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Stability in abundance and niche breadth of gamasid mites across environmental conditions, parasite identity and host pools

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Abstract There is substantial variability among populations of the same species in basic features such as abundance or niche breadth, and it is unclear to what extent these are true species traits as opposed to the product of local environmental factors. In parasites, abundance and niche breadth, i.e. host specificity, show repeatability among different populations of the same species, but may also be influenced by external forces, depending on the parasite taxa studied. We tested whether the abundance and host specificity of gamasid mites parasitic on small mammals from 26 different geographic regions of the Palaearctic, are species-specific or instead determined by host identity and/or parameters of the biotic and abiotic environment. Values of abundance and host specificity (measured as the number of host species used) were significantly more similar among populations of the same mite species than among different mite species; despite also showing consistency within particular host species or regions independently of mite species identity, both abundance and the number of host species used appear to be true mite species traits. In

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contrast, the taxonomic distinctness of host species used by a mite showed little repeatability among populations of the same mite species, and appears mostly determined by the local pool of available host species. Within given mite species, all three variables (abundance, number of host species used, and their taxonomic distinctness) covaried to some extent with one or more environmental factors (e.g., nature of the local host assemblage, temperature, precipitation) across geographical regions, but there was no universal pattern among results from different mite species. These results are similar to those obtained earlier on other taxa, e.g. fleas, and suggest that there are general laws acting on spatial patterns of parasite abundance and host specificity.

Keywords Abundance · Environment · Gamasid mites · Host specificity · Small mammals · Repeatability

Introduction

Phenotypic plasticity is a fundamental property of any species. In simple words, it represents the ability of a species with a given genotype to manifest it via different phenotypes in different environments. Thus, the expression of a trait depends on both species-specific limits of variation and the external environment. The interplay between intrinsic species-specific boundaries of variation and environmental influences is well known for morphological traits such as body size (e.g., Peters 1983) or physiological traits like metabolic rate (e.g., Degen 1997). The plasticity of ecological traits such as population density and niche breadth is less completely understood. Consequently, there is no clear-cut answer to the question of whether a given level of abundance or niche breadth is a species attribute subjected to natural selection, or whether it merely reflects the local constraints exerted by a variety of ecological, morphological, chemical and/or genetic factors (e.g., Fox and Morrow 1981).

The population density (=abundance) of a species is sometimes highly variable and almost unpredictable (e.g., Beissinger and Westphal 1998). This may be related to resource availability (e.g., Newton 1998; Morris 1988) and occurrence of competitors and/or predators (e.g., Boone et al. 2007). However, abundance should also depend on some species-specific traits such as body size (Blackburn and Gaston 2001) and fecundity (Hughes et al. 2000). In addition, lower abundance limits should be determined by species-specific mating system and social structure (e.g., Legendre et al. 1999), whereas upper limits should be determined by the species-specific ability of individuals to withstand crowding (e.g., Debinski and Holt 2000).

The niche breadth of a species is thought to result from adaptive processes (Futuyma and Moreno 1988; Brooks and McLennan 1991) and, thus, represent a true species character. However, niche breadth in terms, say, of the level of resource specialization, may be substantially variable across different populations of the same species (Fox and Morrow 1981; Thompson 1994). This suggests that local factors (e.g., availability of resource) can also profoundly affect niche breadth in a local population.

Parasites are useful models for studying geographic patterns of stability and variation in the ecological parameters of a species, toward a better understanding of the evolution and ecology of abundance and niche breadth. In particular, this is because one can easily obtain replicated samples (e.g., host individuals, host populations, or host species). In addition, the ecological niche of a parasite can be easier to define than that of free-living organisms (Timms and Read 1999) because the main living environment or habitat of a parasite and its food are represented by its host. Consequently, the size of the host spectrum (=host specificity) of a parasite species or population represents both the trophic and spatial dimensions of its niche. Indeed, host specificity is considered as one of the most important properties of a parasitic species (Poulin et al. 2006). It increases as parasites infest (a) a decreasing number and (b) an increasingly narrow phylogenetic range of host species (Poulin and Mouillot 2003).

Despite these advantages, there have been very few attempts to evaluate the relative effect of species identity and extrinsic factors (such as host identity and/or environmental parameters) on abundance and niche breadth of parasites. Three studies dealing with nematodes (Arneberg et al. 1997) and fleas (Krasnov et al. 2006) in mammalian hosts and various metazoans in fish hosts (Poulin 2006) have asked whether the abundance of a parasite is a true species character or the product of extrinsic factors. The patterns they report are very similar. Abundances of nematodes and fleas in mammals as well as those of monogeneans, trematodes, cestodes, nematodes, acanthocephalans and copepods in fish, although showing some among-population variation, were repeatable enough within a parasite species to be considered genuine species character. Abundance of fleas was also repeatable among populations of a host species although to a lesser extent than among populations of the same flea species but on different host species. To the best of our knowledge, the only study that considered the effects of intrinsic species properties versus local factors on parasite host specificity has been carried out for fleas parasitic on small mammals (Krasnov et al. 2004b). It was found that host specificity (measured as both the number of host species exploited and the taxonomic diversity of the host spectrum) was repeatable among different populations of the same flea species and varied significantly more among flea species than within flea species, but also depended to some extent on local environmental parameters.

Although patterns of abundance of various parasites appear similar, the generality of this finding and especially that for host specificity remains to be tested. In particular, the nature of the relationship between a particular parasite taxon and a particular host taxon can affect the pattern of geographic stability versus variability in parasite abundance and host specificity. For example, when the diversity of gamasid mites and fleas were separately examined among roughly the same set of host species in roughly the same geographic area, the former were strongly affected by species-specific host features and less so by the environment (Krasnov et al. 2004a), whereas this was not the case for the latter (Korallo et al. 2007). The greater dependence of mite assemblages than flea assemblages on host features than on environmental parameters was found also when the similarity of community composition of these parasites across different host populations were studied (Krasnov et al. 2005 versus Vinarski et al. 2007). Consequently, abundance and host specificity of mites are expected to depend less strongly on species identity than in fleas, and more strongly on host identity.

