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Habitat variation in species composition of flea assemblages on small mammals in central Europe

Abstract We studied patterns of variation in species composition of flea assemblages on small mammals across different habitats of Slovakia and compared flea species composition within and across host species among habitats. We asked (1) how variable the composition of flea assemblages is among different populations of the same host occurring in different habitats and (2) whether the composition of flea assemblages in a habitat is affected either by species composition of hosts or by environmental affinities of this habitat. Between-habitat similarity in flea species composition increased with an increase in the similarity in host species composition. Species richness of flea assemblages of a host species correlated positively with mean number of cohabitating host species but not with the number of habitats occupied by a host species. Results of the ordination of flea collections from each individual host demonstrated that the first five principal components explained most of the variance in species composition of flea assemblages. The segregation between rodent and insectivore flea assemblages was easily discerned from the ordination diagram when flea assemblages were plotted according to their hosts. When flea assemblages were plotted according to their habitat affinities, the distinction of habitats based on variation in flea composition was not as clear. The results of ANOVA of each principal component showed the significant effect of both host species and habitat type. The variation in each principal component was explained better by the factor of host species compared with the factor of habitat type. Multidimensional scaling of flea assemblages within host species across habitats demonstrated that among-habitat variation in flea composition was manifested differently in different hosts.

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Introduction

Spatial variation in composition of biological communities is one of the central ecological questions (Rosenzweig 1995; Shenbrot et al. 1999). Whereas spatial patterns of communities of free-living organisms have been broadly studied (e.g., Shenbrot et al. 1999, and references therein), communities of parasites have attracted much less attention. One of the reasons for the paucity of studies of spatial variation in parasitic communities is the complicated, multi-level structure of parasite communities. Indeed, composition of parasite communities can vary across host individuals, populations, species and communities (Carney and Dick 2000; Poulin and Valtonen 2002; Calvete et al. 2004). This variation is due, at least in part, to the diversity of host biotic and abiotic environments. For example, a richer community of cohabitating fish increases the probability of lateral transfer of monogenean parasites and, thus, affects monogenean richness and composition in a fish species (Caro et al. 1997). An effect of abiotic environment, namely ambient temperature, has been demonstrated on trematode species composition in *Littorina* mollusks (Galaktionov 1996).

Therefore, some part of a parasite community encountered in a host is due to its specific location, another part due to host identity and yet another part due to the host's environment (Kennedy and Bush 1994). However, the relative importance of spatially

variable factors in variation of community composition is poorly known for most parasite and host taxa. Moreover, most studies of spatial variation in parasite communities were done on helminth communities of teleost fish (e.g., Carney and Dick 2000) and birds (Bush and Holmes 1986; Calvete et al. 2004). Mammalian parasite communities have been much less studied. Therefore, it is not surprising that the hypothesis that the host identity is a major determinant of parasite community structure has been supported (Bell and Burt 1991; Buchman 1991; Guégan et al. 1992). One of the reasons for this may be the relative stability of the internal environment of a host organism (Sukhdeo 1997).

Unlike endoparasites, ectoparasites are influenced not only by the host, but also by the environment of the host. Therefore, a habitat of an ectoparasite should not be just a particular host, but a particular host in a particular habitat. Indeed, Krasnov et al. (1997) showed that species composition of flea assemblages in a particular habitat was determined not only by host species composition, but also by environmental properties of the habitat itself. This study was carried out in the arid environment of the Negev desert. Between-habitat variation in environmental conditions in this area can be great (e.g., Shenbrot et al. 2002) and this can lead to changes in the distribution of ectoparasites among habitats even within the same host species. Indeed, it was found that there was a complete replacement of one flea species (*Xenopsylla conformis*) with another (*Xenopsylla ramesis*) on the same rodent hosts (*Meriones crassus* and *Gerbillus dasyurus*) between two different habitats situated at the opposite sides of a steep precipitation gradient (Krasnov et al. 1998). This replacement was due, in part, to abiotic properties of the habitat (air temperature, relative humidity, and substrate texture), which affected survival and rate of development of preimaginal fleas (e.g., Krasnov et al. 2001). However, the generality of the effect of habitat properties on species composition of flea assemblages remains to be studied. It is unclear what happens in other (e.g., temperate) environments, where among-habitat variation in the environmental parameters is less expressed than in the deserts.

To fill this gap, we studied fleas parasitic on small mammals in different habitats across central and eastern Slovakia. Fleas (Siphonaptera) are obligate holometabolous ectoparasites that are most abundant and diverse on small to medium-sized mammalian species. The larvae are usually not parasitic and feed on organic matter found in the nest or burrow of the host. In most species, larval and pupal development is entirely off-host. To understand spatial patterns of variation in species composition of flea assemblages, we compared flea species composition within and across host species among habitats. First, we asked how variable (if at all) is the composition of flea assemblages among different populations of the same host occurring in different habitats. Second, we asked whether a composition of flea assemblages in a habitat is affected either by species composition of hosts or by environmental affinities of this habitat. If both "environmental" and "host" parameters of a habitat did affect composition of flea assemblages, we attempted to evaluate the relative importance of these groups of parameters.

Materials and methods

Study area, mammal sampling, and flea collection

Mammals were sampled and fleas collected between 1983 and 2001 in 18 locations across Slovakia (see details and maps in Stanko 1987a, b; 1988, 1994; Stanko et al. 2002). Mammals were captured using traps that were deposited following the same protocol at each of 264 trapping sessions (see Stanko 1987a, b, 1988, 1994). Number of trapped mammals ranged from 13 to 3,992 per location, from 8 to 422 per trapping session and from 47 to 1,733 per year. Each trapped animal was identified, sexed, and weighed. The animal's fur was combed thoroughly using a toothbrush over a plastic pan, and fleas were carefully collected. Trapping sessions (on average, 700 traps per session, ranging from 100 to 2,000 traps) lasted 1–3 nights. Trapping plots were distributed across nine habitat types that were distinguished based on their physiognomy. Lowland habitats were those situated at elevations between 100 and 200 m a.s.l. They included (1) lowland river valleys with willow–poplar and ash–alder floodplain forests dominated by *Salix alba*, *Salix fragilis*, and *Populus alba*; (2) woodland belts represented by three to eight rows of poplars (*Populus canadensis*) and various shrubs (*Prunus* sp., *Rosa* sp., *Sambuccus nigra*) with herbal floor composed mainly of *Urtica dioica*; (3) agricultural fields of wheat, maize, and stubble; (4) floodplain lowland forests dominated by *Fraxinus angustifolia*, *Quercus robur*, *Carpinus betulus*, *S. alba*, and *S. fragilis*; and (5) shrubbery dominated by *Prunus spinosus*, *Rosa canina*, and *Crataegus* sp. with sporadic occurrence of poplar and willow trees. Mountain habitats were situated at elevations from 300 to 1,100 m a.s.l. They included (1) narrow submontane and montane brook valleys (hereafter referred to as mountain river valleys) with the main vegetation represented by *Alnus glutinosae*, *Alnus incanae*, *Fagus sylvaticus*, and *Carpinus betulus*; (2) submontane (oak–hornbeam) and montane (beech and beech–maple) forests dominated by *F. sylvaticus*, *Carpinus betulus*, *Q. robur*, and *Acer platanoides*; and (3) shrubbery patches on pastures dominated by *Prunus spinosus*, *Coryllus avellana*, and *Rosa canina*. Finally, urban habitats were represented by gardens and orchards in public green spaces within cities (at elevation 650–750 m a.s.l.).

