

Inferring associations among parasitic gamasid mites from census data

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Received: 4 June 2008 / Accepted: 17 December 2008 / Published online: 3 February 2009
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Abstract Within a community, the abundance of any given species depends in large part on a network of direct and indirect, positive and negative interactions with other species, including shared enemies. In communities where experimental manipulations are often impossible (e.g., parasite communities), census data can be used to evaluate the strength or frequency of positive and negative associations among species. In ectoparasite communities, competitive associations can arise because of limited space or food, but

facilitative associations can also exist if one species suppresses host immune defenses. In addition, positive associations among parasites could arise merely due to shared preferences for the same host, without any interaction going on. We used census data from 28 regional surveys of gamasid mites parasitic on small mammals throughout the Palaearctic, to assess how the abundance of individual mite species is influenced by the abundance and diversity of other mite species on the same host. After controlling for several confounding variables, the abundance of individual mite species was generally positively correlated with the combined abundances of all other mite species in the community. This trend was confirmed by meta-analysis of the results obtained for separate mite species. In contrast, there were generally no consistent relationships between the abundance of individual mite species and either the species richness or taxonomic diversity of the community in which they occur. These patterns were independent of mite feeding mode. Our results indicate either that synergistic facilitative interactions among mites increase the host's susceptibility to further attacks (e.g., via immunosuppression) and lead to different species all having increased abundance on the same host, or that certain characteristics make some host species preferred habitats for many parasite species.

Communicated by Roland Brandl.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-009-1278-0) contains supplementary material, which is available to authorized users.

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Keywords Dermanysoidea · Ectoparasites · Facilitation · Meta-analysis · Phylogenetic contrasts

Introduction

The abundance of a species in a given location depends on a variety of biotic and abiotic factors. In particular, it depends on the relationships with other co-occurring

species. These relationships may affect the abundance of a given species negatively if a community is competitive or positively if a community is facilitative (Rosenzweig 1981). Interspecific interactions that affect the abundance of a given species are not necessarily direct. A variety of indirect interactions can result in variation in the abundances of interacting species. For example, two species may develop a negative association mediated by a shared predator (apparent competition; Holt 1997), or a positive association mediated by a shared competitor (apparent facilitation; Levine 1999). In addition, shared preferences may result in positive associations among species even in the absence of any interspecific interactions.

The occurrence and the form of interspecific interactions in a community can be explicitly demonstrated by field experiments only. Indeed, manipulative experiments have produced convincing examples of pairwise interspecific competitive interactions (see Schoener 1983; Gurevitch et al. 1992, 2000 for reviews). However, field experiments are not only logistically difficult, but are sometimes even impossible. Indeed, few would deny that it is unfeasible to carry out experimental studies on all pairs of species in a community. An alternative is to get an insight into species interactions based on census data (e.g., Crowell and Pimm 1976; Fox and Luo 1996). Some of these methods have been criticized (e.g., Abramsky et al. 1986), but census data nevertheless allow one to identify the potential types of species interactions, and to estimate their relative frequencies, within a community. Furthermore, the biology of some communities simply does not allow species abundances to be manipulated experimentally. For example, communities of parasitic species are very difficult to manipulate. However, it is extremely important to understand the rules that govern parasite communities because parasites form a large proportion of the diversity of life, and because parasitism is a key component in food webs as it is the most common consumer strategy among organisms (Sukhdeo and Bansemir 1996; Poulin and Morand 2004; Lafferty et al. 2008). Moreover, understanding patterns of co-variation of parasite abundances independent of its mechanisms may give us insights into factors associated with the evolution of: (1) selection for a strong or a weak defense system in a host (interhost variation in the number of parasite individuals and species exploiting it), and (2) selection for strong or weak countermeasures against host defenses in a parasite (inter-parasite variation in the number and diversity of co-exploiters). Methods based on census data seem to be almost the only approach available for the study of species interactions within parasite communities (Poulin 2005); some examples of manipulative experiments with parasitic species also exist, though they involve only few species pairs (Patrick 1991; Bush and Malenke 2008).

Recently, we used census data on fleas parasitic on small mammals to better understand the type of species associations that prevail in flea communities (Krasnov et al. 2005). In particular, we tested whether the abundance of any given flea species in a community is affected by either the total abundance of all other co-occurring flea species or the diversity of the flea community. The rationale of this study was based on the hypothesis that suppression of host defense systems resulting from the high abundance of one or more parasite species or/and high parasite diversity (that supposedly requires multiple defense responses) could lead to interspecific facilitation among parasites. If this is true, then the abundance of a given species should be positively correlated with either the abundance of other co-occurring species or their diversity or both. The results of that study suggested that at the level of the component community (an assemblage of parasite species in a host population) as well as the compound community (assemblages of parasite species in a host community), interactions among flea species might be characterized as apparent facilitation mediated via the host and involving suppression of host immune defenses. In other words, the main reason why this type of interspecific interactions occurs in flea communities seems to be the obligate haematophagy of all species in the community. If so, then we may expect that interactions within communities of ectoparasites with different feeding modes will show different patterns. For example, facultative parasites undoubtedly exert less pressure on a host than obligate parasites, and their suppression of host immune response is likely weak (if it occurs at all). Consequently, positive relationships between abundances of facultative parasites resulting from an increase in the host's susceptibility to further attack due to suppression of its defenses should also be weak.

To test this prediction, we used data on haematophagous gamasid mites belonging to the superfamily Dermanyssoidea parasitic on small mammals in the Palaearctic, and examined how the overall abundance and diversity of component mite communities affect the abundance of individual mite species in these communities. In the present study, the analyses are carried out in approximately the same way on more or less the same host species as in our aforementioned study of flea communities (Krasnov et al. 2005), providing a good basis for comparisons between flea and mite community organization. Such comparisons between taxa are necessary to discern any general pattern governing community organization in parasites (Poulin 2007). The interspecific variation in the ecology and feeding mode of gamasids is enormous, ranging from predatory to endoparasitic (see Radovsky 1985 for review). We focused on mites collected from host body surfaces. These mites included both facultative and obligatory haemato- and/or lymphophages. Among the latter, there were species that feed solely on a host's blood (obligate exclusive haematophages) and species that feed on both a host's blood

and small arthropods (obligate non-exclusive haematophages). We expected that facilitative interactions would be: (1) less pronounced across all mite species than across fleas due to the marked variation in the feeding modes of the former, and (2) more pronounced across obligate exclusively haematophagous mites than for obligate non-exclusively and facultatively haematophagous mites.