Gamasids are characterized by extremely high interspecific variation in their ecology and feeding modes. They include soil-dwelling, plant-dwelling and nidicolous predators, and both facultative and obligate vertebrate ecto- and endo-parasites (see Radovsky 1985 for review). Here we focus on haematophagous species collected from host bodies. These mites use their hosts both as food sources and as dispersal vehicles, and the association between these mites and their hosts is thus very intimate (Radovsky 1985).

The aim of this study was to test whether the abundance and niche breadth (expressed as the degree of host specificity) of gamasid mites parasitic on small mammals from 26 different geographic regions of the Palaearctic, are species-specific or instead determined by host identity and/or parameters of the biotic and abiotic environment. We evaluated the repeatability of estimates of mite abundance and host specificity across populations of the same mite species, to determine if these parameters are repeatable within mite species, i.e. if the values of abundance and host specificity are more similar among populations of the same mite species than among different mite species. We also tested the repeatability of mite abundance within host species and regions to assess whether abundance and host specificity are more similar among gamasids occurring on the same host species or in the same region independently of their identity than among gamasids occurring on different host species or in different regions, respectively. In addition, we searched for correlations between the biotic (structure of mite faunas and host assemblages) and abiotic (landscape and climate parameters) characteristics of a region and both mite abundance and host specificity, separately for several mite species.

Materials and methods

Data set

Data on gamasid mites collected from the bodies of small mammals (Soricomorpha, Erinaceomorpha, Lagomorpha and Rodentia) in 26 different regions of the Palaearctic were obtained from published surveys and unpublished data that reported the number of mites of a particular species found on each given small mammal species in a particular location (see Korallo et al. 2007 for the details on the data set). In all studies most rodents and shrews were captured using snap-traps, shrews were also captured using pitfall traps, sciurids and lagomorphs were hunted, whereas moles were captured using mole-traps. Each trapped animal was placed in an individual cloth bag and transported to the laboratory where its fur was thoroughly combed using a toothbrush and all dislodged mites were collected. All species in the dataset were reported to be haematophagous. We used only those sources where sampling effort (the number of examined hosts) was reported. The data set comprised data on 308,368 individual mites belonging to 70 species and collected from 244,389 individual mammals belonging to 76 species.

Estimates of abundance

Initially, we listed all mite-mammal combinations for each region. Then, we excluded those mammal species for which fewer than ten individuals have been examined per region, because estimates of mite abundance could be inaccurate for small samples. The same mite species was often recorded from several different host species within and/or among regions. Abundance values for the same mite species but from several different host species are not comparable. Consequently, we included in the analyses only those mite species that were recorded on the same host species in at least two regions and focused on the principal host species for each mite. The parasite's principal host is the host that supports the largest part of a parasite population. Thus, this host can be identified either as the host species that supports a given mite species across the largest part of its geographic range, or as the host species on which the mite attains its highest abundance (Krasnov et al. 2004c). We used both these approaches. First, we identified the principal host as the host on which a mite occurred most frequently across all regions from which it has been reported. Only records of the mite on the principal host were used in the analyses. Second, we identified the principal host as the mammal species on which the mite achieved its highest average abundance across all populations sampled; we then repeated all analyses using records of mites on these principal hosts. 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 dataset where the principal host of a mite species was identified as the host on which it occurred most frequently across all regions where it was recorded. This data set comprised 38 mite species and 172 mite-region associations. We used the mean number of mite individuals per individual host of a given species as a measure of mite abundance. Other measurements of infection level, such as prevalence, were not available for most of the regions considered. Estimates of mite abundance were negatively correlated with number of examined host individuals (Pearson $r = -0.41$, $N = 171$, $P < 0.05$). Therefore, we corrected estimates of mite abundance for unequal sampling of the same host in different regions by substitution of the original values with their residual deviations from the regression on the number of hosts examined in log-log space.

Estimates of host specificity

The two measures of host specificity we used were (a) the number of mammalian species on which the mite species was found and (b) the specificity index, S_{TD} (Poulin and Mouillot 2003). To calculate these measures, we took into account all host species from which at least 2 individuals of a given mite species were collected. The number of host species was strongly affected by sampling effort (Pearson $r = 0.36$, $N = 171$, $P < 0.05$). Consequently, we substituted original values of host number with their residuals from the regression against sampling effort after log transformation.

The index S_{TD} measures the average taxonomic distinctness of all host species used by a parasite species. When these host species are placed within a taxonomic hierarchy, the average taxonomic distinctness is simply the mean number of steps up the hierarchy that must be taken to reach a taxon common to two host species, computed across all possible pairs of host species (see Poulin and Mouillot 2003 for details). The greater the taxonomic distinctness between host species, the higher the number of steps needed, and the higher the value of the index S_{TD}: thus it is actually inversely proportional to specificity. Using the taxonomic classification of Wilson and Reeder (2005), all mammal species included here were fitted into a taxonomic structure with eight hierarchical levels above species, i.e. subgenus, genus, tribe, subfamily, family, suborder, order, and class (Mammalia). The maximum value that the index S_{TD} can take (when all host species belong to different orders) is thus 8, and its lowest value (when all host species are consubgeners) is 1. However, since the index cannot be computed for parasites exploiting a single host species, we assigned a S_{TD} value of 0 to these mite species, to reflect their strict host specificity. To calculate S_{TD}, RP and DM developed a computer program using Borland C++ Builder 6.0 (available at http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv2).

The number of host species exploited by a mite species correlated positively with S_{TD} (Pearson $r = 0.78$, $N = 171$, $P < 0.001$), indicating that this measure was influenced by the number of species in a mite's host spectrum. Therefore, in the subsequent analyses S_{TD} was corrected for the number of host species in a mite's host spectrum (residuals of the regression after log-transformation).

Estimates of biotic and abiotic characteristics of regions

To characterize host and mite assemblages of each region, we used the total number of mite species and total number of mammal species that were used by these mites as hosts as well as the taxonomic distinctness of mite and host assemblages. For this, we took into account all mite species recorded in a region and all mammals from which at least one individual of a single mite species was collected. Total numbers of mite and host species correlated positively with host sampling effort ($r^2 = 0.23$, $F_{1,24} = 7.3$ and $r^2 = 0.22$, $F_{1,24} = 7.0$, respectively, $P < 0.05$ for both), so these variables were corrected for this confounding effect.

