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ORIGINAL ARTICLE

Geographical patterns of abundance: testing expectations of the 'abundance optimum' model in two taxa of ectoparasitic arthropods

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ABSTRACT

Aim The 'abundance optimum' hypothesis predicts that species abundance peaks in the locality with the most favourable conditions and decreases with an increase of distance from that locality. We tested this prediction for 9 fleas and 13 gamasid mite species.

Location We used published data on fleas and gamasid mites that are parasitic on small mammals throughout the Palaearctic.

Methods For each ectoparasite, we computed the correlation between the relative abundance on its principal host species in a region and the distance from that region to the region of maximum abundance. Then, the correlation coefficients were used in a meta-analysis. We also made a cross-species comparison between relative abundances in localities (a) closest to and (b) furthest from the locality of maximum abundance.

Results Although the relationship between the relative abundance in a region and the distance from that region to the region of maximum abundance was negative in 19 out of 22 ectoparasites, it was only statistically significant in three of them. However, a meta-analysis of coefficients of correlations across all species revealed a significant negative effect of the distance from the region of maximum abundance on relative abundance in a particular region. A cross-species comparison between relative abundances in the localities closest to and furthest from the locality of maximum abundance demonstrated that the former were significantly higher than the latter.

Main conclusions A lack of strict host specificity in the ectoparasites studied, and the absence of any strong spatial correlations among the environmental variables affecting ectoparasite reproduction and abundance, may provide an explanation for the spatial independence in abundance values of most species. However, a preference for a particular host even in host-opportunistic parasites combined with species-specific environmental preferences could be the reason behind the weak, but significant, negative abundance–distance relationship across species. The contradiction between results obtained when separate species were considered and when the overall pattern was analysed across species suggests that there exists a general underlying spatial pattern that can often be masked by other factors.

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INTRODUCTION

Almost universally, distributions of species abundance are strongly positively skewed (Gaston, 2003). In other words, a species is abundant in only a few localities where it occurs, whereas it is rare in most other localities. One of the explanations for this pattern is that a species' abundance decreases from the centre to the periphery of its geographical range (Hengeveld & Haeck, 1982; Hengeveld, 1990). This explanation is based on the assumptions that: (1) abundance represents the response of a local population to local conditions; (2) local abundance reflects the relationship between local environmental conditions and the Hutchinsonian niche requirements of a species; and (3) environmental variables that affect abundance are spatially autocorrelated (Brown, 1984). Additional reasons for this pattern include variation in species interactions (Husak & Linder, 2004) and negative effects of gene flow from the core populations (Kirkpatrick & Barton, 1997). This spatial pattern, called the 'abundant-centre hypothesis' by Sagarin *et al.* (2006), became an important paradigm in biogeography and has been repeatedly invoked as an explanation of species distributions (e.g. Brown, 1984) as well as for decision-making in conservation (e.g. Leppig & White, 2006).

Recent analyses of numerous data sets have demonstrated that the 'abundant-centre' model is far from a universal pattern (Sagarin & Gaines, 2002; Gaston, 2003; Sagarin, 2006; Sagarin *et al.*, 2006). There can be a variety of reasons behind the lack of a decrease in abundance from the centre of a range to its periphery (see Sagarin & Gaines, 2002; Sagarin, 2006; Sagarin *et al.*, 2006 for reviews). One of these reasons is that the geometric centre of a geographical range does not necessarily coincide with the locality with the most favourable conditions (see Brown, 1995; Gaston, 2003; Sagarin *et al.*, 2006). Nevertheless, if spatial variation of abundance results from species responses to the environment, if this response is hump-shaped and if environmental variables are spatially autocorrelated, then the 'abundant-centre' hypothesis would hold with the 'centre' being at the locality in which the environment meets most of a species' requirements (i.e. the species' ecological optimum) rather than at the geometric centre of its geographical range (Hengeveld, 1990; Gaston, 2003). In other words, the 'abundant-centre' pattern represents a particular case of the 'optimum response surface model' (Gaston, 2003). Furthermore, a necessary condition for a unimodal pattern of spatial variation of abundance to arise is that there is a single 'most favourable' locality for a species across its geographical range. Consequently, another simple explanation, not involving any complicated mechanisms, for the lack of the 'abundant-centre' pattern reported by Sagarin & Gaines (2002) is that a species meets more than one locality with highly favourable conditions across its range (Brown, 1995).