Materials and methods

Data set

Data on gamasid mites collected from the bodies of small mammals (Soricomorpha, Erinaceomorpha, Lagomorpha and Rodentia) in 28 different regions of the Palaearctic were obtained from published surveys and unpublished data that reported the number of mites of each of the different species found on each given small mammal species in a particular location (see Supplementary data). Details of the sampling methods used in these studies are published elsewhere (Korallo et al. 2007). We used only those sources where sampling effort (the number of examined hosts) was reported. The data set comprised data on 310,098 individual mites collected from 248,031 individual mammals. Information on feeding mode of mites was taken from Zemskaya (1969, 1973), Radovsky (1985) and Tagiltsev and Tarasevich (1982).

Estimates of mite abundance and diversity

We selected mite species that were recorded on at least eight host species across regions. For each mite species on each host species in each region we calculated the mean abundance of this species, the pooled abundance of other co-occurring mite species, overall mite species richness and values of the taxonomic distinctness (Δ^+) of the co-occurring mite assemblage (see below). We used the mean number of mite individuals per individual host of a given species as a measure of mean mite abundance. Other measurements of infection level, such as prevalence and intensity of mite infestation, were not available for the majority of the regions considered. Some host and mite species occurred in more than one region; measurements of abundance and diversity for these combinations were averaged across regions. Each host–mite combination was treated as an independent data point. Unequal study effort among host species may result in confounding variation in estimates of parasite abundance. In addition, hosts of different body size can support different numbers of ectoparasites. To ensure that variation in among-host sampling effort and body size did not bias estimates of mite abundance, we regressed log-transformed estimates of mite abundance per host against

the log-transformed number of hosts examined and the log-transformed body surface area of a host for each mite-host association. Body surface area of a host species was estimated from host body mass following Walsberg and Wolf (1995). Data on mean body mass were obtained either from original sources or from Silva and Downing (1995). Estimates of mite abundance per host were affected by both sampling effort and host body surface ($r^2 = 0.22$, $F_{2,650} = 89.9$ for a “target” mite abundance and $r^2 = 0.70$, $F_{2,650} = 775.1$ for pooled abundance of co-occurring mite species, $P < 0.0001$). Consequently, in subsequent analyses we substituted the original values of mite abundance by residuals of the regression of log-transformed mite abundance against the log-transformed number of hosts examined and log-transformed host body surface area.

The two measures of mite species diversity we used were: the number of mite species found on a host species, or species richness; and the average Δ^+ of the mites present. When these mite species are placed within a taxonomic hierarchy, the average Δ^+ is the mean number of steps up the hierarchy that must be taken to reach a taxon common to two species, computed across all possible pairs of species (Clarke and Warwick 1998, 1999; Warwick and Clarke 2001; Poulin and Mouillot 2003). The greater the Δ^+ between mite species, the higher the number of steps needed, and the higher the value of the index Δ^+ . To calculate Δ^+ , we used the taxonomic classification of Bregetova (1956), Radovsky (1985) and Halliday (1998) and fitted all mite species into a taxonomic structure with four hierarchical levels above species, i.e., genus, subfamily, family and superfamily (Dermanyssoidea). Calculations were made with a computer program developed by D. M. and R. P. using Borland C++ Builder 6.0 (available at <http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>).

Estimates of parasite species richness may also be biased due to unequal host sampling effort (Morand and Poulin 1998). Indeed, log-transformed values of mite richness were strongly affected by number of hosts examined ($r^2 = 0.47$, $F_{1,651} = 587.5$, $P < 0.001$). In addition, the species richness of a mite assemblage (i.e., the number of mite species exploiting a host species in a region) was weakly, but significantly correlated with Δ^+ ($r^2 = 0.07$, $F_{1,651} = 43.2$, $P < 0.001$), indicating that this measure was influenced by the number of species in a host’s mite assemblage. Consequently, values of mite richness and Δ^+ were substituted by their residual deviations from log–log linear regressions on the number of hosts examined or the number of mite species in an assemblage, respectively.

Data analysis

We analyzed relationships between the abundance of a mite species and: (1) the pooled abundance of co-occurring mite

species in the assemblage, and (2) species richness and Δ^+ of the mite assemblage. This was done using Pearson product-moment correlation coefficients within mite species among all host species on which they occurred. Nevertheless, treating values of abundance and diversity of mites calculated for different host species as independent observations can introduce a bias in the analysis. To control for the effects of host phylogeny, we used the method of independent contrasts (Felsenstein 1985). The phylogenetic trees of hosts were derived from various sources (see Grenyer and Purvis 2003; Krasnov et al. 2004 for details). To compute independent contrasts, we used the PDAP: PDTREE program (Garland et al. 1993; Midford et al. 2007) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2007). Independent contrasts were standardized as suggested by Garland et al. (1992). To test for the correlation between a mite's abundance (dependent variable) and the abundance of all other co-occurring mites, or the species richness and Δ^+ of mite assemblages (independent variables), we regressed standardized contrasts of the dependent variable against standardized contrasts of the independent variables using major axis regression forced through the origin (Pagel 1992; Garland et al. 1992) for each mite species.

Then, Pearson's rank correlation coefficients between dependent and independent variables were Fisher's z -transformed and used as measures of effect size for meta-analyses across mite species. We used the number of host species on which a mite was recorded across regions as sample size for each observation. A combined estimate of the effect size was calculated using both fixed effects and random effects algorithms, which produced similar results. To assess heterogeneity among mite species, we calculated the inconsistency index (I^2) (Higgins and Thompson 2002; Higgins et al. 2003) as $I^2 = [(Q - df)/Q] \times 100\%$, where Q is the χ^2 statistic. Because substantial heterogeneity among mite species was revealed (value of I^2 50%, see below), we present the results using the random effects algorithm only. Meta-analysis was carried out using the software package Comprehensive Meta-Analysis version 2 (Biostat, Englewood, N.J.).

When multiple tests are carried out, the probability of achieving significant results is greater because there is an increased probability of rejecting the null hypothesis. To overcome this problem, adjustment of the α level is usually suggested in order to reduce the probability of obtaining spurious results (e.g., Bonferroni correction). However, this approach has been shown to often lead to the incorrect acceptance of the false null hypothesis, so it has been increasingly criticized by statisticians and ecologists in recent years (Rothman 1990; Perneger 1998, 1999; Moran 2003; Garcia 2004). Hence, we report our results prior to and after the Bonferroni correction.

Results

Across the 28 regions, there were a total of 1,801 mite species-host species-region combinations involving 78 mite species and 79 host species. There were 29 mite species that occurred in at least eight host species across all regions. Among them, three species were facultative haematophagous, nine species were obligate exclusive haematophages and the remaining 17 species were obligate non-exclusive haematophages. These mites were recorded on average on 4.3 host species per region (a maximum of 23 host species) and comprised 654 mite-host associations.