The index of average taxonomic distinctness (Δ^+) of mite or host assemblages is a measure analogous to the index of host specificity, S_{TD} (Clarke and Warwick 1998, 1999; Warwick and Clarke 2001; Poulin and Mouillot 2003). For hosts, this index was calculated exactly as the index S_{TD} (see above), whereas for mite assemblages it was calculated using the taxonomic classification of Bregetova (1956), Radovsky (1985), and Halliday (1998) and fitting all mite species into a taxonomic structure with 4 hierarchical levels above species, i.e. genus, subfamily, family and superfamily (Dermanyssoidea). No effect of number of either mite or host species on their respective Δ^+ was found ($r^2 = 0.02$, $F_{1,24} = 0.6$ and $r^2 = 0.11$, $F_{1,24} = 2.9$, respectively; $P > 0.10$ for both), so Δ^+ for mites and hosts (Δ^+_m and Δ^+_h, respectively) were used in the analyses after log-transformation.

To characterize environmental conditions of a geographic locality, we computed climatic variables (annual, winter and summer precipitation, mean surface air temperature of January, mean surface air temperature of July, and mean annual surface air temperature) and elevation parameters for each region, using the Global Ecosystems database (Kineman et al. 2000; see Vinarski et al. 2007 for details). Because some of these variables strongly correlated with each other, we substituted them with the scores of a principal component analysis (PCA).

Data analyses

To determine whether mite abundance and host specificity are true mite species attributes, i.e. parameters that vary less among populations of the same mite species than among different mite species, we performed (a) correlation analyses between the values of mite abundance or host specificity and (b) repeatability analyses following that of Arneberg et al. (1997). In the former analyses, we correlated the lowest abundance or host specificity values (number of host species or S_{TD}) recorded for a given mite species with all other values of abundance or host specificity, respectively, recorded in other regions for this species, across all mite species. If abundance or host specificity values of the same mite species are consistent with each other across different regions, then a positive correlation is expected between the lowest value and other values of abundance or host specificity.

In the repeatability analyses, we analysed the variation in mite abundance or host specificity by one-way ANOVAs in which mite species was the independent factor. A significant effect of mite species would indicate that the abundance or host specificity is repeatable within mite species, i.e. that values for the same mite species from different geographic regions are more similar to each other than to values from other mite species. We estimated the proportion of the total variance originating from differences among mite species, as opposed to within species, following Sokal and Rohlf (1995). To assess whether mite abundance and host specificity are determined also by host identity and/or the particular biotic and abiotic conditions of a locality, we performed the repeatability analyses using host species or region (as a proxy for geographic differences in a set of biotic and abiotic conditions) as the single factor. A significant effect of host species or region would indicate that the mite abundance or host specificity values are repeatable within host species or region, respectively, independently of mite species identity. For the repeatability analysis within host species, we used only those 27 mite species that were recorded in at least two host species (in total 14 hosts and 139 mite-host associations).

To understand whether and how the biotic and abiotic environment of a geographic location affects the abundance and host specificity of a mite species, we analysed the effect of biotic and abiotic environmental components separately (expressed either as species richness and taxonomic distinctness of mite and host assemblages or as three composite variables extracted from original environmental measures using PCA, see above) on variation in abundance and host specificity within a mite species across regions. This was done for each of eight mite species which occurred in at least six regions using Generalized Linear Models (GLM) with a normal distribution and power-link function, searching for the best model using the Akaike's Information Criterion. Then, we tested the significance of the parameter estimates in each best model using the Wald statistic.

We did not apply the Bonferroni adjustment of alpha-level as this approach has been increasingly criticized by statisticians and ecologists in recent years, because it often leads to the incorrect acceptance of the false null hypothesis (Rothman 1990; Perneger 1998, 1999; Moran 2003; Garcia 2004). Thus we present unadjusted results.

Results

Correlation analyses

The lowest abundances were strongly positively correlated with all other abundance values across mite species (Pearson $r = 0.57$, $N = 133$, $P < 0.0001$). In other words, different mites demonstrated a relatively narrow range of abundances when exploiting the same host species in different regions (Fig. 1).

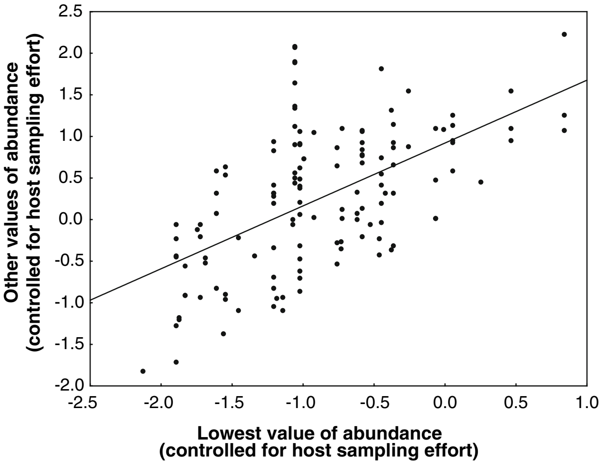

Fig. 1 Relationship between the lowest abundance and other abundance values on the same host species for 72 mite species recorded in at least two regions

The lowest number of host species exploited and the lowest value of taxonomic distinctness (S_{TD}) of the host spectrum also correlated positively with all other values of these parameters (Pearson $r = 0.58$ and $r = 0.032$, respectively; $N = 133$, $P < 0.05$ for both). However, the data points on the scatterplots for both measures of host specificity (Figs. 2, 3) form somewhat triangular patterns. This means that some mite species are characterized by high variation in host specificity across localities, whereas other species demonstrate similar degrees of host specificity wherever they occur.

Repeatability analyses

The repeatability analyses for the 72 mite species recorded in least two regions supported the results of the correlation analyses (Table 1). Abundances of the same mite species on the same host species were more similar to each other than expected by chance, and vary significantly among mite species, with 47.4% of the variation among samples explained by differences between mite species. Mean mite abundance per host individual can, therefore, be considered as a mite species character because estimates of abundance are repeatable within the same mite species. Furthermore, mite abundance was also repeatable independently of mite species identity, either across populations within a host species or within a region, but to a lesser degree than within a mite species (Table 1). The same was true for host specificity evaluated as the number of host species exploited. It was highly repeatable within a mite species and less, albeit significantly, so within a host species or a region (Table 1). However, host specificity evaluated as the taxonomic diversity of a mite's host spectrum was too variable within mite species across regions: it was not repeatable within the same mite species and cannot be considered as a mite species attribute (Table 1). This parameter was also not repeatable within host species. However, the taxonomic diversity of the mite's host spectrum was repeatable across mite species within a region, although the amount of variation associated with differences between regions was not especially high (Table 1).