In addition, Sagarin & Gaines (2002) noted some geographical, ecological and taxonomic limitations of the data sets they used to test the generality of the 'abundant-centre' pattern. The vast majority of the studies concerned terrestrial species from Europe and North America, and none of the studies dealt with parasitic organisms, although parasites form a large proportion of the diversity of life (Sukhdeo & Bansemir, 1996; Poulin & Morand, 2004).

The only test of the 'abundance optimum' pattern in parasites has been carried out by Poulin & Dick (2007) using data on eight helminth endoparasites of the fish *Perca flavescens* in continental North America. Assuming that body condition and antiparasite defence systems do not vary substantially among different populations of conspecific hosts, the general lack of an 'abundance optimum' pattern in helminths reported by Poulin & Dick (2007) is not particularly surprising. In addition, endoparasite dynamics may be affected by factors other than those related to the definitive host, such as the availability of intermediate hosts and the environmental factors affecting infective stages.

A parasite's environment is highly predictable, much more so than the environment of most free-living species (Sukhdeo, 1997). This may be true for endoparasites, but it is not entirely accurate for ectoparasites. The latter are influenced not only by the host itself but also by the characteristics of their off-host environment, which are much less predictable than the in-host environment. Consequently, there are more convincing reasons to expect the 'abundance optimum' pattern in ectoparasitic species. Here, we tested the occurrence of this pattern using data on the abundance of several species from two taxa of haematophagous ectoparasitic arthropods, fleas and gamasid mites, parasitic on Palaearctic small mammals. Although the abundance of a parasite is somewhat stable within bounds set by species-specific life-history traits, it still varies among different populations (e.g. Krasnov *et al.*, 2006 for fleas and Korallo-Vinarskaya *et al.*, 2008 for mites). A search for geographical patterns may improve our understanding of this variation.

Fleas (Siphonaptera) are typical ectoparasites of mammals and are most diverse on small and medium-sized host species. They usually alternate between periods when they occur on the host body and periods when they occur in its burrow or nest. In most cases, the pre-imaginal development is entirely off-host. Gamasid mites belonging to the superfamily Dermanyssoidea and exhibit a huge variety of ecological and feeding modes, including soil-dwelling and nidicolous predators and facultative and obligatory vertebrate ecto- and endoparasites (see Radovsky, 1985 for review). Here we focused on haematophagous mites collected from the bodies of small mammalian hosts. These mites use their hosts both as food sources and as dispersal vehicles (Radovsky, 1985).

Data on the position of the centre of the geographical range or on the abundance in this centre are unavailable for most flea and mite species. Consequently, for each studied species we considered the locality where its abundance peaks as the most 'favourable' and studied the relationship between local abundances and the distance from the most 'favourable' locality. If the 'abundance optimum' hypothesis holds, local ectoparasite abundance should decrease with increasing distance from the most favourable locality. However, the relationship between abundance and the distance to the ecological optimum may not be manifested by a monotonic decrease. It could instead be that the abundance tends to be high in the localities close to the ecological optimum and low far from it, with abundances between the most optimal and the least optimal localities being highly variable (Brown, 1995; Enquist *et al.*, 1995; Gaston, 2003). Consequently, we also compared abundances between the 'closest-to-optimum' localities and the 'furthest-to-optimum' localities across species. Finally, we combined the results of separate species analyses and carried out a meta-analysis to get an overall picture of the relationship between the relative abundance of a species in a locality and the distance from that locality to the locality of maximum abundance.

MATERIALS AND METHODS

Data on fleas and gamasid mites collected from the bodies of small mammals (Erinaceomorpha, Soricomorpha, Lagomorpha and Rodentia) in different regions of the Palaearctic were obtained from published surveys (48 surveys for fleas and 22 surveys for mites) and unpublished data (4 surveys for mites) that reported the number of fleas or mites of a particular species found on each given small mammal species in a particular location. Details on the data sets can be found elsewhere (see Krasnov *et al.*, 2006 for fleas and Korallo *et al.*, 2007 for mites).

We used the mean number of fleas or mites per individual host of a given host species as a measure of abundance. Other measurements of infection level, such as prevalence and intensity of infestation, were not available for the majority of the regions considered. Estimates of parasite abundance are unreliable if the host sample size is small (Rózsa *et al.*, 2000). Consequently, data for a flea or a mite species collected from a particular host in a particular region were only included if at least 15 individual hosts from this region had been examined.