On average, there were 23 replicated samples per habitat type, ranging from a minimum of four for lowland shrubbery and urban habitats to a maximum of 59 for belts. A total of 14,080 individuals from 24 species of

small mammals (rodents and insectivores) were trapped, of which 5,876 individuals were infested with parasites. Thirty flea species (16,980 individuals) were collected (see species lists in Stanko et al. 2002). Information on mean abundance and prevalence of each flea species on each host species, on the abundance of host species as well as on host range of individual fleas can be found elsewhere (Stanko 1994; Stanko et al. 2002; Morand et al. 2004).

Data analysis

To test for matching between host species composition and flea species composition in a set of habitats, for each habitat type we calculated the (1) mean abundance of each flea species (for which at least ten individuals were collected) per individual host across all host species (for which at least ten infested host individuals were recorded) and (2) overall abundance of each host species. After excluding flea and host species with fewer than ten individuals from the analysis, there were 14 host species and 25 flea species (see Appendix). Then, we calculated the Bray-Curtis similarity (Bray and Curtis 1957) for either flea or host species composition between each pair of habitats from standardized (see details in Clarke and Warwick 2001) abundance data. The index was calculated as

$$S_{il} = 100 * \left\{ 1 - \frac{\sum\limits_{j=1}^{n} |y_{ij} - y_{lj}|}{\sum\limits_{j=1}^{n} (y_{ij} + y_{lj})} \right\},$$

where y_{ij} represents the abundance of the jth flea or host species in the ith habitat. Bray-Curtis similarity index is commonly used in ecological studies (Legendre and Legendre 1998). Justification of the suitability of the Bray-Curtis index for ecology can be found elsewhere (Clarke and Warwick 2001).

Next we applied multidimensional non-parametric scaling (Kruskal and Wish 1978) to ordinate flea assemblages and host assemblages across habitats. We tested whether and how closely the two sets of host and flea habitat distributions were related. This was done by calculating rank correlation coefficients between all elements of the two resulting between-habitat similarity matrices (for hosts and for fleas) (Clarke and Warwick 2001). The rank correlation coefficient ρ can vary from 0 (no relation between two similarity matrices) to 1 (perfect match between two matrices). Statistical significance of ρ was estimated by permutation procedure with 999 permutations. These calculations were performed by the RELATE routine implemented in the program Primer-5 (Clarke and Gorley 2001). In addition, we tested for the relationship between similarities in flea and host composition by regressing similarity in flea composition against similarity in host composition across all pairs of habitats.

To understand the relationships between the structure of flea community and host habitat distribution, we calculated three parameters of flea species richness for each of the 14 host species, namely flea "fauna" (overall number of flea species recorded), mean infracommunity flea species richness (mean number of flea species per infested individual) and mean component community flea species richness (evaluated as mean number of flea species per host species within a trapping session). We regressed each of these parameters against the number of occupied habitats and mean number of co-occurring host species. A host was considered as an occupier of a habitat if at least five individuals of this host were captured there. The results did not change when the cut-off number was established at a minimum of two, three, and four individuals of a particular species captured in a habitat. A single capture of a host species in a habitat was considered occasional and was not included in the analyses. All dependent and independent variables (except for mean infracommunity flea species richness) in these analyses were positively correlated with the number of captured individuals ($r^2 = 0.32$–0.85, $F_{1,12} = 5.8$–66.1; $P < 0.03$ for all). Consequently all relevant variables were controlled for the differences in among-species sampling effort by substitution of the original data values with their residual deviations of the regressions against the sampling effort in log–log space. In addition, the relationships between measurements of flea species richness and numbers of occupied habitats and co-occurring host species were also analyzed using independent contrasts (Felsenstein 1985), which controls for the confounding effect of phylogeny. A phylogenetic tree for hosts was constructed using various sources (see Krasnov et al. 2004a for details). To compute independent contrasts, we used the PDAP:PDTREE program (Midford et al. 2004) implemented in Mesquite modular system for evolutionary analysis (Maddison and Maddison 2004). Regression of independent contrasts was forced through the origin (Garland et al. 1992).

We ordinated flea assemblages from each host individual in each trapping grid by principal component analysis to test for the relative effect of host and habitat affinity in species composition of flea assemblages. We included in this analysis 14 flea species for which at least 50 individuals were recorded. Axes of ordination space are linear combinations of log-transformed abundances of each flea species. Prior to analysis, the abundances of each flea species on an individual host were weighted by overall abundance of fleas on this individual. Thus, the axes represented main directions of change in flea species composition among hosts and were obtained independently of host species and habitat affinity. Then, we analyzed each of the first five principal components (see Results) using separate one-way ANOVAs with either host species or habitat type as independent factors. We estimated the proportion of the total variance originating from differences among host species or habitats, as opposed to within species or habitats, following Sokal and Rohlf (1995).

To understand how flea species composition within a host species changes among habitats, we applied multi-dimensional non-parametric scaling to ordinate flea assemblages across habitats for each of eight host species that occur in several habitat types and for which flea species composition differed significantly among habitats as revealed by within-host among-habitat ANOVAs of the scores of five principal components (see Results). A matrix of Bray-Curtis similarities between each pair of habitats was used as input data. For each host species, we identified those flea species that primarily accounted for the observed assemblage differences between the most differing habitats (Clarke and Gorley 2001). This was carried out by decomposition of Bray-Curtis similarity into contribution of each species using the routine SIMPER implemented in the program Primer-5 (Clarke and Gorley 2001).