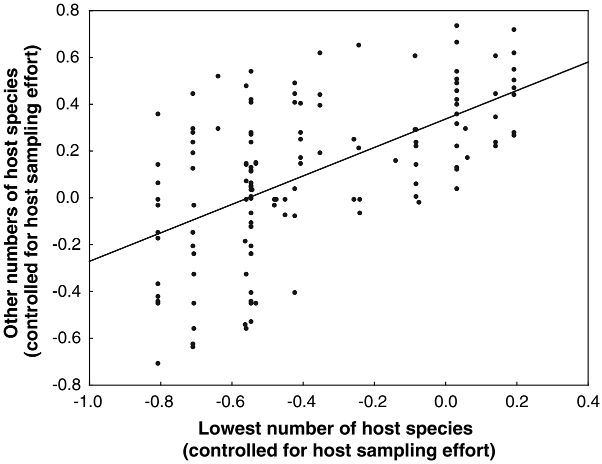

Fig. 2 Relationship between the lowest number of host species exploited in a region and other region-specific values of the number of host species exploited for 72 mite species recorded in at least two regions

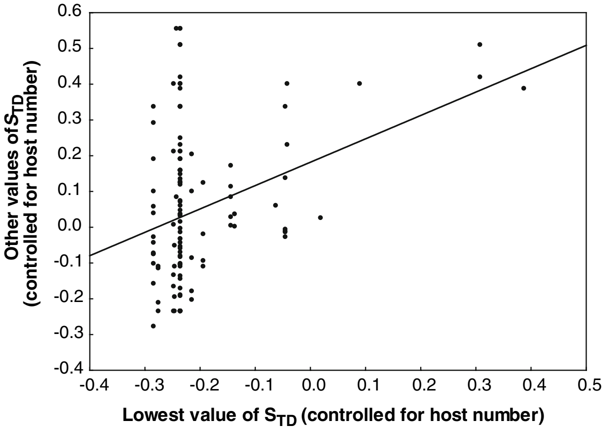

Fig. 3 Relationship between the lowest value of host specificity measured as taxonomic distinctness of the host spectrum (S_{TD}) in a region and other region-specific values of S_{TD} for 72 mite species recorded in at least two regions

Table 1 Summary of the repeatability analyses of mite abundance and host specificity within mite species, within host species, and within regions

Mite parameter	Independent factor	*F*	df	*P*	%V
Abundance	Mite species	11.1	37,133	<0.001	47.4
# Host species exploited		3.6	37,133	<0.001	33.3
S_{TD}		1.7	37,133	0.16	5.8
Abundance	Host species	5.2	12,126	0.001	29.4
# Host species exploited		2.7	12,126	0.003	14.1
S_{TD}		0.7	12,126	0.79	3.4
Abundance	Region	1.0	24,146	0.02	10.3
# host species exploited		0.8	24,146	0.04	8.1
S_{TD}		2.2	24,146	0.03	9.3

%V—percentage of variation associated with differences between mite species, host species, or regions

Generalized linear models

Principal component analysis of environmental variables resulted in three factors. These three factors explained 91.5% of the variance, and their eigenvalues were 3.58, 1.59 and 1.23. The first factor (F1) represented an increase in air temperature (loadings of temperature variables were 0.88, 093 and 0.74, respectively), whereas the second factor (F2) represented an increase in winter precipitation (factor loading 0.92) and the third factor (F3) represented an increase in annual and summer precipitation (factor loadings 0.84 and 0.91, respectively).

Results of best model selection using Akaike's Information Criterion (AIC) are presented in Tables 2 and 3. In general, in six of eight mite species abundance was affected by biotic factors and in six of eight mite species it was affected by abiotic factors. In five of these six species, both types of factors affected abundance, whereas no effect of any measured variable on abundance was detected in *Laelaps clethrionomydis*. Host specificity evaluated as the number of host species exploited was affected by biotic factors in all species except *Hyperlaelaps amphibius* and *Laelaps hilaris*. However, in these mites only,

Table 2 The significant best models of biotic and abiotic local environmental factors (EF) explaining variance in abundance (A), number of hosts exploited (HN) and taxonomic distinctness of the host spectrum (S_{TD}) for eight species of gamasid mites

Mite species	Mite character	EF	Model	AIC	Likelihood ratio χ^2	*P*
Haemogamasus nidiformis	A	Biotic	Δ_h^+	13.11	7.7	0.02
		Abiotic	F1, F3	12.4	8.3	0.01
	HN	Biotic	Δ_m^+, HSR	−10.33	9.18	0.03
	S_{TD}	Biotic	HSR, Δ_h^+	−14.17	11.30	0.001
Hirstionyssus isabellinus	A	Biotic	HSR	25.63	12.72	0.01
		Abiotic	F2	27.69	6.66	0.01
	HN	Biotic	HSR	−22.99	22.71	0.001
	S_{TD}	Biotic	HSR	−19.28	13.65	0.001
Hyperlaelaps amphibius	A	Biotic	MSR	17.08	7.83	0.02
		Abiotic	F2	7.88	12.03	0.001
	HN	Abiotic	F1, F3	3.46	9.74	0.01
	S_{TD}	Biotic	Δ_m^+	−9.47	5.02	0.04
		Abiotic	F1	−11.99	5.54	0.02
Hyperlaelaps arvalis	A	Abiotic	F2	22.9	6.5	0.01
	HN	Biotic	Δ_m^+	2.9	8.5	0.03
	S_{TD}	Biotic	Δ_m^+	−10.9	6.7	0.03
Laelaps clethrionomydis	HN	Biotic	HSR	−3.89	2.57	0.05
	S_{TD}	Biotic	MSR, Δ_m^+, HSR	−22.25	27.30	0.001
		Abiotic	F2, F3	−15.90	18.94	0.001
Laelaps hilaris	A	Biotic	MSR, HSR	6.36	13.73	0.001
	HN	Abiotic	F1	−0.49	9.71	0.001
	S_{TD}	Biotic	Δ_m^+	−9.08	5.90	0.02
		Abiotic	F1, F2, F3	−9.95	10.76	0.01
Laelaps muris	A	Biotic	MSR	26.25	10.32	0.001
		Abiotic	F1, F2, F3	24.93	15.64	0.001
	HN	Biotic	MSR, HSR	5.99	7.88	0.02
Laelaps pavlovskyi	A	Biotic	Δ_m^+, HSR, Δ_h^+	9.45	10.17	0.02
		Abiotic	F1	9.33	6.29	0.01
	HN	Biotic	Δ_m^+, Δ_h^+	4.53	7.14	0.03
	S_{TD}	Abiotic	F3	−2.13	5.29	0.02