Abundance values for the same parasite species but from several different host species are not comparable. Moreover, even a highly host-opportunistic parasite varies in its abundance among different host species. Often the difference in the abundance of a parasite on different hosts stems from different fitness rewards in these hosts, so that different hosts play different roles in the long-term persistence of a parasite population (Poulin, 2007). In such cases the parasite population would thus mainly depend on one or a few key host species. The best estimate of the abundance of a parasite in a locality is that obtained by looking at how well it performs on its principal host species. On the other hand, for the parasite species as a whole, throughout its entire range, we might expect a degree of specialization on those host species that are most likely to be encountered across all localities where the parasite occurs. Consequently, if the parasite's principal host is the host that supports the largest part of a parasite population, then this host can be identified either as the host species that supports a given parasite species across the largest part of its geographical range or as the host species on which the parasite attains its highest abundance (Krasnov *et al.*, 2004a). In this study, we focused on the principal host species for each flea or mite, using the former approach. Only records of each flea or mite species on its principal host were used in the analyses. We identified the principal host as the host on which a flea or a mite occurred most frequently across all regions from which it has been reported. Then, we selected only those fleas and mites that were recorded on their principal host in at least eight (for fleas) or seven (for mites) regions. This resulted in 9 flea and 13 mite species whose principal hosts consisted of nine species (eight rodents and one soricomorph) (Table 1). In addition, to guarantee the robustness of the results independently of our method of identification of the principal host, we subsequently selected the principal host as the mammal species on which the flea or mite achieved its highest average abundance across all regions sampled. We then repeated the analyses using records of parasites on these principal hosts for five of nine flea species and eight of thirteen mite species (because in the remaining four flea and five mite species, the identity of principal hosts using the two approaches was the same). This second run of analyses yielded the same results as the previous one. Consequently, here we report only the results of analyses performed on the data set where the principal host of a parasite species was identified as the host on which it occurred most frequently across all regions where it was recorded.

For each flea or mite species, the region with the highest abundance value was used as a reference point for other regions. In other words, the abundance of a flea or a mite on its principal host in a region was expressed as a relative value, i.e. as a proportion of the value observed in the region where the abundance of this species was the highest. The use of relative values allows the comparison of abundance values that vary greatly in absolute terms among regions.

The geographical distances between each region and the region of maximum abundance were calculated as the linear distances between the centres of these regions (described in the respective sources) and obtained from a map using the ArcView 9.1 software. Distributions of relative abundances and distances deviated from normal (Shapiro–Wilk's tests, $W = 0.68–0.72$; $P < 0.05$ for all) and none of the usual transformations of values provided normal distributions. Consequently, we applied nonparametric statistics.

First, for each ectoparasite species, Spearman rank correlation coefficients were computed between the relative abundance in a region and the distance from the centre of that region to the centre of the region of maximum abundance. This provides a test of the 'abundance optimum' hypothesis for each parasite species, as local ectoparasite abundance should decrease with increasing distance from the most favourable locality where the parasite achieves maximum abundance. In these analyses, values from the region of maximum abundance were not included because this would generate a spurious negative relationship due to the occurrence of the highest recorded value at a zero distance.

Second, for each species we selected the locality closest to the locality of maximum abundance and the locality furthest

Table 1 Data on 9 flea (Siphonaptera) and 13 mite (Dermanyssoidea) species included in the analyses (see Appendix S1 in Supporting Information for sources).