Results

Among-habitat similarity in host species composition averaged 52.6% and ranged from a minimum of 8.2% between fields and mountain shrubbery to a maximum of 90.5% between lowland river valleys and belts. Similarity in flea species composition averaged 61.5% and ranged from a minimum of 30.5% between lowland and mountain shrubbery to a maximum of 91.8% between lowland river valleys and belts. Among-habitat similarity in flea species composition was reflected by among-habitat similarity in host species composition as revealed by the ρ statistic ($\rho = 0.36$, $P = 0.02$). This statistic correlates the elements of two similarity matrices and, thus, indicates significant agreement between these matrices. Furthermore, between-habitat flea composition similarity was significantly positively correlated with between-habitat host composition similarity ($r^2 = 0.19$, $F_{1,34} = 7.8$, $P < 0.01$). In other words, the similarity in flea species composition increased with an increase in the similarity in host species composition (Fig. 1). Distribution of
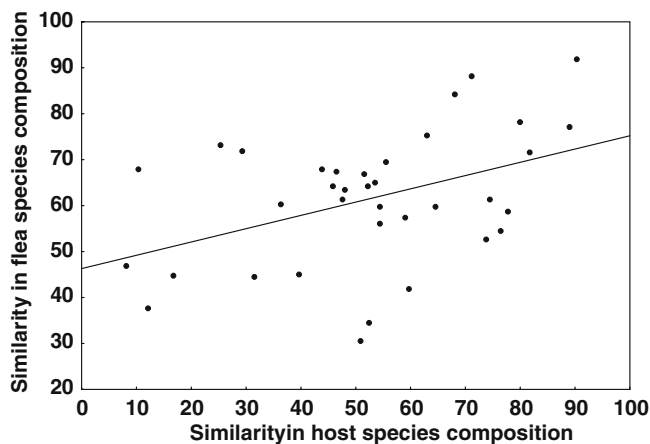
habitats in the ordination space constructed using non-parametric multidimensional scaling is represented in Fig. 2. Comparison of the diagrams based on the similarities in flea and host composition allows groups of habitats that are more similar to each other than to other habitats in both flea and host species composition to be distinguished. These were three mountain habitats (river valleys, forests, and shrubbery) and three lowland habitats (river valleys, forests, and woodland belts). Field and urban habitats differed sharply from other habitat types by their flea and host composition. However, lowland shrubbery was similar in its host species composition to other lowland habitats, but flea species composition in this habitat differed drastically from any other habitat.

In across-host comparisons, no significant relationship was found between any of the measurements of flea species richness and number of habitats occupied by a host species ($r^2 = 0.01$–0.14, $F_{1,12} = 0.1$–1.2; $P > 0.2$ for all for conventional statistics and $r = -0.02$, $r = -0.04$ and $r = -0.28$; $P > 0.3$ for all for independent contrasts).
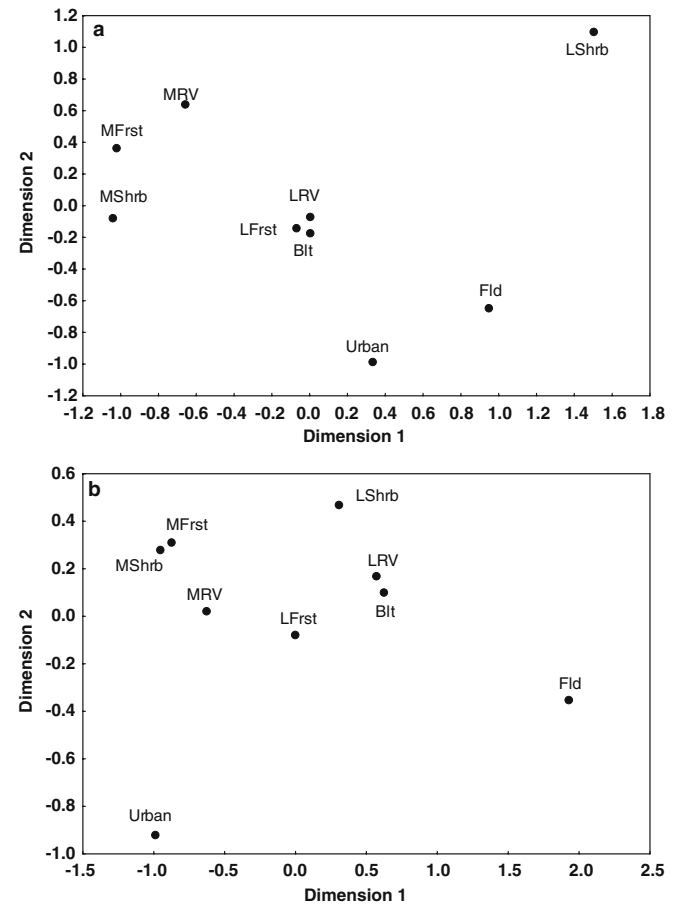

Fig. 1 Relationship between similarity in flea species composition and similarity in host species composition across pairs of habitats

Fig. 2 Multidimensional scaling distribution of habitats based on Bray-Curtis similarity in flea (**a**) and host (**b**) composition. *LRV* Lowland river valleys, *Blt* lowland woodland belts, *Fld* lowland agricultural fields, *LFrst* lowland forests, *LShrb* lowland shrubbery, *MRV* mountain river valleys, *MFrst* mountain forests, *MShrb* mountain shrubbery, and *Urban* urban habitats

By contrast, species richness of flea assemblages of a host species expressed as flea fauna, mean infracommunity richness or mean component community richness correlated positively with the mean number of cohabiting host species ($r^2 = 0.38$, $F_{1,12} = 7.2$; $r^2 = 0.66$, $F_{1,12} = 23.5$, and $r^2 = 0.35$, $F_{1,12} = 6.4$, respectively, $P < 0.02$ for all). The same was true when the method of independent contrasts was used ($r = 0.49$, $r = 0.76$, and $r = 73$, respectively; $P < 0.05$ for all). An illustrative example with mean infracommunity flea species richness is presented in Fig. 3.