In 16 out of these 29 mite species, the mean abundance was significantly correlated either with the mean abundance of all other co-occurring mite species or with one of the measures of the diversity of mite assemblages, or both. In particular, across host species, the mean abundance of a mite was significantly positively correlated with the mean abundance of co-occurring heterospecific mites in 12 cases (four obligate exclusive haematophages, seven obligate non-exclusive haematophages and one facultative haematophagous) and significantly negatively correlated in one mite species (obligate exclusive haematophagous; Table 1). However, after the Bonferroni adjustment of α level, significant positive correlations between the mean abundance of a mite and the mean abundance of co-occurring mites were recorded for three obligate non-exclusive haematophages only (Table 1). When the method of independent contrasts was applied, a significant positive correlation between the mean abundance of a mite and the mean abundance of co-occurring heterospecific mites was found in ten mite species (six species after the Bonferroni adjustment), whereas no significant negative correlation was found in any species (Table 1). The correlations based on phylogenetic contrasts support the results of conventional statistics for seven mites (an illustrative example using the mite *Androlaelaps casalis* is presented in Fig. 1), but not for three obligate non-exclusive haematophages (*Hyperlaelaps amphibius*, *Hyperlaelaps arvalis* and *Laelaps multispinosus*); the correlation was only revealed using phylogenetic contrasts in the facultative haematophagous *Eulaelaps stabularis*. Interestingly, the occurrence of a significant association between abundance of a mite and abundance of all co-occurring mites differed between the two largest gamasid genera present in our dataset. Significant positive correlation was found in six of eight species of *Haemogamasus* and in two (or one if the method of independent contrasts was used) of nine species of *Laelaps* (Table 1).

The results of the meta-analyses showed a significant overall positive effect of the abundance of co-occurring mites of all species on the mean abundance of a given mite across all 29 species (Fig. 2). Meta-analysis of the Fisher's z -transformed Pearson's correlation coefficients produced

Table 1 Summary of correlation analysis [Pearson product-moment correlation using conventional statistics (CS) and independent contrasts (IC)] between the abundance of a mite species and the abundance of all other co-occurring mite species across different host species, for 28 mite species

Mite species	CS	IC
<i>Androlaelaps casalis</i> (ONEH)	0.64*	0.54*
<i>Androlaelaps fahrenheitzi</i> (ONEH)	0.16 n.s.	−0.22 n.s.
<i>Androlaelaps pavlovskiyi</i> (ONEH)	−0.62 n.s.	−0.31 n.s.
<i>Echinonyssus apodemi</i> (OEH)	−0.33 n.s.	−0.14 n.s.
<i>Echinonyssus criceti</i> (OEH)	−0.11 n.s.	−0.14 n.s.
<i>Echinonyssus eusoricis</i> (OEH)	−0.37*	0.09 n.s.
<i>Echinonyssus isabellinus</i> (OEH)	0.34**	0.38**
<i>Echinonyssus transiliensis</i> (OEH)	0.05 n.s.	0.17 n.s.
<i>Eulaelaps stabularis</i> (FH)	0.05 n.s.	0.28*
<i>Haemogamasus ambulans</i> (ONEH)	0.62**	0.50**
<i>Haemogamasus dauricus</i> (ONEH)	0.68**	0.81**
<i>Haemogamasus hirsutus</i> (OEH)	0.84**	0.88**
<i>Haemogamasus liponyssoides</i> (OEH)	0.01 n.s.	0.02 n.s.
<i>Haemogamasus mandschuricus</i> (ONEH)	0.58**	0.50**
<i>Haemogamasus nidi</i> (FH)	−0.07 n.s.	−0.28 n.s.
<i>Haemogamasus nidiformis</i> (FH)	0.44*	0.43*
<i>Haemogamasus serdjukovae</i> (OEH)	0.65**	0.76**
<i>Hyperlaelaps amphibius</i> (ONEH)	0.75**	0.19 n.s.
<i>Hyperlaelaps arvalis</i> (ONEH)	0.40*	0.16 n.s.
<i>Laelaps agilis</i> (ONEH)	0.08 n.s.	0.01 n.s.
<i>Laelaps algericus</i> (ONEH)	0.22 n.s.	0.34 n.s.
<i>Laelaps clethrionomydis</i> (ONEH)	−0.04 n.s.	−0.10 n.s.
<i>Laelaps hilaris</i> (ONEH)	−0.28 n.s.	−0.37 n.s.
<i>Laelaps jetmari</i> (ONEH)	−0.28 n.s.	0.09 n.s.
<i>Laelaps lemmi</i> (ONEH)	−0.14 n.s.	−0.16 n.s.
<i>Laelaps multispinosus</i> (ONEH)	0.64**	0.45 n.s.
<i>Laelaps muris</i> (ONEH)	0.01 n.s.	−0.36 n.s.
<i>Laelaps nuttalli</i> (ONEH)	0.74**	0.81**
<i>Myonyssus ingricus</i> (OEH)	−0.39 n.s.	−0.40 n.s.

Italicized coefficients of correlation remained significant after the Bonferroni adjustment. Feeding modes of mite (*in parentheses*) are obligate non-exclusive haematophagy (ONEH), obligate exclusive haematophagy (OEH), facultative haematophagy (FG)
 * $P < 0.05$, ** $P < 0.01$, n.s. non-significant (prior to the Bonferroni adjustment)

by conventional statistics demonstrated that the combined effect size was 0.31 ± 0.11 and the 95% confidence interval for the point estimate ranged from 0.11 to 0.49, and did not overlap 0. Heterogeneity among species was high as evaluated by I^2 (82.8%). When correlation coefficients produced by the method of independent contrasts were used, the results of the meta-analysis were essentially the same. The combined effect size was 0.26 ± 0.11 , whereas the 95% confidence interval for the point estimate ranged from 0.05 to 0.48. Heterogeneity among species was also high ($I^2 = 82.3%$). Meta-analyses carried out separately for the