Taxon	Species	Principal host	Number of regions	Sources
Siphonaptera	*Amalaraeus penicilliger*	*Myodes rutilus*	14	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14
	Amphipsylla rossica	*Microtus arvalis*	8	7, 15, 16, 17, 18, 19, 20, 21
	Catallagia dacenkoi	*Myodes rutilus*	9	2, 4, 5, 6, 9, 10, 12, 13, 14
	Ctenophthalmus assimilis	*Microtus arvalis*	8	1, 7, 8, 10, 15, 16, 21, 22
	Hystrichopsylla talpae	*Microtus arvalis*	9	1, 7, 8, 10, 15, 16, 17, 18, 20
	Leptopsylla segnis	*Mus musculus*	17	2, 4, 7, 10, 13, 15, 17, 18, 19, 20, 23, 24, 25, 26, 27, 28, 29
	Megabothris rectangulatus	*Myodes rutilus*	10	2, 3, 4, 5, 6, 7, 8, 10, 11, 12
	Megabothris turbidus	*Myodes glareolus*	9	4, 6, 7, 8, 10, 15, 17, 21, 25
	Palaeopsylla soricis	*Sorex araneus*	11	1, 4, 7, 8, 10, 15, 16, 17, 21, 25, 30
Dermanyssoidea	*Androlaelaps glasgowi*	*Myodes rutilus*	7	2, 12, 31, 32, 33, 34, 35
	Echinonyssus eusoricis	*Myodes rutilus*	11	9, 31, 32, 34, 36, 37, 38
	Echinonyssus isabellinus	*Myodes rutilus*	16	2, 9, 12, 14, 31, 32, 34, 35, 36, 37, 38
	Eulaelaps stabularis	*Myodes rutilus*	10	9, 14, 31, 32, 33, 34, 36, 37, 39
	Haemogamasus ambulans	*Myodes rutilus*	15	2, 9, 12, 14, 31, 32, 34, 35, 36, 37, 38
	Haemogamasus nidi	*Myodes rutilus*	7	9, 14, 31, 32, 35, 37
	Haemogamasus nidiformes	*Myodes rutilus*	7	31, 32, 34, 36, 38
	Hyperlaelaps amphibius	*Arvicola amphibius*	10	31, 36, 40, 41, 42
	Hyperlaelaps arvalis	*Microtus oeconomus*	12	31, 34, 36, 37, 38
	Laelaps clethrionomydis	*Myodes rutilus*	15	2, 9, 12, 31, 32, 33, 34, 35, 36, 37, 38
	Laelaps hilaris	*Microtus oeconomus*	10	31, 32, 34, 36, 37
	Laelaps muris	*Arvicola amphibius*	13	2, 31, 32, 36, 38, 40, 41, 42
	Laelaps pavlovskyi	*Apodemus agrarius*	7	31, 32, 33, 36, 40, 42

from the locality of maximum abundance. We compared relative abundances between these localities across all 22 species using a sign test (because these abundances are not independent).

Finally, Spearman rank correlation coefficients between the relative abundance in a region and the distance from the centre of that region to the centre of the region of maximum abundance were used as measures of effect size for meta-analysis. We used the number of regions in which an ectoparasite was recorded as the sample size for each observation. A combined estimate of the effect size was calculated using both fixed effects and random effects algorithms, which produced identical results. Heterogeneity was evaluated using *Q*-statistics. Meta-analysis was carried out using the software package Comprehensive Meta-Analysis, version 2 (Biostat Inc., Englewood, NJ, USA).

RESULTS

Nine flea species were recorded from between 8 and 17 regions, and 13 gamasid mite species were recorded from between 7 and 16 regions. The minimum distance between two regions in which a flea or mite was recorded on the same principal host was 286 km (for *Ctenophthalmus assimilis*) and 106 km (for *Echinonyssus isabellinus*), whereas the maximum distance was 5505 km (for *Amalaraeus penicilliger*) and 4835 km (for *Haemogamasus ambulans*).

The results of correlation analyses between relative abundance in a region and the distance to the centre of the region where maximum abundance on this host was recorded are presented in Table 2. Significant negative relationships were found only for one flea species (*Catallagia dacenkoi*) and two mite species (*Echinonyssus eusoricis* and *Hyperlaelaps amphibius*) (see illustrative example in Fig. 1a). No relationships between these two variables were found in the remaining 8 fleas and 10 mites (see illustrative example in Fig. 1b). Nevertheless, in 19 out of 22 parasite species studied, the values of the Spearman rank correlation coefficient between the two parameters were negative.

A cross-species comparison between relative abundances in the localities closest to the locality of maximum abundance and those furthest from the locality of maximum abundance demonstrated that the former were significantly higher than the latter (sign test, $Z = 4.05$, $P < 0.001$; Fig. 2).

The results of the meta-analysis showed a significant overall negative effect of distance from the locality of maximum abundance on abundance across 22 species (Fig. 3). The combined effect size (± SE) was -0.32 ± 0.08. The 95% confidence interval for the point estimate ranged from -0.46 to -0.17, and did not overlap zero. Heterogeneity among species as evaluated by *Q*-statistics was relatively low (12.2) and the *P*-value was not significant (0.93). This suggests a slight tendency for the relative abundance in a locality to decrease with increasing distance between this and the most preferable (in terms of abundance) locality.