The results of the ordination of the flea collections from each individual host demonstrated that the first five principal components explained 64% of the total variance in species composition among flea assemblages from individual hosts (Table 1). The contributions of the first and second axes to segregation of flea assemblages exceeded twice that of the remaining axes, which contributed similarly to the segregation. Each of the ordination axes corresponded to a change in flea species composition with similar contribution of each axis. For example, the first axis represented mainly the change in the abundance of *Amalaraeus penicilliger* and *Rhadinopsylla integella*, whereas the second axis represented

the change in the abundance of *Doratopsylla dasycnema* and *Palaeopsylla soricis*. The ordination diagram suggests that these changes occurred within rodent and insectivore hosts, respectively. Indeed, the segregation between rodent and insectivore flea assemblages could be easily discerned when flea assemblages were plotted according to their hosts (Fig. 4a). When flea assemblages were plotted according to their habitat affinities, the distinction of habitats based on variation in flea composition was not as clear (Fig. 4b). However, habitats with richer and poorer flea assemblages can be discerned as suggested by the size of 95%-confidence ellipses in Fig. 4a. Moreover, the results of ANOVA of each principal component demonstrated the significant effect of both host species and habitat type (independent variables) (Table 2). The variation in each principal component was explained better by the factor of host species than by the factor of habitat type.

Nevertheless, habitat type, in general, affected flea species composition within a host species (Table 3). However, the effect of habitat type on principal component scores was manifested differently in different hosts. The results of one-way ANOVAs with habitat
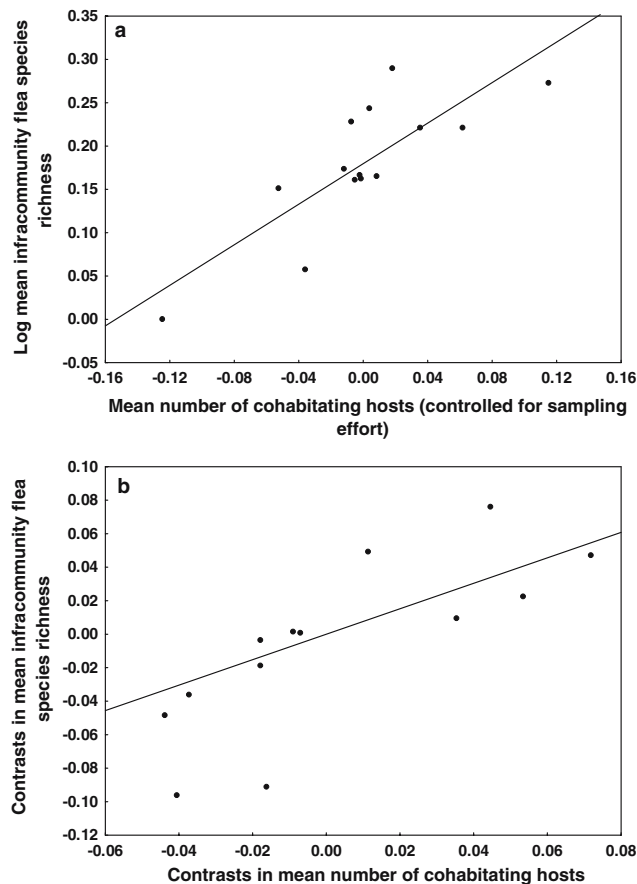

Fig. 3 Relationship between mean infracommunity flea species richness and number of cohabiting hosts (controlled for sampling effort) across 14 host species in the conventional space (**a**) and in the space of independent contrasts (**b**)
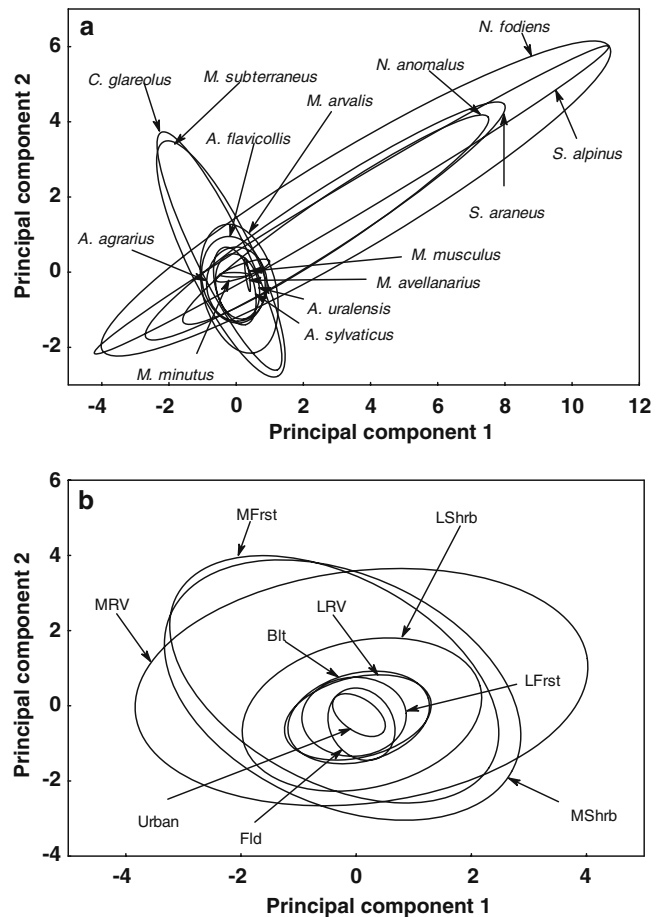

Fig. 4 Ninety-five percent confidence ellipses for flea assemblages from each individual host in the space of two first principal component axes according to the host species (**a**) and habitat type (**b**). See Fig. 2 for the abbreviations of habitat names

type as the independent variable carried out separately for each host species (Table 3) demonstrated that among-habitat within-host differences in flea species composition were due to either many flea species (e.g., *Apodemus flavicollis*) or only a few flea species (e.g., *Microtus subterraneus*). The contribution of different flea species to among-habitat variation in flea assemblage composition was different. For example, *D. dasycnema* and *P. soricis* (PCA 2, Table 2) contributed to among-habitat variation in flea composition in the majority of host species, whereas the role of *Megabothris turbidus* and *Nosopsyllus fasciatus* (PCA 4, Table 2) in this variation was important for *Apodemus* species and *Clethrionomys glareolus* only (Table 3).