The modelling was carried out using a Generalized Linear Model with the application of Akaike's Information Criterion (AIC) for the best model selection. Biotic components of the environment of a region include mite species richness (MSR), taxonomic distinctness of the mite fauna (Δ_m^+), host species richness (HSR) and taxonomic distinctness of the host assemblage (Δ_h^+). Abiotic environmental components are represented by factors F1, F2 and F3 (composite variables extracted from seven environmental variables calculated for each region, see text for explanations)

the number of host species exploited was found to be affected by abiotic factors. Variation in taxonomic distinctness of the host spectrum was best explained by both biotic and abiotic factors in three species, by biotic factors only in three species and by abiotic factors only in one species.

Estimates of the parameters of the best models (Table 3) suggest that in the majority of mites, abundance generally decreased with an increase in the number of either mite or host

Table 3 Parameter estimates for the significant best models explaining variance in abundance (A), number of hosts exploited (HN) and taxonomic distinctness of the host spectrum (S_{TD}) for eight species of gamasid mites

Mite species	Mite character	Environment	Model	Wald statistic
Haemogamasus nidiformis	A	Biotic	$1.6\Delta_{\mathrm{h}}^{+}$	4.6
		Abiotic	−0.9F1–0.8F3	11.2/13.6
	HN	Biotic	$-11.4\Delta_{\mathrm{m}}^{+}$+1.1HSR	15.9/14.1
	S_{TD}	Biotic	−0.8HSR+$1.4\Delta_{\mathrm{h}}^{+}$	12.8/3.8
Hirstionyssus isabellinus	A	Biotic	−0.8HSR	12.8
		Abiotic	−0.7F2	4.6
	HN	Biotic	1.1HSR	38.7
	S_{TD}	Biotic	−0.9HSR	24.0
Hyperlaelaps amphibius	A	Biotic	−6.2MSR	6.7
		Abiotic	−0.7F2	20.5
	HN	Abiotic	−0.2F1–0.2F3	5.2/3.7
	S_{TD}	Biotic	$-7.3\Delta_{\mathrm{m}}^{+}$	5.9
		Abiotic	−0.1F1	4.5
Hyperlaelaps arvalis	A	Abiotic	−0.6F2	4.1
	HN	Biotic	$-13.7\Delta_{\mathrm{m}}^{+}$	5.9
	S_{TD}	Biotic	$-8.1\Delta_{\mathrm{m}}^{+}$	4.5
Laelaps clethrionomydis	HN	Biotic	0.84HSR	5.7
	S_{TD}	Biotic	−0.7MSR–$16.8\Delta_{\mathrm{m}}^{+}$−1.2HSR	22.1/95.6/401.3
		Abiotic	−0.23F2–0.22F3	52.7/99.6
Laelaps hilaris	A	Biotic	−4.5MSR–1.5HSR	6.8/3.3
	HN	Abiotic	−0.5F1	8.8
	S_{TD}	Biotic	$8.7\Delta_{\mathrm{m}}^{+}$	4.9
		Abiotic	0.3F1+0.3F2–0.2F3	9.7/17.8/23.6
Laelaps muris	A	Biotic	−6.4MSR	7.1
		Abiotic	−0.4F1–0.9F2+0.7F3	5.6/10.9/13.6
	HN	Biotic	−2.9MSR+1.6HSR	9.2/9.4
Laelaps pavlovskyi	A	Biotic	$56.5\Delta_{\mathrm{m}}^{+}$−2.9HSR+$6.4\Delta_{\mathrm{h}}^{+}$	10.1/9.8/5.5
		Abiotic	−1.1F1	5.3
	HN	Biotic	$28.1\Delta_{\mathrm{m}}^{+}$+$4.9\Delta_{\mathrm{h}}^{+}$	3.9/5.0
	S_{TD}	Abiotic	0.3F3	4.7

See Table 2 for factor names. All parameters are significant ($P < 0.05$)

species, or both, in a region as well as with an increase of temperature and winter precipitation. In the majority of mites, the effect of the biotic environment on host specificity evaluated as the number of hosts exploited was expressed as an increase of this number concomitantly with an increase in the richness of regional host assemblages. In contrast, taxonomic distinctness of the host spectrum did not demonstrate any clear trend in its association with either biotic or abiotic parameters of a region. For example, S_{TD} increased with a decrease in taxonomic diversity of the mite fauna in three species and with regional host species richness in three other species.

Discussion

Abundance and host specificity (expressed as the number of hosts exploited) of mites were strongly determined by species identity and to a much lesser extent by host identity and the biotic and abiotic characteristics of a locality exactly as observed for fleas (Krasnov et al. 2005, 2006). These two characters are thus genuine attributes of a mite species. In contrast, host specificity measured as the taxonomic diversity hosts used was too variable within mite species to be considered as a species character. Nevertheless, both abundance and host specificity were somewhat variable among host species and among regions with the former affected by both local biotic and abiotic factors, and the latter mainly by biotic factors.

The results of this study have implications on two fronts. First, our results provide the first analysis of abundance and host specificity patterns in gamasid mites, an important taxon of arthropod ectoparasites. Second, when compared with previous findings on several parasite–host associations, they add to our understanding of whether there are general rules that apply to all or at least most parasite–host associations. The elucidation of spatial patterns of parasitism is crucially important for epidemiology, veterinary medicine, conservation and pest management. Below, we discuss both these issues.