Table 2 Spearman's rank correlation coefficients between local relative abundance and distance to the centre of the region with maximum abundance for the 9 flea (Siphonaptera) and 13 gamasid mite (Dermanyssoidea) species.

Taxon	Species	Spearman's *R*	*P*
Siphonaptera	*Amalaraeus penicilliger*	−0.39	0.19
	Amphipsylla rossica	−0.17	0.70
	Catallagia dacenkoi	−0.73	0.03
	Ctenophthalmus assimilis	0.17	0.70
	Hystrichopsylla talpae	−0.42	0.29
	Leptopsylla segnis	−0.32	0.22
	Megabothris rectangulatus	−0.55	0.12
	Megabothris turbidus	−0.24	0.57
	Palaeopsylla soricis	−0.03	0.93
Dermanyssoidea	*Androlaelaps glasgowi*	−0.43	0.39
	Echinonyssus eusoricis	−0.71	0.02
	Echinonyssus isabellinus	−0.01	0.98
	Eulaelaps stabularis	−0.27	0.49
	Haemogamasus ambulans	0.09	0.76
	Haemogamasus nidi	−0.54	0.26
	Haemogamasus nidiformes	0.08	0.87
	Hyperlaelaps amphibius	−0.67	0.04
	Hyperlaelaps arvalis	−0.42	0.20
	Laelaps clethrionomydis	−0.23	0.41
	Laelaps hilaris	−0.43	0.24
	Laelaps muris	−0.46	0.13
	Laelaps pavlovskyi	−0.26	0.61

DISCUSSION

The results of this study suggest that on the one hand the 'abundance optimum' model is not an adequate representation of the geographical structure of abundance in an individual ectoparasite species, as in the case of helminth parasites of fish (Poulin & Dick, 2007). On the other hand, the results of our meta-analysis demonstrate that there is an overall across-species tendency for a decrease of abundance with increasing distance from the presumably most favourable locality in ectoparasitic arthropods.

There are several possible reasons why our study did not uncover significant decreases of abundance with distance from the locality of maximum abundance in most studied species. First, the input data could be confounded by taxonomic errors, for instance if several different parasites from different areas have been lumped under the same name (e.g. Blouin, 2002). Although such taxonomic errors remain a possibility in our data set because the surveys were conducted at different times and in most cases by different people, in this study we considered the most common and well-known flea and mite species, a fact that makes taxonomic errors unlikely.

Second, it is possible that estimation of parasite abundance as the mean number of parasites per host individual is not exactly appropriate in the present context because of the aggregated distribution of a parasite population across a host population (Anderson & May, 1978; Poulin, 2007). Consequently, an adequate description of the abundance of a parasite for comparisons between different locations should include not only the mean but also the variance in the number of parasites per host individual. However, these data are not available for any flea or mite in our data set.