Diagrams of multidimensional scaling of flea assemblages within hosts and across habitats demonstrated that among-habitat variation in flea composition was manifested differently in different hosts (Fig. 5). Furthermore, in different hosts, the main differences in species composition of flea assemblages among habitats
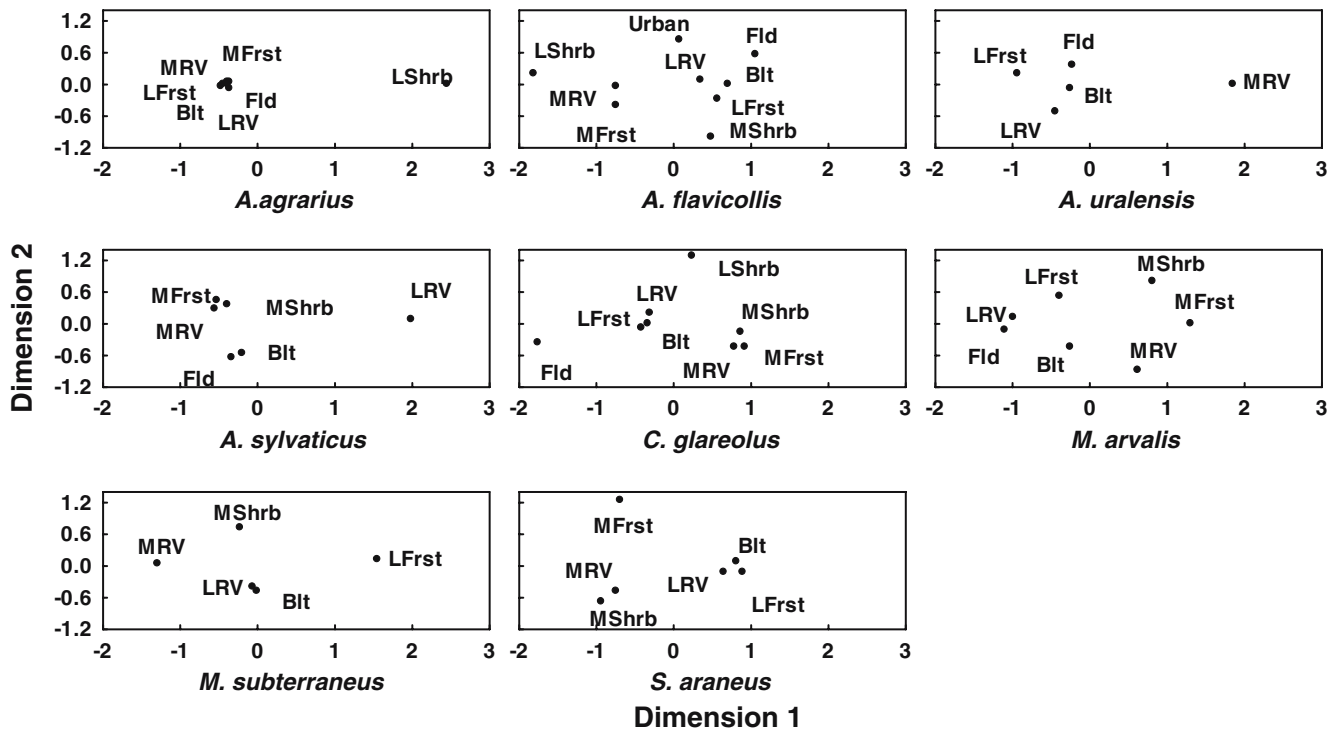

Fig. 5 Multidimensional scaling distribution of habitats based on Bray-Curtis similarity in flea composition. See Fig. 2 for the abbreviations of habitat names

Table 1 Summary of principal component analysis of flea assemblages from each individual host

		Principal component				
		1	2	3	4	5
	Eigenvalue	1.81	1.64	1.12	1.08	1.06
	Proportion of variance explained	0.16	0.15	0.12	0.11	0.10
R	*Amalaraeus penicilliger*	0.67*	0.34	−0.01	0.06	−0.12
	Ctenophthalmus agyrtes	0.48	−0.23	0.16	−0.18	−0.42
	Ctenophthalmus assimilis	−0.10	−0.38	−0.68*	0.30	−0.16
	Ctenophthalmus solutus	−0.17	−0.15	0.43	−0.49	0.28
	Ctenophthalmus uncinatus	0.14	0.03	0.73*	−0.12	−0.14
	Doratopsylla dasycnema	−0.46	0.64*	−0.02	0.07	−0.23
	Hystrichopsylla orientalis	0.03	0.01	−0.15	−0.04	−0.79*
	Megabothris turbidus	−0.03	−0.40	0.13	0.66*	0.03
	Nosopsyllus fasciatus	−0.11	−0.28	−0.36	−0.68*	−0.05
	Peromyscopsylla bidentata	0.33	0.30	−0.16	0.00	0.69*
	Palaeopsylla similis	0.06	−0.21	0.00	0.06	0.08
	Palaeopsylla soricis	−0.49	0.65*	−0.04	0.05	−0.17
	Rhadinopsylla integella	0.66*	0.39	−0.21	0.10	0.02
	Rhadinopsylla pentacantha	0.30	0.14	−0.34	0.13	−0.52

R is linear correlation between each ordination axis and abundance of each species in the observation vector
*Indicates coefficient of correlation > 0.6

Table 2 Summary of ANOVAs of the effect of host species and habitat type on the principal component scores

Factor		Principal component				
		1	2	3	4	5
Host	F	365.4	137.4	17.2	24.3	30.9
	V	52.7	29.4	5.2	6.6	8.4
Habitat	F	12.3	153.6	31.9	11.9	35.8
	V	1.9	21.2	4.7	1.9	5.8

V is proportion of the total variance originating from differences among hosts or habitats as opposed to that within hosts or habitats, respectively

All F are significant, $P < 0.05$

Table 3 F statistics of one-way ANOVAs of principal component scores dependent on habitat type

Host	Principal component				
	1	2	3	4	5
Apodemus agrarius	2.4*	14.8*	3.3*	4.1*	4.3*
Apodemus flavicollis	4.4*	28.4*	16.0*	9.6*	7.8*
Apodemus uralensis	1.8	1.4	5.1*	10.5*	3.9*
Apodemus sylvaticus	6.0*	13.8*	16.9*	3.3*	2.2
Clethrionomys glareolus	29.7*	36.9*	3.3*	7.3*	5.5*
Microtus arvalis	4.0*	19.3*	2.2	1.6	8.6*
Muscardinus avellanarius	0.02	0.5	1.1	0.2	1.3
Microtus subterraneus	1.4	3.3*	0.4	1.7	0.3
Sorex araneus	3.3*	3.9*	4.3*	1.7	1.9