Variability of abundance and host specificity in gamasid mites

The reason for the repeatability of abundance within mite species is most likely that some species-specific life history traits determine the limits of abundance. Given that we considered the abundance of mites collected from host bodies and that some mite species are obligate haematophages, whereas others are opportunistic blood feeders (Radovsky 1985), the lower limits of mite abundance can depend on the relative need of a mite species to feed on blood as well as the species-specific relationship between reproduction and blood feeding. For example, a female *Ornithonyssus bursa* requires at least two blood meals to be able to reproduce (Sikes and Chamberlain 1954), whereas a female *Dermanyssus gallinae* begins to lay eggs after a single blood meal (Tucci et al. 2005). Among gamasid mites parasitic on mammals, the number of blood meals necessary for oviposition is 4–5 for *Hirstionyssus meridianus*, but at least 6 for *Hirstionyssus criceti* (Goncharova 1958). Upper limits of abundance can be determined by species-specific reproductive outputs and generation times. For example, the ovoviviparous *Haemogamasus ambulans* produces at most one larva every 2 days (Furman 1959), whereas the mean daily egg production of *Chiroptonyssus robustipes* attains three eggs per day (Radovsky 1967; see Radovsky 1985 for additional examples). Generation time also varies among gamasid species, from about 5–7 days in *O. bursa* (Sikes and Chamberlain 1954) to as long as 16–17 days in *D. gallinae* (Maurer and Baumgärtner 1992).

Variability in mite abundance among different populations of the same species is definitely associated also with the effect of host- and physical environment-related factors. These effects are reflected in the repeatability of mite abundance within host species and within region, independently of mite species identity, as well as in the effect of biotic and abiotic parameters of a geographic locality on mite abundance. In other words, some host or environmental properties may constrain the number of mites co-exploiting an individual host. An example of host properties that may affect mite abundance is immunocompetence (i.e. the ability to cope with parasitism), which often differs among different species (e.g., Klein and Nelson 1998; Mendes et al. 2006).

Local physical factors such as air temperature and relative humidity may strongly influence feeding rate (Kozlova 1982; Zeman 1988), reproduction (Sikes and Chamberlain 1954; Kozlova 1983, 1987) and survival (Kozlova 1983, 1987; Maurer and Baumgärtner 1992) of gamasids. A locality is characterized not only by abiotic, but also by biotic factors. In particular, each locality harbours a certain fauna of host species and a certain number of mite species. It appears that both the number of host species and the number of mite species can affect local mite abundance. The consistent decrease of mite abundance with an increase of either host or mite species richness (or both) in a region suggests that (a) mites may be "diluted" among various host species (Ostfeld and Keesing 2000a, b) and/or (b) there can be some competitive interactions within the mite community.

The degree of host specificity of a parasite species is determined by the range of host-related conditions under which this species can successfully perform. These conditions are associated with morphological, physiological and ecological traits of particular host taxa (Ward 1992). As for any taxon of arthropod parasites, in haematophagous mites these traits include the structure of host skin, the physical and chemical properties of host blood, the details of the host's immune response, and the environmental conditions of the host shelter (Krasnov et al. 2005). As with the evolution of niche breadth in free-living organisms, the level of tolerance of a mite species to the range of these conditions can be subjected to natural selection and result in either a broad (=low host specificity) or a narrow (=high host specificity) niche.

Nevertheless, host specificity values from different populations of the same mite species are still somewhat variable. To some extent, this reflects geographic differences in host availability. Indeed, the increase in the number of hosts exploited with an increase of regional host species richness suggests that whenever a new host species appears in a regional pool, at least of some species of mites add it to their host spectrum. This process is facilitated by generally low host specificity in many gamasid species. Indeed, some mites demonstrate a high degree of opportunism in the number of host species they can utilize. For example, *Haemogamasus nidi* in the Krasnodar region of southern Russia was recorded on as many as 14 host species (Shevchenko et al. 1975), whereas *Hirstionyssus isabellinus* in the northern part of Russian Far East was found to parasitize as many as 12 hosts (Yudin et al. 1976). *Laelaps echidninus*, although considered as oligoxenous by earlier authors (e.g., Bregetova 1956), was recorded on as many as 11 host species (rodents, soricomorphs and scandentians) in the Yunnan Province of China (Luo et al. 2007).

The taxonomic distinctness of the host spectrum among different populations of the same mite species was extremely variable and seems to be the product of current ecological conditions. The two main determinants of this facet of mite host specificity are the regional host pool and the regional mite community. The decrease in S_{TD} values with increasing regional host species richness is likely associated with the ability of some mite species to select from the available pool those host species that are closely related to their principal hosts (see Krasnov et al. 2004c). Interestingly, this ability is demonstrated by both obligatory (e.g., *H. isabellinus*) and opportunistic (e.g., *H. nidiformis*) blood feeders. The increase in S_{TD} with a decrease in the taxonomic diversity of the mite fauna means that as species composing a mite assemblage become taxonomically closer, some mite species such as *Hyperlaelap amphibius*, *Hyperlaelaps arvalis* and *Laelaps clethrinomydis* start to exploit more taxonomically distant hosts, possibly compensating for some negative effects of interspecific competition. The exact mechanisms behind this phenomenon remain to be studied.

Are there general patterns in parasite ecology?

One of the most important results of this study is that the relative stability of abundance within a mite species appears to be the manifestation of a more general trend. Similarity in abundance level among different populations of the same parasite species has been reported for various parasite taxa exploiting various host taxa, suggesting that there are some fundamental rules governing parasite ecology. Moreover, the percentage of variation originating from differences among parasite species, as opposed to within species appeared to be strikingly similar among vastly different parasite–host associations. Indeed, this percentage was approximately 52% in nematodes parasitic in mammals (Arneberg et al. 1997) and fish (Poulin 2006) and 47% in fleas (Krasnov et al. 2006) and mites (this study) parasitic on mammals. However, within-species repeatability of abundance appears to be higher in monogeneans and acanthocephalans (84% of variation explained by among-species difference for both: Poulin 2006).