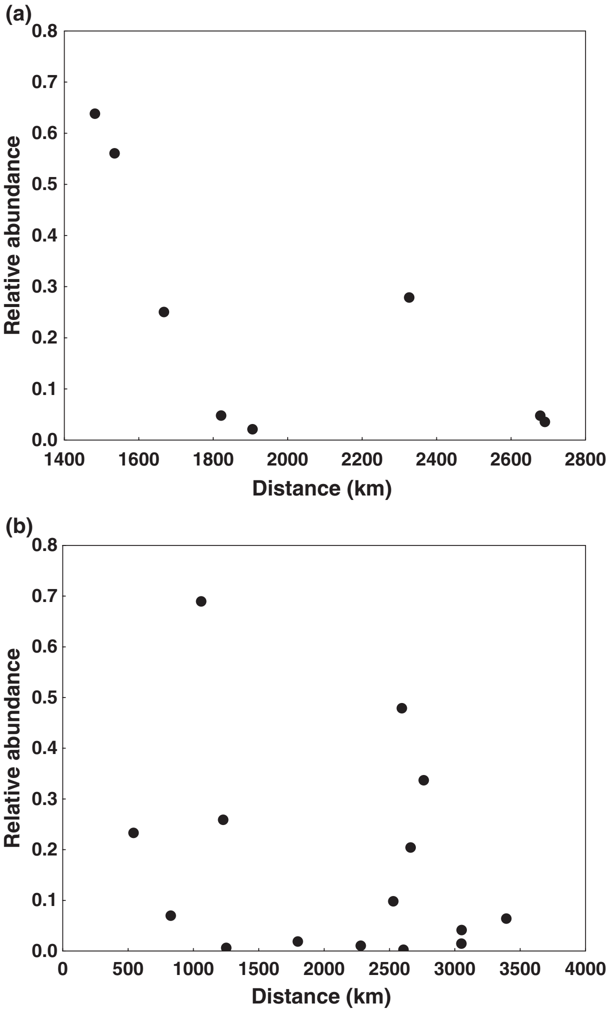

Figure 1 Relationship between local abundance on the principal host and the distance to the centre of the region where maximum abundance on this host was recorded, for the flea *Catallagia dacenkoi* (a) and the gamasid mite *Laelaps clethrionomydis* (b).

Third, it is likely that the data used in this study did not cover the true optimum localities which occur at the centres of the geographical ranges of the fleas and mites studied. However, no 'abundance optimum' pattern was found even when the region of maximum abundance was relatively close to the true geometric centre of a geographical range (e.g. 380 km for *Amalaraeus penicilliger*; B.R. Krasnov & G.I. Shenbrot, unpublished data). Moreover, as mentioned above, the geometric centre of a range does not necessarily coincide with the most favourable locality in terms of abundance (Sagarin *et al.*, 2006). For example, this can be true for discontinuous ranges and ranges across which biotic and abiotic environmental conditions change irregularly.

Fourth, the abundance of individual fleas and mites is often characterized by strong seasonal variation (e.g. Krasnov, 2008

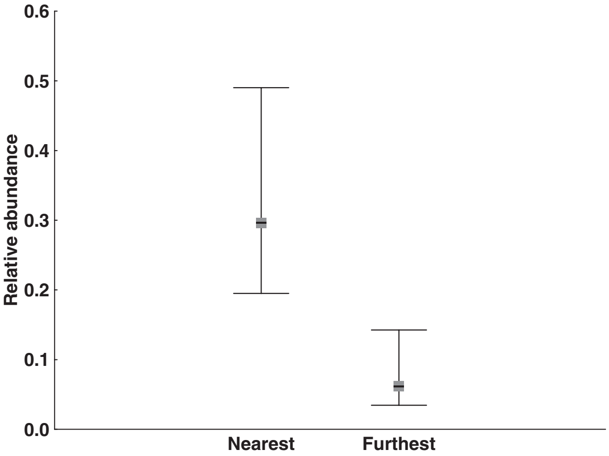

Figure 2 Median and upper and lower quartiles of relative abundances in the locality closest to and furthest from the locality of maximum abundance across 22 ectoparasite species.

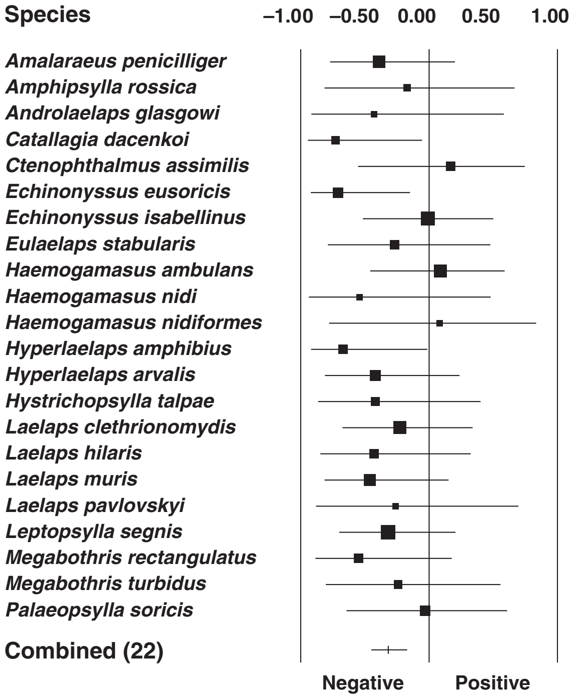

Figure 3 Forest plot for the meta-analysis of the relationship between local relative abundance and distance to the locality of maximum abundance across 22 ectoparasite species. Each point represents the value of the correlation coefficient (either negative from –1 to 0 or positive from 0 to 1) and the line indicates the 95% confidence intervals, for each species separately and for all species combined; the size of the point is proportional to the number of localities involved.

for fleas). However, the data used in our study were collected over several years. This makes the effect of seasonal variation in abundance unimportant.