ANOVAs were carried out separately for each host species
*$P < 0.05$

were due to different flea species. For example, flea assemblages on *Apodemus agrarius* and *Apodemus uralensis* were similar across most habitats except for lowland shrubbery or mountain river valleys, respectively. Flea assemblages on *A. agrarius* in lowland shrubbery differed drastically from all other habitats because of high abundance of *Ctenophthalmus solutus* (contribution of this species to pairwise habitat dissimilarity was 38–45%), whereas *Megabothris turbidus* was mainly responsible for the difference in *A. uralensis* flea composition between mountain river valleys and the rest of the habitats (39–46% of contribution to pairwise habitat dissimilarity). Flea assemblages on *Microtus arvalis* and *Sorex araneus* within lowland habitats and within mountain habitats tended to cluster together along the first dimension, but differed sharply between these two habitat groups. The reason for these differences on *M. arvalis* was relatively high abundance of *Ctenophthalmus assimilis* in lowland habitats (34–50% of contribution to pairwise habitat dissimilarity). Lowland and mountain flea assemblages of *S. araneus* differed due to relatively high abundance of *P. soricis* (14–34% contribution) and relatively low abundance of *P. similis* (13–40% contribution) in lowland compared to mountain habitats. Apparent clusters of habitats (= similar flea assemblages) were also evident for *A. sylvaticus*, *C. glareolus* and *M. subterraneus*. In most

cases, these clusters were represented by habitats belonging to either lowland or mountain areas. The flea species that primarily contributed to among-habitat differences in *A. sylvaticus* was *N. fasciatus* (33–35% of contribution). Flea assemblages of both voles (*C. glareolus* and *M. subterraneus*) differed among habitats mainly due to *Megabothris turbidus* (28–50% of contribution), *A. penicilliger* (24–42% of contribution) and *C. assimilis* (25–43% of contribution).

Discussion

This study demonstrated that species composition of flea assemblages in a given host in a given habitat is determined by both host identity and habitat identity. Furthermore, host identity seems to be a more important factor affecting structure of flea assemblage compared to habitat identity. Indeed, a significant effect of either host species or habitat type in ANOVAs of principal component scores suggested that flea species composition expressed as principal components was repeatable both within host species and within habitat type. In other words, flea species composition varied less (1) among populations of the same host species than among host species and (2) among habitats of the same type than among different habitats. However, proportion of the total variance in flea species composition originating from differences among host species, as opposed to within species, averaged 20.5% across principal components, whereas proportion of the total variance originating from differences among habitat types, as opposed to within habitat type, averaged 7.1% across principal components.

The importance of host identity reflects strong dependence of a given flea on a given host species. In highly host-specific parasites, a species can become adapted to various traits of a particular host species (Ward 1992; Poulin 1998; Combes 2001). Nevertheless, even a highly host-opportunistic parasite varies in its abundance among different host species because of the different reproductive (e.g., Krasnov et al. 2002a, 2004b) or exploitative (e.g., Krasnov et al. 2003) performance of a parasite on different host species. Furthermore, the abundance of a flea on different host species was found to decrease with increasing taxonomic distance between these hosts (Krasnov et al. 2004c). The net result of all these relationships is that high abundance of a flea species is linked with one or a few closely related host species. In addition, spatial overlap among related hosts is likely high because the hosts often have similar ecological preferences (Brooks and McLennan 1991). As a consequence, habitat distribution of flea species mirrors habitat distribution of host species. Comparison of multidimensional scaling diagrams of the distribution of fleas and hosts among habitats as well as apparent distinctness between flea assemblages of rodent and insectivore hosts (Fig. 4a) support this idea.

Nevertheless, the between-habitat similarity in host species composition explained only about 20% of the variance in the between-habitat similarity in flea species composition. This means that some habitat pairs were characterized by similar flea assemblages but different host compositions, whereas other habitat pairs were occupied by similar host communities harboring strikingly different flea assemblages. For example, the difference in dominant host species between mountain shrubbery (*A. flavicollis* and *C. glareolus*) and agricultural fields (*A. agrarius*, *A. uralensis* and *M. arvalis*) led to a coefficient of similarity as low as 8%. However, flea assemblages on these hosts in both habitats were dominated by *Ctenophthalmus agyrtes*, *C. assimilis*, *C. solutus*, and *Megabothris turbidus*, leading to coefficient of similarity as high as 47%. On the other hand, mountain and lowland shrubbery habitats were occupied by host communities with 51% similarity, although the presence of *A. penicilliger*, *A. rossica*, *Ctenophthalmus bisoctodentatus*, *D. dasycnema*, *Hystrichopsylla talpae*, *Ceratophyllus sciurorum*, *Peromyscopsylla bidentata*, *Palaeopsylla similis*, and all *Rhadinopsylla* species in mountains and their absence in lowland resulted in only 30% similarity in flea assemblages. The reason for this difference may be due to the difference in elevation and, consequently, in air temperature between mountain and lowland areas, which can be an important factor for survival of immature fleas (Kern et al. 1999; Krasnov et al. 2001).

Another, not necessarily alternative, explanation for the relatively low proportion of variance in between-habitat similarity in flea species composition explained by between-habitat similarity in host species composition is the habitat effect on flea community structure. This effect can be associated with both biotic and abiotic components of a habitat. Among-habitat variation in biotic components can be related, for example, to the number of cohabiting hosts. Indeed, flea species richness in a host species increased with an increase in host community size. High numbers of cohabiting hosts can facilitate flea exchange between hosts (Ryckman 1971; Rödl 1979; Krasnov and Khokhlova 2001). High probability of flea exchange between host species might, therefore, mask the effect of host identity on the within-host, among-habitat composition of flea assemblages. Another biotic component of a habitat is represented by fleas themselves. Different combinations of flea species compositions might be a result of competition between some flea species (Day and Benton 1980; Krasnov et al. 2005) and can lead to competitive exclusion (Krasnov et al. 2005).

Abiotic components of a habitat are represented by environmental factors, such as air temperature, relative humidity, and substrate structure. All these components have a strong effect on survival and development of both pre-imaginal and imago fleas (see Marshall 1981 and references therein). Moreover, both habitat and geographic distributions of some flea species are limited by these factors (Krasnov et al. 2002b). Comparison of among-habitat variation in composition of flea assemblages within host species (Fig. 5) supports, albeit indirectly, the important role of environmental factors in determining flea community structure. Apparent clusters of flea assemblages corresponding to lowland and mountain habitats can be distinguished in six of eight species. Environmental variation between these two areas is likely more pronounced than that among habitats within each of these areas.