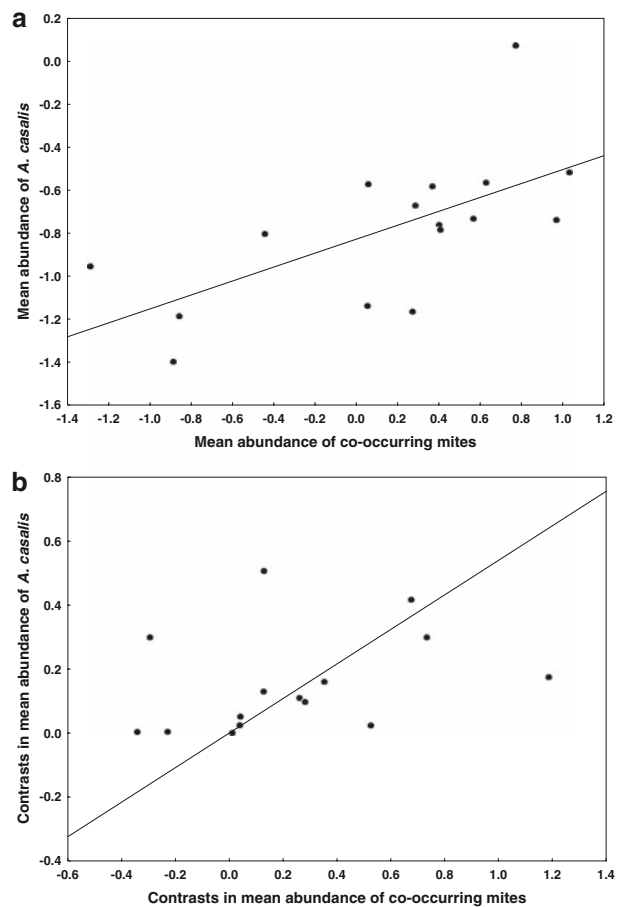


Fig. 1 Relationships between the mean abundance of *Androlaelaps casalis* and the abundance of all other co-occurring mite species using conventional statistics (a) and the method of independent contrasts (b)

two largest genera supported the existence of a positive relationship between a mite’s abundance and that of all other mites in *Haemogamasus* (conventional statistics, combined effect 0.60 ± 0.20 , 95% confidence interval 0.29–0.80, $I^2 = 81.5%$; method of independent contrasts, combined effect 0.72 ± 0.33 , 95% confidence interval 0.25–0.92, $I^2 = 92.9%$), but not in *Laelaps* (conventional statistics, combined effect 0.20 ± 0.19 , 95% confidence interval from -0.16 to 0.51 , $I^2 = 76.5%$; method of independent contrasts, combined effect -0.07 ± 0.10 , 95% confidence interval from -0.25 to 0.12 , $I^2 = 15.3%$).

Significant relationships between the mean abundance of a mite and either measurement of mite assemblage diversity were found in 12 mite species (seven or ten species when either conventional statistics or the method of independent contrasts was used, respectively; Table 2). Of these, the mean abundance of a mite increased with an increase in the species richness of the mite assemblages in five species (two obligate exclusive haematophages and three obligate non-exclusive haematophages) and with a decrease in species richness in an other five species (two obligate

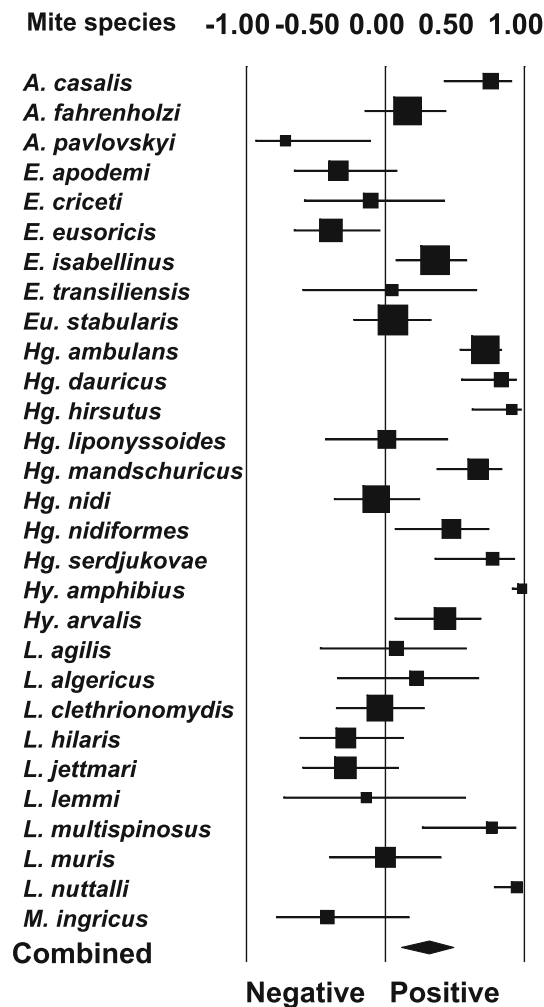


Fig. 2 Forrest plot for the meta-analysis of the relationship between the mean abundance of a given mite on a host and that of all co-occurring mites of all other species across 29 mite species. Each point represents the value of the Fisher's z -transformed correlation coefficient (using conventional statistics) and the line indicates the 95% confidence intervals, for each species separately; the size of the point is proportional to the number of host species on which the mite species was recorded. For species names, see Table 1

exclusive haematophages and three obligate non-exclusive haematophages) (see illustrative examples with *Haemogamasus hirsutus* and *Echinonyssus apodemi* in Fig. 3). After the Bonferroni adjustment, only three correlations (negative) remained significant (for obligate non-exclusive haematophages; Table 2).

The Δ^+ of mite assemblages correlated negatively with the abundance of three mite species (two obligate exclusive haematophages and one obligate non-exclusive haematophage) and positively in two species (one obligate exclusive haematophage and one obligate non-exclusive haematophage; Table 2). After the Bonferroni adjustment, only one correlation (negative) remained significant (for the obligate non-exclusive haematophage; Table 2).

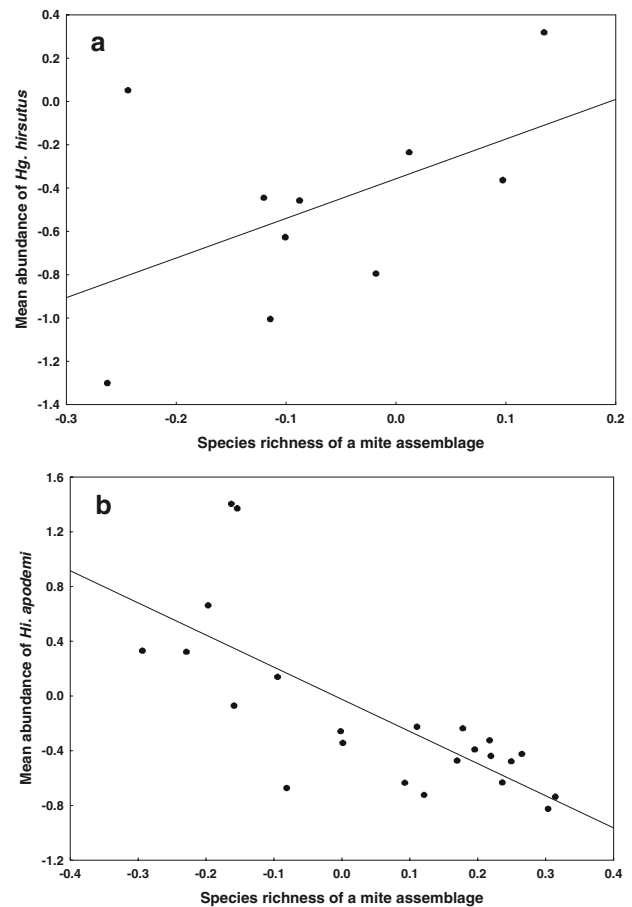


Fig. 3 Relationships between the abundance of *Haemogamasus hirsutus* (a) and *Echinonyssus apodemi* (b) and species richness of a mite assemblage across different host species using conventional statistics