Fifth, some of the variation in ectoparasite abundance across localities can be due to variation in sampling intensity and sampling technique across surveys. Nevertheless, the data that we used were collected using commonly accepted methods of small mammal sampling (see Krasnov *et al.*, 2006 for fleas and Korallo *et al.*, 2007 for mites) so this effect should be inconsequential.

The aforementioned reasons for the lack of an 'abundance optimum' pattern in individual species are related to the possible inadequacy of the data. However, there could also be biological reasons for this absence of a clear pattern. In particular, a geographical replacement of the principal host species of a given parasite species across its geographical range (Shenbrot *et al.*, 2007) would obviously result in spatial independence of the abundance peaks.

Finally, the apparent spatial independence of local abundances in most fleas and mites found in this study may be real. For example, the local abundance of a parasite may strongly depend on the occurrence of alternative hosts. A parasite may respond to the occurrence of alternative hosts in a community in two different ways. Its abundance or prevalence could either increase because of an increase in the amount of available resources (i.e. the total number of hosts) or decrease in its principal host because the parasite becomes 'diluted' among principal and auxiliary hosts. Telfer *et al.* (2005) reported the effect of the rodent *Myodes glareolus*, introduced to Ireland, on the relationships between prevalence of fleas (*Amalaraeus penicilliger*, *Ctenophthalmus nobilis* and *Hystrichopsylla talpae*) and abundance of the native host *Apodemus sylvaticus*. In areas where *M. glareolus* was absent, an increase in density of *A. sylvaticus* led to an increase in flea prevalence. However, in areas invaded by *M. glareolus*, flea prevalence in *A. sylvaticus* decreased with an increase in density of this host. The fleas and mites considered in our study are not strongly host-specific. The mean number of host species per region ranges from 5.0 (in *Amphipsylla rossica*) to 10.2 (in *C. assimilis*) for fleas, and from 2.4 (in *Hyperlaelaps amphibius*) to 15.0 (in *Eulaelaps stabularis*) for mites. Interestingly, a significant negative relationship between local abundance and distance from the site of maximum abundance was found in the relatively host-specific *H. amphibius*, thus supporting the above explanation. However, this relationship has also been found to be significant in the generalist *Echinonyssus eusoricis* (mean number of host species per region = 8.7), thus contradicting this explanation. It is possible that different mechanisms produce similar spatial patterns of abundance in different species because of some unknown species-specific responses.

Nevertheless, the results of this study suggested predominantly negative relationships between local abundance and distance from the locality of maximum abundance (19 of 22 species), and in three species these relationships were statistically significant. This was further supported by both cross-species comparisons and the meta-analysis, which uncovered an overall trend that was probably masked by specific responses of separate species. The reasons behind this trend can be related to the effect of host species and environmental conditions on the reproduction of ectoparasites. Indeed, a strong effect of the host species on the reproductive success of even host-opportunistic parasites has been repeatedly reported (e.g. Gerasimova, 1973; Prasad, 1973; Krasnov *et al.*, 2004b). Abiotic factors such as microclimate and the texture of the substrate of the host burrow have also been shown to affect various parameters of ectoparasite reproduction (e.g. Heeb *et al.*, 2000; Dean & Meola, 2002 for fleas; Sikes & Chamberlain, 1954 for mites). It is thus possible that favourable conditions for reproduction of ectoparasites and maintenance of their high abundance are determined by interactions among host-related and environment-related factors. The spatial coincidence of the occurrence of the most preferable host and most preferable environment may well be rare. As a result, a negative relationship between distance from such a locality to other localities and ectoparasite abundance may arise.

The lack of significance of the correlation between abundance and distance to the optimal locality in most studied species, coupled with a significant difference between relative abundances in the localities closest to and furthest from the locality of maximum abundance in cross-species analysis, suggests that the shape of the 'abundance optimum' pattern may not be merely a monotonic decline of abundance with increasing distance from the optimal locality, but also involve a sharp step-wise drop of abundance in the most remote locality. Indeed, a variety of patterns of geographical variation in abundance have been reported (see Brown, 1995 and Gaston, 2003 for reviews), and monotonic decreases are not the rule.

The 'abundance optimum' pattern thus appears to be generally weak and easily masked by other factors. The contradiction between results obtained (1) when separate species were considered, and (2) when the pattern was analysed across species deserves further investigation and should be addressed in future studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Sources for Table 1.

BIOSKETCH

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