This study confirms the conclusions of Krasnov et al. (1997, 1998) that species composition of fleas on a host species is determined not only by host–flea relations, but also by host–habitat relations. Consequently, a habitat for a flea is not a particular host or a group of hosts but rather a particular host or a group of hosts in a particular habitat. Nevertheless, among-habitat differences in flea assemblages within a host species in Slovakia appeared to be less pronounced than those in the Negev desert. Indeed, flea assemblages of some desert hosts were composed, at least seasonally, of completely different species (Krasnov et al. 1998). This was not the case for any host species in this study. Flea assemblages of the same host in different habitats differed by relative abundances of fleas rather than by their species assortment. The explanation of this difference between temperate and arid environments may be related to differences in the sheltering pattern of host species. Imago fleas spend a considerable part of their lives in a host shelter, whereas this shelter is the ultimate habitat for pre-imagoes. Most desert hosts construct deep below-ground burrows, whereas most temperate rodents and insectivores either construct above-ground nests or dig shallow burrows (Kucheruk 1983). Between-habitat differences in the environmental conditions of the burrows are likely more pronounced than those of the above-ground nests. An alternative explanation might be related to the frequency of interspecific visits to other small mammals' burrows, which presumably is higher in temperate regions (Kucheruk 1983) because of relatively higher small mammal density than in deserts. This could increase host-switching and, therefore, lead to a more scattered presence of flea species across the populations of a host species occupying different habitats.

In conclusion, our results suggest that the composition of a flea assemblage in a small mammalian host in a habitat is related to both host and habitat characteristics. Nevertheless, host identity plays a more important role than habitat identity in structuring flea assemblages.

Appendix Fleas and small mammals collected in different habitat types in Slovakia

Habitat type	Small mammals	Fleas
Lowland river valleys	*Apodemus agrarius, Apodemus flavicollis, Apodemus uralensis, Apodemus sylvaticus, Clethrionomys glareolus, Microtus arvalis, Microtus subterraneus, Neomys anomalus, Neomys fodiens, Sorex alpinus, Sorex araneus*	*Amphipsylla rossica, Ctenophthalmus agyrtes, Ctenophthalmus assimilis, Ctenophthalmus bisoctodentatus, Ctenophthalmus solutus, Ctenophthalmus uncinatus, Doratopsylla dasycnema, Hystrichopsylla orientalis, Megabothris turbidus, Nosopsyllus fasciatus, Palaeopsylla similis, Palaeopsylla soricis, Peromyscopsylla bidentata, Rhadinopsylla pentacantha*
Lowland woodland belts	*A. agrarius, A. flavicollis, A. uralensis, A. sylvaticus, C. glareolus, M. arvalis, M. subterraneus, N. fodiens, S. araneus*	*Amalaraeus arvicolae, C. agyrtes, C. assimilis, C. bisoctodentatus, C. solutus, D. dasycnema, H. orientalis, Leptopsylla segnis, M. turbidus, N. fasciatus, P. similis, P. soricis, P. bidentata*
Lowland agricultural fields	*A. agrarius, A. flavicollis, A. uralensis, A. sylvaticus, Mus musculus, C. glareolus, M. arvalis, M. subterraneus*	*C. agyrtes, C. assimilis, C. solutus, D. dasycnema, H. orientalis, L. segnis, M. turbidus, N. fasciatus, P. soricis*
Lowland forests	*A. agrarius, A. flavicollis, C. glareolus, M. arvalis, M. subterraneus, S. araneus*	*C. agyrtes, C. assimilis, C. solutus, D. dasycnema, H. orientalis, L. segnis, M. turbidus, N. fasciatus, P. soricis, P. bidentata*
Lowland shrubbery	*A. agrarius, A. flavicollis, A. uralensis, C. glareolus, M. subterraneus, N. anomalus, S. araneus*	*C. agyrtes, C. assimilis, C. solutus, H. orientalis, M. turbidus, N. fasciatus, P. soricis*
Mountain river valleys	*A. agrarius, A. flavicollis, A. uralensis, A. sylvaticus, Micromys minutus, C. glareolus, M. arvalis, M. subterraneus, Muscardinus avellanarius, N. anomalus, N. fodiens, S. alpinus, S. araneus*	*A. arvicolae, Amalaraeus penicilliger, A. rossica, Atyphloceras nuperus, C. agyrtes, C. assimilis, C. bisoctodentatus, C. solutus, C. uncinatus, Ceratophyllus sciurorum, D. dasycnema, H. orientalis, Hystrichopsylla talpae, L. segnis, M. turbidus, N. fasciatus, Palaeopsylla kohauti steini, P. similis, P. soricis, P. bidentata, Peromyscopsylla silvatica, Rhadinopsylla integella, Rhadinopsylla isacantha, R. pentacantha*
Mountain forests	*A. agrarius, A. flavicollis, A. uralensis, A. sylvaticus, C. glareolus, M. arvalis, M. subterraneus, M. avellanarius, N. anomalus, S. alpinus, S. araneus*	*A. arvicolae, A. penicilliger, A. rossica, A. nuperus, C. agyrtes, C. assimilis, C. solutus, C. uncinatus, Ceratophyllus sciurorum, D. dasycnema, H. orientalis, H. talpae, L. segnis, M. turbidus, N. fasciatus, P. similis, P. soricis, P. bidentata, P. silvatica, R. integella, R. isacantha, R. pentacantha*
Mountain shrubbery	*A. flavicollis, A. sylvaticus, C. glareolus, M. arvalis, M. subterraneus, M. avellanarius, N. fodiens, S. araneus*	*A. penicilliger, A. rossica, C. agyrtes, C. assimilis, C. bisoctodentatus, C. solutus, C. sciurorum, D. dasycnema, M. turbidus, N. fasciatus, P. k. steini, P. similis, P. soricis, P. bidentata, R. integella, R. isacantha, R. pentacantha*
Urban habitats	*A. flavicollis, M. musculus, M. arvalis,*	*C. agyrtes, C. assimilis, C. solutus, L. segnis, M. turbidus*

References

Bell G, Burt A (1991) The comparative biology of parasite species diversity: intestinal helminths of freshwater fishes. J Anim Ecol 60:1046–1063

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

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

Buchman K (1991) Relationship between host size of *Anguilla anguilla* and the infection level of the monogeneans *Pseudodactylogyrus* spp. J Fish Biol 35:599–601

Bush AO, Holmes JC (1986) Intestinal helminths of lesser scaup ducks: an interactive community. Can J Zool 64:142–152