The extent of repeatability of parasite abundance within a host species is also similar among mammalian nematodes (22% of variation explained by differences among host species as opposed to within host species; Arneberg et al. 1997), fleas (24%; Krasnov et al. 2006) and mites (29%; this study). However, this percentage was lower in metazoan parasites of fish (13%; Poulin 2006). This difference may have something to do with differences between fish and mammals leading to a higher degree of independence of parasite population parameters from host identity in fish compared to mammals. A possible reason for this may be the lower interspecific diversity of immunological defences in fish. Indeed, the fish immune system is less complex than that of mammals (Bird et al. 2006). However, this hypothesis remains to be tested.

The extent of the repeatability of abundance within regions was similar between fleas (13% of variation explained by differences among regions as opposed to within region; Krasnov et al. (2006)) and mites (10%; this study). Both taxa are ectoparasitic and are thus subjected to the influence of environmental factors. Indeed, the effect of factors such as climate and soil structure on abundance is well known for both fleas (e.g., Krasnov et al. 2001) and mites (e.g., Crystal 1986).

Data on the repeatability of host specificity among different populations of the same parasite species are available for fleas (Krasnov et al. 2005) and mites (this study) only. When host specificity is expressed as the number of hosts exploited, it appeared to be a true attribute of both flea and mite species to approximately the same extent (30% and 33% of variation originating from differences among parasite species, as opposed to within species, respectively; Krasnov et al. (2005) and this study). However, when host specificity is evaluated as the taxonomic diversity of the host spectrum, it was found to be weakly, albeit significantly, repeatable within flea species (14.4% of variation accounted for by differences among flea species), but not repeatable within mite species. Still, the repeatability of host taxonomic distinctness (index S_{TD}) within regions suggests that the set of species in the host spectrum is determined mainly by the pool of available host species. This is supported by the effect of the number of hosts in a region and their taxonomic diversity on the values of the index S_{TD} in many separate mite species. In contrast, the characteristics of the host assemblage used by a flea were unaffected by the characteristics of the regional pool of host species (Krasnov et al. 2005). This means that, in general, local host availability (in terms of host number and taxonomic diversity of the host pool) does not influence flea host specificity, but affects that of gamasids.

Both abundance and host specificity are characteristics of individual parasite species and parasite populations. Comparison of the results of this study with those of earlier studies shows that geographic patterns shown by parasites (e.g., fleas and mites) at the population and species level demonstrate a high degree of generality. However, when we looked at geographic patterns of the same two taxa at a higher hierarchical level, namely their communities, we found no universal trend. For example, the distance decay of community similarity (sensu Nekola and White 1999) holds for fleas (Krasnov et al. 2005) but not for gamasids (Vinarski et al. 2007). The effect of host body size and metabolic rate on species richness of mite assemblages is pronounced (Korallo et al. 2007), whereas flea assemblages are not associated with these host features (Krasnov et al. 2004a). This supports Poulin's (2007) suggestion that, although general laws apply to the lower (e.g., population) scales of parasite ecological studies, most patterns observed at the parasite community level are highly contingent and far from universal.

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References

Arneberg P, Skorping A, Read AF (1997) Is population density a species character? Comparative analyses of the nematode parasites of mammals. Oikos 80:289–300

Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. J Wildl Manage 62:821–841

Bird S, Zou J, Secombes C (2006) Advances in fish cytokine biology give clues to the evolution of a complex network. Curr Pharm Des 12:3051–3069

Blackburn TM, Gaston KJ (2001) Linking patterns in macroecology. J Anim Ecol 70:338–352

Boone MD, Semlitsch RD, Little EE, Doyle MC (2007) Multiple stressors in amphibian communities: effects of chemical contamination, bullfrogs, and fish. Ecol Appl 17:291–301

Bregetova NG (1956) Gamasoidea. Keys to the fauna of the USSR, Issue 61. Academy of Science of USSR, Leningrad (in Russian)

Brooks DR, McLennan DA (1991) Phylogeny, ecology, and behavior. A research program in comparative biology. University of Chicago Press, Chicago

Clarke KR, Warwick RM (1998) A taxonomic distinctness index and its statistical properties. J Appl Ecol 35:523–531

Clarke KR, Warwick RM (1999) The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Mar Ecol Prog Ser 184:21–29

Crystal MM (1986) Artificial feeding of northern fowl mites, *Ornithonyssus sylviarum* (Canestrini and Fanzago) (Acari: Macronyssidae), through membranes. J Parasitol 72:550–554

Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. Conserv Biol 14:342–355

Degen AA (1997) Ecophysiology of small desert mammals. Springer, Berlin

Fox LR, Morrow PA (1981) Specialization: species property or local phenomenon? Science 211:887–893

Furman DP (1959) Observations on the biology and morphology of *Haemogamasus ambulans* (Thorell) (Acarina: Haemogamasidae). J Parasitol 45:274–280

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. Annu Rev Ecol Syst 19:207–233

Garcia LV (2004) Escaping the Bonferroni iron claw in ecological studies. Oikos 105:657–663

Goncharova AA (1958) Biology of a gamasid mite *Hirstionyssus criceti* Sylz in the Trans-Baikalia. Sci Trans Chita Res Inst Epidemiol Microbiol Hygiene [Nauchnye Zapiski Chitinskogo Nauchno-Issledovatelskogo Instituta Epidemiologii. Microbiologii i Gigieny] 4:65–70 (in Russian)

Halliday RB (1998) Mites of Australia: a checklist and bibliography. CSIRO, Melbourne

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81:2241–2249

Kineman JJ, Hastings DA, Ohrenschall MA, Colby J, Schoolcraft DC, Klaus J, Knight J, Krager L, Hayes P, Oloughlin K., Dunbar P, Ikleman J, Anderson C, Burland J, Dietz J, Fisher H, Hannaughan A, Kelly M, Boyle S, Callaghan M, Delamana S, Di L, Gomolski K, Green D, Hochberg S, Holquist W, Johnson G, Lewis L, Locher A, Mealey A, Middleton L, Mellon D, Nigro L, Panskowitz J, Racey S, Roake B, Ross J, Row L, Schacter J, Weschler P (eds) (2000) Global ecosystems database version II: database, user's guide, and dataset documentation. US Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center. http://www.ngdc.noaa.gov/seg/ecosys/ecosys.shtml (accessed on 22 Nov 2007)

Klein SL, Nelson RJ (1998) Adaptive immune responses are linked to the mating system of arvicoline rodents. Am Nat 151:59–67