Meta-analyses of the relationships between the mean abundance of a mite and the species richness of mite assemblages did not find any tendency. When the results of conventional statistics were used, the combined effect was -0.03 ± 0.09 with 95% confidence intervals from -0.21 to 0.15 . For correlations produced by the method of independent contrasts, the combined effect was -0.01 ± 0.10 with 95% confidence intervals from -0.20 to 0.18 . The same was true for the relationships between the mean abundance of a mite and the Δ^+ of mite assemblages. The combined effects were -0.04 ± 0.05 for correlations obtained from conventional analyses and -0.04 ± 0.05 for correlations obtained from the method of independent contrasts. Ninety-five percent of confidence intervals were from -0.15 to 0.07 and from -0.13 to 0.06 , respectively.

Discussion

The results of this study demonstrate that, in general, the abundance of an individual mite species correlates positively,

Table 2 Summary of correlation analysis (Pearson product-moment correlation using CS and IC) between the abundance of a mite species and species richness (SR) and taxonomic distinctness (Δ^+) of the mite assemblage, across different host species, for 28 mite species

Mite species	CS		IC	
	SR	Δ^+	SR	Δ^+
<i>A. casalis</i> (ONEH)	0.54*	0.15 n.s.	0.41 n.s.	0.05 n.s.
<i>A. fahrenheitzi</i> (ONEH)	−0.07 n.s.	−0.21 n.s.	−0.33*	−0.01 n.s.
<i>A. pavlovskiyi</i> (ONEH)	−0.24 n.s.	0.62 n.s.	−0.32 n.s.	0.01 n.s.
<i>Echinonyssus apodemi</i> (OEH)	−0.73**	0.02 n.s.	−0.71**	−0.40*
<i>Echinonyssus criceti</i> (OEH)	−0.19 n.s.	0.14 n.s.	−0.32 n.s.	−0.12 n.s.
<i>Echinonyssus eusoricis</i> (OEH)	−0.18 n.s.	−0.38*	0.37*	0.07 n.s.
<i>Echinonyssus isabellinus</i> (OEH)	0.15 n.s.	−0.02 n.s.	0.25 n.s.	−0.13 n.s.
<i>Echinonyssus transiliensis</i> (OEH)	0.43 n.s.	0.01 n.s.	0.49 n.s.	0.04 n.s.
<i>Eulaelaps stabularis</i> (FH)	−0.07 n.s.	−0.18 n.s.	0.22 n.s.	0.01 n.s.
<i>Haemogamasus ambulans</i> (ONEH)	0.25 n.s.	0.02 n.s.	0.26 n.s.	0.07 n.s.
<i>Haemogamasus dauricus</i> (ONEH)	0.60*	−0.34 n.s.	0.53*	−0.16 n.s.
<i>Haemogamasus hirsutus</i> (OEH)	0.75*	0.67*	0.70**	0.35 n.s.
<i>Haemogamasus liponyssoides</i> (OEH)	−0.23 n.s.	−0.21 n.s.	−0.12 n.s.	−0.28 n.s.
<i>Haemogamasus mandschuricus</i> (ONEH)	0.27 n.s.	0.10 n.s.	0.17 n.s.	0.21 n.s.
<i>Haemogamasus nidi</i> (FH)	0.10 n.s.	−0.02 n.s.	0.04 n.s.	0.02 n.s.
<i>Haemogamasus nidiformis</i> (FH)	−0.06 n.s.	0.01 n.s.	0.18 n.s.	−0.03 n.s.
<i>Haemogamasus serdjukovae</i> (OEH)	0.15 n.s.	−0.16 n.s.	0.18 n.s.	0.02 n.s.
<i>Hyperlaelaps amphibius</i> (ONEH)	−0.65 n.s.	0.54 n.s.	−0.52 n.s.	0.69**
<i>Hyperlaelaps arvalis</i> (ONEH)	−0.07 n.s.	0.09 n.s.	−0.22 n.s.	0.21 n.s.
<i>L. agilis</i> (ONEH)	0.38 n.s.	0.11 n.s.	0.61*	0.01 n.s.
<i>L. algericus</i> (ONEH)	0.11 n.s.	−0.52 n.s.	0.10 n.s.	−0.40 n.s.
<i>L. clethrionomydis</i> (ONEH)	0.06 n.s.	0.01 n.s.	0.04 n.s.	0.01 n.s.
<i>L. hilaris</i> (ONEH)	−0.34 n.s.	0.16 n.s.	−0.66**	0.03 n.s.
<i>L. jettmari</i> (ONEH)	−0.33 n.s.	−0.47*	−0.01 n.s.	−0.51**
<i>L. lemmi</i> (ONEH)	−0.24 n.s.	0.17 n.s.	−0.08 n.s.	−0.02 n.s.
<i>L. multispinosus</i> (ONEH)	−0.42 n.s.	−0.41 n.s.	−0.79**	0.26 n.s.
<i>L. muris</i> (ONEH)	−0.15 n.s.	0.20 n.s.	0.08 n.s.	0.20 n.s.
<i>L. nuttalli</i> (ONEH)	−0.02 n.s.	−0.43 n.s.	0.11 n.s.	−0.64 n.s.
<i>Myonyssus ingricus</i> (OEH)	−0.59*	0.21 n.s.	−0.19 n.s.	−0.04 n.s.

Italicized coefficients of correlation remained significant after the Bonferroni adjustment. See Table 1 for other abbreviations
* $P < 0.05$, ** $P < 0.01$, n.s. (prior to the Bonferroni adjustment)

albeit weakly, with the abundance of all other mite species in a component community, whereas the correlation of mite abundance against the diversity of the mite community may be both negative and positive. However, our expectation that these patterns will differ between mites with different feeding modes did not receive any support except that no relationship between mite abundance and diversity of the surrounding mite community was found in mites that feed on the blood of their hosts only facultatively.