Calvete C, Blanco-Aguiar JA, Virgós E, Cabezas-Díaz S, Villafuerte R (2004) Spatial variation in helminth community structure in the red-legged partridge (*Alectoris rufa* L.): effects of definitive host density. Parasitology 129:101–113

Carney JP, Dick TA (2000) Helminth community in yellow perch (*Perca flavescens* (Mitchill)): determinants of pattern. Can J Zool 78:538–555

Caro A, Combes C, Euzet L (1997) What makes a fish a suitable host for Monogenea in the Mediterranean. J Helminthol 71:203–210

Clarke KR, Gorley RN (2001) Primer v5: user manual/tutorial. Primer-E, Plymouth Marine Laboratory, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. Primer-E, Plymouth Marine Laboratory, Plymouth

Combes C (2001) Parasitism. The ecology and evolution of intimate interactions. University of Chicago Press, Chicago

Day JF, Benton AH (1980) Population dynamics and coevolution of adult siphonapteran parasites of the southern flying squirrel (*Glaucomys volans volans*). Am Midl Nat 103:333–338

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Galaktionov KV (1996) Life cycles and distribution of seabird helminthes in Arctic and subarctic regions. Bull Scand Soc Parasitol 6:31–49

Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. Am Nat 41:8–32

Guégan J-F, Lambert A, Leveque C, Euzet L (1992) Can host body size explain the parasite species richness in tropical freshwater fishes? Oecologia 90:197–204

Kennedy CR, Bush AO (1994) The relationship between pattern and scale in parasite communities: a stranger in a strange land. Parasitology 109:187–196

Kern WH, Richman DL, Koehler PG, Brenner RJ (1999) Outdoor survival and development of immature cat fleas (Siphonaptera: Pulicidae) in Florida. J Med Entomol 36:207–211

Krasnov BR, Khokhlova IS (2001) The effect of behavioural interactions on the transfer of fleas (Siphonaptera) between two rodent species. J Vector Ecol 26:181–190

Krasnov BR, Shenbrot GI, Medvedev SG, Vatschenok VS, Khokhlova IS (1997) Host–habitat relation as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. Parasitology 114:159–173

Krasnov BR, Shenbrot GI, Medvedev SG, Khokhlova IS, Vatschenok VS (1998) Habitat-dependence of a parasite–host relationship: flea assemblages in two gerbil species of the Negev Desert. J Med Entomol 35:303–313

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, Khokhlova IS, Oguzoglu I, Burdelova NV (2002a) Host discrimination by two desert fleas using an odour cue. Anim Behav 64:33–40

Krasnov BR, Khokhlova IS, Fielden LJ, Burdelova NV (2002b) The effect of substrate on survival and development of two species of desert fleas (Siphonaptera: Pulicidae). Parasite 9:135–142

Krasnov BR, Sarfati M, Arakelyan MS, Khokhlova IS, Burdelova NV, Degen AA (2003) Host-specificity and foraging efficiency in blood-sucking parasite: feeding patterns of a flea *Parapulex chephrenis* on two species of desert rodents. Parasitol Res 90:393–399

Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004a) Relationship between host diversity and parasite diversity: flea assemblages on small mammals. J Biogeogr 31:1857–1866

Krasnov BR, Khokhlova IS, Burdelova NV, Mirzoyan NS, Degen AA (2004b) Fitness consequences of density-dependent host selection in ectoparasites: testing reproductive patterns predicted by isodar theory in fleas parasitizing rodents. J Anim Ecol 73:815–820

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, Burdelova NV, Khokhlova IS, Shenbrot GI, Degen AA (2005) Pre-imaginal interspecific competition in two flea species parasitic on the same rodent host. Ecol Entomol 30:146–155

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage, Beverly Hills

Kucheruk VV (1983) Mammal burrows: their structure, topology and use (in Russian). Fauna Ecol Rodents 15:5–54

Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier, Amsterdam

Maddison WP, Maddison DR (2004) Mesquite: a modular system for evolutionary analysis, version 1.05. http://mesquiteproject.org

Marshall AG (1981) The ecology of ectoparasitic insects. Academic, London

Midford PE, Garland T Jr, Maddison WP (2004) PDAP:PDTREE package for Mesquite, version 1.06. http://mesquiteproject.org/pdap_mesquite/index.html

Morand S, Gouy de Bellocq J, Stanko M, Miklisova D (2004) Is sex-biased ectoparasitism related to sexual size dimorphism in small mammals of Central Europe? Parasitology 129:505–510

Poulin R (1998) Evolutionary ecology of parasites. From individuals to communities. Chapman and Hall, London

Poulin R, Valtonen T (2002) The predictability of helminth community structure in space: a comparison of fish populations from adjacent lakes. Int J Parasitol 32:1235–1243

Rödl P (1979) Investigation of the transfer of fleas among small mammals using radioactive phosphorus. Folia Parasitol 26:265–274

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Ryckman RE (1971) Plague vector studies. Part I. The rate of transfer of fleas among *Citellus*, *Rattus* and *Sylvilagus* under field conditions in southern California. J Med Entomol 8:535–540

Shenbrot GI, Krasnov BR, Rogovin KA (1999) Spatial ecology of desert rodent communities. Springer, Berlin Heidelberg New York

Shenbrot GI, Krasnov BR, Khokhlova IS, Demidova T, Fielden LJ (2002) Habitat-dependent differences in architecture and microclimate of the Sundevall's jird (*Meriones crassus*) burrows in the Negev Desert, Israel. J Arid Environ 51:265–279

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

Stanko M (1987a) Siphonaptera of small mammals in the northern part of the Krupina plain (in Slovakian). Stred Slov Zborn Stredoslov Múz Bansk Bystr 6:108–117

Stanko M (1987b) Fleas (Siphonaptera) of small mammals from Javorie mountains (in Slovakian). Acta Res Nat Mus Nat Slov 33:95–108

Stanko M (1988) Fleas (Siphonaptera) of small mammals in eastern part of Volovské vrchy mountains (in Slovakian). Acta Res Nat Mus Nat Slov 34:29–40

Stanko M (1994) Fleas synusy (Siphonaptera) of small mammals from the central part of the East-Slovakian lowlands. Biologia (Bratislava) 49:239–246

Stanko M, Miklisova D, Gouy De Bellocq J, Morand S (2002) Mammal density and patterns of ectoparasite species richness and abundance. Oecologia 131:289–295

Sukhdeo MVK (1997) Earth's third environment: the worm's eye view. Bioscience 47:141–149

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