Korallo NP, Vinarski MV, Krasnov BR, Shenbrot GI, Mouillot D, Poulin R (2007) Are there general rules governing parasite diversity? Small mammalian hosts and gamasid mite assemblages. Divers Distrib 13:353–360

Kozlova RG (1982) Life cycle, feeding and reproduction in mites *Haemogamasus ambulans* (Gamasoidea, Haemogamasidae). Parazitologiya 16:219–223 (in Russian)

Kozlova RG (1983) The effect of air moisture on development, survival and behaviour of the mite *Haemogamasus nidi* (Gamasoidea, Haemogamasidae). Parazitologiya 17:293–298 (in Russian)

Kozlova RG (1987) Some questions about biology of mites *Haemolaelaps glasgowi* (Gamasoidea). Parazitologiya 21:496–499 (in Russian)

Krasnov BR, Khokhlova IS, Fielden LJ, Burdelova NV (2001) The effect of temperature and humidity on the survival of pre-imaginal stages of two flea species (Siphonaptera: Pulicidae). J Med Entomol 38:629–637

Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004a) Flea species richness and parameters of host body, host geography and host "milieu". J Anim Ecol 73:1121–1128

Krasnov BR, Mouillot D, Shenbrot GI, Khokhlova IS, Poulin R (2004b) Geographical variation in host specificity of fleas (Siphonaptera): the influence of phylogeny and local environmental conditions. Ecography 27:787–797

Krasnov BR, Shenbrot GI, Khokhlova IS, Poulin R (2004c) Relationships between parasite abundance and the taxonomic distance among a parasite's host species: an example with fleas parasitic on small mammals. Int J Parasitol 34:1289–1297

Krasnov BR, Shenbrot GI, Mouillot D, Khokhlova IS, Poulin R (2005) Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographic distance or faunal similarity? J Biogeogr 32:633–644

Krasnov BR, Shenbrot G, Khokhlova IS, Poulin R (2006) Is abundance a species attribute of haematophagous ectoparasites? Oecologia 150:132–140

Legendre S, Clobert J, Møller AP, Sorci G (1999) Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. Am Nat 153:449–463

Luo L-P, Guo X-G, Quian T-J, Wu D, Men X-Y, Dong W-G (2007) Distribution of gamasid mites on small mammals in Yunnan province, China. Insect Sci 14:71–78 (in Chinese)

Maurer V, Baumgärtner J (1992) Temperature influence on life table statistics of the chicken mite *Dermanyssus gallinae* (Acari: Dermanyssidae). Exp Appl Acarol 15:27–40

Mendes L, Piersma T, Hasselquist D, Matson KD, Ricklefs RE (2006) Variation in the innate and acquired arms of the immune system among five shorebird species. J Exp Biol 209:284–291

Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405

Morris DW (1988) Habitat-dependent population regulation and community structure. Evol Ecol 2:253–269

Nekola JC, White PS (1999) The distance decay of similarity in biogeography and ecology. J Biogeogr 26:867–878

Newton I (1998) Population limitation in birds. Academic Press, London

Ostfeld RS, Keesing F (2000a) The function of biodiversity in the ecology of vector-borne zoonotic diseases. Can J Zool 78:2061–2078

Ostfeld RS, Keesing F (2000b) Biodiversity and disease risk: the case of Lyme disease. Conserv Biol 14:722–728

Perneger TV (1998) What's wrong with Bonferroni adjustments. Br Med J 316:1236–1238

Perneger TV (1999) Adjusting for multiple testing in studies is less important than other concerns. Br Med J 318:1288

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Poulin R (2006) Variation in infection parameters among populations within parasite species: intrinsic properties versus local factors. Int J Parasitol 36:877–885

Poulin R (2007) Are there general laws in parasite ecology? Parasitology 134:763–776

Poulin R, Mouillot D (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. Parasitology 126:473–480

Poulin R, Krasnov BR, Morand S (2006) Patterns of host specificity in parasites exploiting small mammals. In: Morand S, Krasnov BR, Poulin R (eds) Micromammals and macroparasites: from evolutionary ecology to management. Springer, Tokyo, pp 233–256

Radovsky FJ (1967) The Macronyssidae and Laelapidae (Acarina: Mesostigmata) parasitic on bats. Univ Calif Publ Entomol 46:1–288

Radovsky FJ (1985) Evolution of mammalian mesostigmatid mites. In: Kim KC (ed) Coevolution of parasitic arthropods and mammals. John Wiley, New York, pp 441–504

Rothman KJ (1990) No adjustments are needed for multiple comparisons. Epidemiology 1:43–46

Shevchenko ZG, Strihanova EV, Petrova RA, Timofeev MN, Meleshko NS (1975) Materials of the study of Gamasina mites of the Krasnodar region. Problems Particularly Dangerous Infect 43–44:103–111 (in Russian)

Sikes RK, Chamberlain RW (1954) Laboratory observations on three species of bird mites. J Parasitol 40:691–697

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Thompson JN (1994) The coevolutionary process. University of Chicago Press, Chicago

Timms R, Read AF (1999) What makes a specialist special? Trends Ecol Evol 14:333–334

Tucci EC, Prado AP, Araújo RP (2005) Fecundidade de *Dermanyssus gallinae* (De Geer, 1778) (acari, dermanyssidae) em laboratório. Arq Inst Biol São Paulo 72:29–32

Vinarski MV, Korallo NP, Krasnov BR, Shenbrot GI, Poulin R (2007) Decay of similarity of gamasid mite assemblages parasitic on Paleoarctic small mammals: geographic distance, host species composition or environment? J Biogeogr 34:1691–1700

Ward SA (1992) Assessing functional explanations of host specificity. Am Nat 139:883–891

Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. Oceanogr Mar Biol 39:207–231

Wilson DE, Reeder DM (eds) (2005) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. John Hopkins University Press, Baltimore

Yudin BS, Krivosheev VG, Belyaev VG (1976) Small mammals of the Northern Far East. Nauka, Novosibirsk (in Russian)

Zeman P (1988) Surface skin lipids of birds – a proper host kairomone and feeding inducer in the poultry red mite, *Dermanyssus gallinae*. Exp Appl Acarol 5:163–173