increase or decrease over evolutionary time. Recent studies on other animal groups have challenged the paradigm that specialization is both directional and irreversible. In his review of studies on evolutionary transitions between specialized and generalized host-plant use, Nosil (2002) found that generalist-to-specialist transitions were more frequent overall among phytophagous insects, but that in some groups the opposite was true. Also, Stireman (2005) reported that transitions from specialist to generalist strategies have occurred more frequently than the reverse during the evolutionary history of tachinid flies, a group of endoparasitoids of insect hosts. The result is that generalist tachinid species tend to be the most derived,

i.e. they tend to occupy branch tips in the phylogeny of the group (Stireman, 2005).

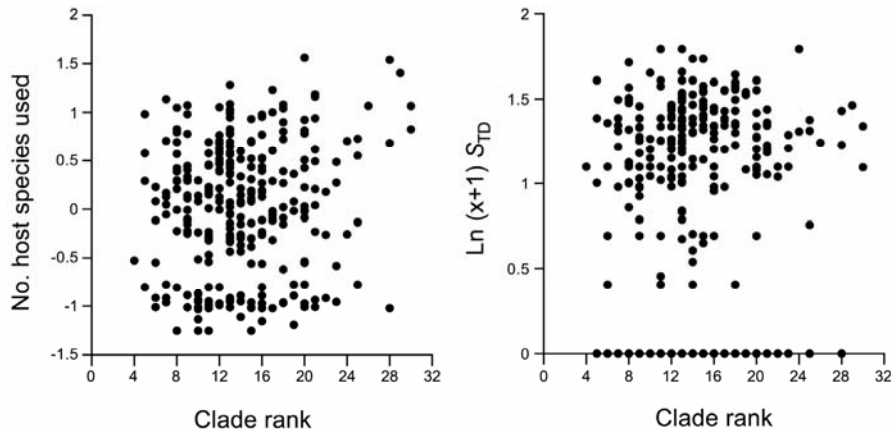


Fig. 8. Relationship between either the number of host species used by a flea species or the taxonomic distinctness of these hosts (measured by the index S_{TD}) and clade rank, among 297 species of fleas parasitic on small mammals. The number of host species used is corrected for sampling effort, i.e. data shown are residuals of the regression of the log-transformed number of host species on which the flea species was found against the log-transformed number of host individuals sampled (data from Poulin et al. 2006)

So what about true parasites? Poulin et al. (2006) tested for directionality in the evolution of host specificity in fleas parasitic on small mammals. They determined whether host specificity, measured both as the number of host species used and their taxonomic diversity, i.e. the index S_{TD} , was related to clade rank of the flea species. Clade rank is the number of branching events between an extant species and the root of the phylogenetic tree; it can be used to distinguish flea species that are basal in the phylogenetic tree from those that are highly derived, i.e. those with low and high clade rank, respectively (Poulin et al. 2006). Both across all flea species in the dataset, and within some families or genera, there were weak positive relationships between clade rank and the number of host species used, but none with the index S_{TD} (Fig. 8). These results suggest a slight evolutionary trend of decreasing host specificity, with many flea lineages increasing over evolutionary time the number of host species they can exploit. However, using a more conservative test, these trends could not be distinguished from a non-directional random walk model, suggesting a lack of directionality in the evolution of host specificity in fleas (Poulin et al.

2006). This can be seen from the scatter of points in Fig. 8. Given the fact that generalist fleas achieve higher abundances on their hosts, as we discussed earlier, it is not surprising that host specificity shows signs, albeit not strong ones, of having loosened over time. Once again, evidence from other parasite taxa would be welcome.

6 Concluding remarks

Host specificity is arguably one of the most important properties of a parasite, because it can determine, among other things, whether a parasite can survive the extinction of a host species, whether a parasite has the potential to invade new habitats such as islands, or whether a parasite can become established and spread following its introduction to a new geographical area. Macroparasites of micromammals have received relatively little attention in this regard. The available evidence suggests that some ecological features of small mammals may interact with parasite transmission mode to determine what levels of host specificity are observed. Still, large-scale patterns of host specificity have only been investigated in fleas, and studies on other parasite taxa are definitely needed. In addition, since many rodent species are now universal laboratory models in many branches of biology, it should prove possible to investigate host specificity in an experimental context. For instance, the mechanisms responsible for the failure or success of a particular parasite species in different host species could be examined using controlled laboratory infections. In addition, selection experiments like that of Gemmill et al. (2000) can be envisaged with host species like mice with short generation times, to track the evolution of host specificity under different selection regimes. The evolution and ecology of host specificity will remain an important research area for years to come. This is particularly true in the light of the global environmental changes occurring at present, and the possibility that, by altering transmission conditions, they will lead to the expansion of the host range of many parasite species.

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