Positive correlations between the abundance of a mite and the pooled abundances of all other co-occurring mites may be a manifestation of apparent interspecific facilitation mediated via the host. Hereafter, for simplicity, we consider interspecific facilitation only. However, intraspecific facilitation could act in parallel, with higher numbers of both conspecific and heterospecific mites resulting in facilitation of subsequent attacks. Nevertheless, the potential for

intraspecific facilitation within mite species seems to vary strongly among species. This is because: (1) abundance of a mite species varies among different populations of the same species only within relatively narrow species-specific boundaries, and (2) many mite species are characterized by low levels of abundance (Korallo-Vinarskaya et al. 2009). In other words, intraspecific facilitation may compensate for the lack of interspecific facilitation in some mite species, but this will undoubtedly not be the case for other mite species.

The pressure due to parasitism by one abundant mite species may cause the host species to be more prone to attacks by mites belonging to other species. One of the mechanisms behind this may be immunosuppression caused by high numbers of attackers (Barriga 1999; Duerr et al. 2003). Another mechanism can be related to the cost of the immune defense system which is presumably high (Sheldon and Verhulst 1996). Consequently, if the parasite

pressure is too heavy, a host attacked by a great number of parasites may be forced to give up its immune response and yield to parasites (Combes 2001). These two mechanisms can apply to any parasite taxon. The pattern found in this study for gamasid mites can also be explained by some peculiarities in their feeding ecology. Indeed, “cooperative feeding” has been described in some mites such as *Androlaelaps fahrenheitsi* (Furman 1959a), *Androlaelaps centocarpus* (Furman 1966) and *Haemogamasus liponyssoides* (Radovsky 1960) when multiple individuals feed from a single skin lesion or puncture. It is possible that “feeding cooperation” may take place not only between conspecific individuals but also between heterospecific individuals, although the latter has never been documented. Nevertheless, indirect evidence of cross-resistance of a host not only against closely related (e.g., McTier et al. 1981), but also against distantly related arthropod ectoparasites (e.g., den Hollander and Allen 1986) suggests the likelihood of heterospecific feeding cooperation.

However, there can be at least two reasons other than interspecific interactions mediated via the host behind positive correlations between mite abundances. First, some host species may represent better habitats for multiple mite species than other host species due to some of their inherent characters. Obviously, characters that make a host species preferred over other host species by a haematophagous parasite could be the same for different taxa of haematophages. These are characters that allow a parasite either to obtain more food or to obtain food of higher quality, or that make food acquisition easier (Kelly and Thompson 2000; Krasnov et al. 2005). For example, hosts may differ in their skin structure which may be extremely important for mite feeding. Indeed, mouth apparatuses in many mite species, even in those that are obligate parasites, do not demonstrate sharp morphological changes from the generalized dermanysoid type (Radovsky 1985; Dowling 2006). Furthermore, some mite species do not possess special cheliceral adaptations for host skin penetration and typically feed from pre-existing wounds (Furman 1959a, b; Radovsky 1985; Dowling 2006). The abundance of these mites will likely vary among hosts if intraspecific agonistic interactions are more frequent in some host species than others. Interspecific variation in the level of intraspecific aggression is pronounced in small mammals (Adams 1980). Another explanation for preferences of one host species over another host species by any haematophage may involve interspecific differences in blood composition (e.g., amino acid ratio; Harrington et al. 2001; Lehane 2005). This variation causes differences in the energy expenditure necessary for digestion by a parasite feeding on the blood of different host species (e.g., Sarfati et al. 2005). Among-host differences in defensive abilities (e.g., immunocompetence) may also lead to a preference for weakly defended

host species over well-defended hosts by any blood-sucking ectoparasite (Gouy de Bellocq et al. 2006).

Second, some host species may tolerate higher densities of gamasids of all species than other host species. For example, there can be a species-specific limit to a host's ability to cope with multiple mite attacks, such that hosts belonging to some species die faster when infested by mites than hosts belonging to other species. However, the two explanations involving interspecific variation in either host suitability for mites or tolerance to mite attacks, albeit plausible, are weakened by the fact that the percentages of the variation in mite diversity explained by differences between host species are relatively low (10.3% for Δ^+ of mite assemblages and 24.2% for mite species richness; Krasnov et al. 2008). In other words, the diversity of gamasid mites is only weakly determined by host identity (although it is repeatable among populations of the same mite species), whereas the opposite would be the case if the between-host variation in their suitability for any mite species or their tolerance to all mite species were pronounced. Nevertheless, the role of shared host preferences in generating positive associations among parasite species (due to either suitability of a particular host species for, or its high tolerance to, all parasites) could not be a priori ruled out and deserves further investigation.

The relationships between the abundance of a given mite species and the diversity of the mite assemblages were not consistent. In other words, an increase in mite diversity was accompanied by an increase in abundance in some species and a decrease in abundance in other species. This suggests that both positive and negative interactions may exist in mite communities. The mechanisms of facilitation could be similar to those proposed for the explanation of the positive correlation between the abundance of a given mite species and pooled abundances of all other co-occurring mites. For example, low immunocompetence of a host species supposedly leads not only to an increase in the number of individual mites attacking this host but also to an increase in the number of mite species that it harbors. Negative interactions among mites may include both competition and interspecific predation. Although, to the best of our knowledge, competition between parasitic gamasids has never been studied, it cannot be ruled out a priori. Interspecific predation in gamasid mites has repeatedly been reported, although the majority of examples come from soil-dwelling rather than parasitic taxa (e.g., Walzer and Schausberger 1999). However, among five species for which we found a negative association between their abundance and species richness of mite assemblages, there were both species which fed exclusively on blood and those which utilized a mixed diet of blood and small arthropods.

The results of this study thus support the idea that both positive and negative interspecific interactions occur in

communities consisting of the same species (Callaway and King 1996; Callaway and Walker 1997; Lortie et al. 2004). These processes may operate either simultaneously or with the magnitude of each process being spatially or temporally variable (Levine 1999). In other words, species interactions in a community are represented by complex combinations of negative and positive components that can be both direct and indirect, and these interactions all contribute to shaping the relative abundances of the different species in the community (Levine 1999).

Our prediction that the relationships between mite abundance and abundance and/or diversity of the entire mite community will be manifested differently in mites with different feeding modes was not validated by the data. For example, a positive correlation between the abundance of a mite and the pooled abundances of all other co-occurring mites was found in *Haemogamasus liponyssoides* and *Haemogamasus mandschuricus*. Despite these two species being congeners, the former feeds solely on blood and has mouthparts that puncture the skin of a host (Radovsky 1960), whereas the latter feeds not only on blood but also on a variety of small arthropods and does not possess chelicerae adapted for skin penetration (Goncharova and Buyakova 1960). The degree of host specificity does not play any substantial role in the occurrence of a link between the mean abundance of a mite and the abundance and/or diversity of co-occurring mites. For example, *Haemogamasus ambulans* is a highly host opportunistic species (Korneev 2003), whereas the only two species of *Laelaps* for which the relationship between mean abundance and pooled abundance of all other mites was found are strictly host specific. The only host of *Laelaps multispinosus* is *Ondatra zibethica* (e.g., Grundmann and Tsai 1967) and the only host of *Laelaps nuttalli* is *Rattus norvegicus* (e.g., Fox 1951; Tipton 1960; Soliman et al. 2001).

A comparison of the present results with those of Krasnov et al. (2005) on the abundance patterns in component communities of fleas parasitic on small mammals suggests that some rules governing the communities of different parasite taxa within the same host taxon are similar, whereas other rules vary among parasite taxa. For example, the relationships between the mean abundance of a parasite species and the pooled abundances of other co-occurring parasites belonging to the same taxon were predominantly positive in both fleas and gamasids. Furthermore, the proportion of species in which this relationship was statistically significant among studied mites was only slightly lower than that among studied fleas (12 of 29 species versus 25 of 41 species). The main reason for this similarity is undoubtedly that many of the mechanisms of interspecific facilitation proposed above (such as interhost variation in the level of immunocompetence or immunosuppression of a host by high number of haematophagous attackers) apply equally

well to practically all taxa of blood-sucking arthropods. The lower proportion of mite species demonstrating the positive correlation between abundances as compared with fleas can be explained by the fact that even obligatory haematophagous mites do not always have to penetrate the host skin to get access to its blood but often satisfy their need for blood by utilizing dried blood drops or dead lice or fleas that previously fed on a host (Radovsky 1985; Dowling 2006).

In contrast to abundance–abundance patterns, the relationships between the abundance of a parasite and the diversity of parasite assemblages appears to be substantially different between mites and fleas. The main pattern in fleas was that the mean abundance of a given species decreased with an increase in the value of one or more measurements of their diversity (Krasnov et al. 2005), whereas mites demonstrated either a negative or positive pattern with equal frequency. The reason for this difference may lie in the similarity of life histories in fleas as opposed to the diversity of life histories seen in gamasid mites. Along those lines, it is also possible that flea species abundance increases with their diversity because fleas may act synergistically on host defenses, while there is no reason to expect an effect of mite diversity on mite abundance since facilitation is unlikely among species having a high diversity of life histories and strategies. All fleas are obligate haematophages, whereas the feeding habits of mites are incredibly diverse. Although we did not find an association between abundance–diversity patterns and the feeding mode of mites in this study, the lack of any such pattern in facultative haematophages suggests that this association may indeed exist. This issue remains to be further studied when data on more mite species become available.

Acknowledgements We thank Lajos Rózsa and two anonymous referees for their helpful comments on the earlier version of the manuscript. This study was partly supported by the Israel Science Foundation (grant no. 249/04 to Boris R. Krasnov). This is publication no. 623 of the Mitrani Department of Desert Ecology.

References

- Abramsky Z, Bowers MA, Rosenzweig ML (1986) Detecting interspecific competition in the field: testing the regression method. *Oikos* 47:199–204
- Adams DB (1980) Motivational systems of agonistic behavior in murid rodents: a comparative review and neural model. *Aggress Behav* 6:295–346
- Barriga OO (1999) Evidence and mechanisms of immunosuppression in tick infestations. *Genet Anal Biomol Eng* 15:139–142
- Bregetova NG (1956) Gamasoidea. Keys to the fauna of the USSR, issue 61. Academy of Science of USSR, Leningrad (in Russian)
- Bush SE, Malenke JR (2008) Host defence mediates interspecific competition in ectoparasites. *J Anim Ecol* 77:558–564
- Callaway RM, King L (1996) Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* 77:1189–1195

- Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965
- 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
- Crowell KL, Pimm SL (1976) Competition and niche shifts introduced onto small islands. *Oikos* 27:251–258
- Combes C (2001) Parasitism: the ecology and evolution of intimate interactions. University of Chicago Press, Chicago
- den Hollander N, Allen JR (1986) Cross-reactive antigens between a tick *Dermacentor variabilis* (Acari: Ixodidae) and a mite *Prosopites cuniculi* (Acari: Psoroptidae). *J Med Entomol* 23:44–50
- Dowling APG (2006) Mesostigmatid mites as parasites of small mammals: systematics, ecology, and the evolution of parasitic associations. In: Morand S, Krasnov BR, Poulin R (eds) *Micromammals and macroparasites: from evolutionary ecology to management*. Springer, Tokyo, pp 103–117
- Duerr HP, Dietz K, Schulz-Key H, Büttner DW, Eichner M (2003) Density-dependent parasite establishment suggests infection-associated immunosuppression as an important mechanism for parasite density regulation in onchocerciasis. *Trans R Soc Trop Med Hyg* 97:242–250
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15
- Fox I (1951) Relative and seasonal abundance of the common rat ectoparasites of San Juan, Puerto Rico. *J Parasitol* 37:85–95
- Fox BJ, Luo J (1996) Estimating competition coefficients from census data: a re-examination of the regression technique. *Oikos* 77:291–300
- Furman DP (1959a) Feeding habits of symbiotic mesostigmatid mites of mammals in relation to pathogen-vector potentials. *Am J Trop Med Hyg* 8:5–12
- Furman DP (1959b) Observations on the biology and morphology of *Haemogamasus ambulans* (Thorell) (Acarina: Haemogamasidae). *J Parasitol* 45:274–280
- Furman DP (1966) Biological studies on *Haemolaelaps centrocarpus* Berlese (Acarina: Laelapidae) with observations on its classification. *J Med Entomol* 2:331–335
- García LV (2004) Escaping the Bonferroni iron claw in ecological studies. *Oikos* 105:657–663
- Garland T, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol* 41:18–32
- Garland T, Dickerman AW, Janis CM, Jones JA (1993) Phylogenetic analysis of covariance by computer simulation. *Syst Biol* 42:265–292
- Goncharova AA, Buyakova TG (1960) Biology of *Haemogamasus mandschuricus* Vtzh. in Trans-Baikalia (Far Eastern area). *Parasitol Collect* 19:155–163 (in Russian)
- Gouy de Belloq J, Krasnov BR, Khokhlova IS, Pinshow B (2006) Temporal dynamics of a T-cell mediated immune response in desert rodents. *Comp Biochem Physiol A* 145:554–559
- Grenyer R, Purvis A (2003) A composite species-level phylogeny of the “Insectivora” (Mammalia: Order Lipotyphla Haeckel, 1866). *J Zool* 260:245–257
- Grundmann AW, Tsai Y-H (1967) Some parasites of the muskrat, *Ondatra zibethicus osoyoosensis* (Lord, 1863) Miller, 1912 from the Salt Lake Valley, Utah. *Trans Am Microsc Soc* 86:139–144
- Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in field experiments. *Am Nat* 140:539–572
- Gurevitch J, Morrison JA, Hedges LV (2000) The interaction between competition and predation: a meta-analysis of field experiments. *Am Nat* 155:435–453
- Halliday RB (1998) *Mites of Australia: a checklist and bibliography*. CSIRO, Melbourne
- Harrington LC, Edman JD, Scott TW (2001) Why do female *Aedes aegypti* (Diptera: Culicidae) feed preferentially and frequently on human blood? *J Med Entomol* 38:411–422
- Higgins JPT, Thompson SG (2002) Quantifying heterogeneity in a meta-analysis. *Stat Med* 21:1539–1558
- Higgins JPT, Thompson SG, Deeks JJ, Altman DG (2003) Measuring inconsistency in meta-analysis. *Br Med J* 327:557–560
- Holt RD (1997) Predation, apparent competition, and the structure of prey communities. *Theor Popul Biol* 12:197–229
- Kelly DW, Thompson CE (2000) Epidemiology and optimal foraging: modeling the ideal free distribution of insect vectors. *Parasitology* 120:319–327
- 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
- Korallo-Vinarskaya NP, Krasnov BR, Vinarski MV, Shenbrot GI, Mouillot D, Poulin R (2009) Stability in abundance and niche breadth of gamasid mites across environmental conditions, parasite identity and host pools. *Evol Ecol* (in press)
- Korneev VA (2003) Ecological connections between gamasid mites (Arachnida, Gamasoidea) and small mammals in forest biotopes of the Middle Volga region. *Russ J Ecol* 34:133–137
- Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004) 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 (2005) Abundance patterns and coexistence processes in communities of fleas parasitic on small mammals. *Ecography* 28:453–464
- Krasnov BR, Korallo-Vinarskaya NP, Vinarski MV, Shenbrot GI, Mouillot D, Poulin R (2008) Searching for general patterns in parasite ecology: host identity vs. environmental influence on gamasid mite assemblages in small mammals. *Parasitology* 135:229–242
- Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R, Thieltges DW (2008) Parasites in food webs: the ultimate missing links. *Ecol Lett* 11:533–546
- Lehane MJ (2005) *The biology of blood-sucking in insects*, 2nd edn. Cambridge University Press, Cambridge
- Levine JM (1999) Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80:1762–1769
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI, Callaway RM (2004) Rethinking plant community theory. *Oikos* 107:433–438
- Maddison WP, Maddison DR (2007) Mesquite: a modular system for evolutionary analysis, version 2.0. <http://mesquiteproject.org>
- McTier TL, George JE, Bennet SN (1981) Resistance and cross-resistance of guinea pigs to *Dermacentor andersoni* Stiles, *D. variabilis* (Say), *Amblyomma americanum* (Linnaeus) and *Ixodes capularis* Say. *J Parasitol* 67:813–822
- Midford PE, Garland T, Maddison W (2007) PDAP:PDTree package for Mesquite, version 1.09. http://mesquiteproject.org/pdap_mesquite/index.html
- Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100:403–405
- Morand S, Poulin R (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evol Ecol* 12:717–727
- Pagel MD (1992) A method for the analysis of comparative data. *J Theor Biol* 156:431–442
- Patrick MJ (1991) Distribution of enteric helminths in *Glaucomys volans* L. (Sciuridae): a test for competition. *Ecology* 72:755–758
- 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
- Poulin R (2005) Detection of interspecific competition in parasite communities. *J Parasitol* 91:1232–1235
- Poulin R (2007) Are there general laws in parasite ecology? *Parasitology* 134:763–776
- Poulin R, Morand S (2004) Parasite biodiversity. Smithsonian Institution Press, Washington
- Poulin R, Mouillot D (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology* 126:473–480
- Radovsky FJ (1960) Biological studies on *Haemogamasus liponyssoides* Ewing (Acarina: Haemogamasidae). *J Parasitol* 46:410–417
- Radovsky FJ (1985) Evolution of mammalian mesostigmatid mites. In: Kim KC (ed) *Coevolution of parasitic arthropods and mammals*. Wiley, New York, pp 441–504
- Rosenzweig ML (1981) A theory of habitat selection. *Ecology* 62:327–335
- Rothman KJ (1990) No adjustments are needed for multiple comparisons. *Epidemiology* 1:43–46
- Sarfati M, Krasnov BR, Ghazaryan L, Khokhlova IS, Fielden LJ, Degen AA (2005) Energy costs of blood digestion in a host-specific haematophagous parasite. *J Exp Biol* 208:2489–2496
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Sheldon BC, Verhulst S (1996) Ecological immunology: costly parasite defenses and trade offs in evolutionary ecology. *Trends Ecol Evol* 11:317–321
- Silva M, Downing JA (1995) *CRC handbook of mammalian body masses*. CRC, Boca Raton
- Soliman S, Marzouk AS, Main AJ, Montasser AA (2001) Effect of sex, size, and age of commensal rat hosts on the infestation parameters of their ectoparasites in a rural area of Egypt. *J Parasitol* 87:1308–1316
- Sukhdeo MVK, Bansemir AD (1996) Critical resources that influence habitat selection decisions by gastrointestinal helminth parasites. *Int J Parasitol* 26:483–498
- Tagiltsev AA, Tarasevich LN (1982) Arthropods of the burrow complex in the natural foci of arboviral infections. Siberian Branch, Novosibirsk, Nauka (in Russian)
- Tipton VJ (1960) The genus *Laelaps*. With a review of the Laelapinae and a new subfamily Alphalaelaptinae (Acarina: Laelapidae). *Univ Calif Publ Entomol* 16:233–356
- Walsberg GE, Wolf BO (1995) Effects of solar radiation and wind speed on metabolic heat-production by two mammals with contrasting coat color. *J Exp Biol* 198:1499–1507
- Walzer A, Schausberger P (1999) Cannibalism and interspecific predation in the phytoseiid mites *Phytoseiulus persimilis* and *Neoseiulus californicus*: predation rates and effects on reproduction and juvenile development. *Biocontrol* 43:457–468
- Warwick RM, Clarke KR (2001) Practical measures of marine biodiversity based on relatedness of species. *Oceanogr Mar Biol* 39:207–231
- Zemskaya AA (1969) Types of parasitism of gamasid mites. *Med Parasitol Parasit Dis* 38:393–405 (in Russian)
- Zemskaya AA (1973) Parasitic gamasid mites and their medical significance. *Meditcina*, Moscow (in Russian)