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Co-occurrence of ectoparasites on rodent hosts: null model analyses of data from three continents

Boris R. Krasnov, Sonja Matthee, Marcela Lareschi, Natalia P. Korallo-Vinarskaya and Maxim V. Vinarski

B. R. Krasnov (krasnov@bgu.ac.il), Mitrani Dept of Desert Ecology, Swiss Inst. for Dryland Environmental Research, Jacob Blaustein Inst. for Desert Research, Ben-Gurion Univ. of the Negev, Sede-Boqer Campus, IL–84990 Midreshet Ben-Gurion, Israel – S. Matthee, Dept Conservation Ecology and Entomology, Stellenbosch Univ., 7602 Stellenbosch, South Africa – M. Lareschi, Center for Parasitological Studies and Vectors, National Research Council of Argentina and School of Natural Sciences and Museum of La Plata National Univ., Calle 2 N 584, AR–1900 La Plata, Argentina – N. P. Korallo-Vinarskaya, Laboratory of Arthropod-Borne Viral Infections, Omsk Research Inst. of Natural Foci Infections, Mira str. 7, RU–644080 Omsk, Russia – M. V. Vinarski, Dept Zoology and Physiology, Faculty of Chemistry and Biology, Omsk State Pedagogical Univ., Tukhachevskogo emb. 14, RU–644099 Omsk, Russia.

We studied patterns of species co-occurrence in communities of ectoparasitic arthropods (ixodid ticks, mesostigmate mites and fleas) harboured by rodent hosts from South Africa (*Rhabdomys pumilio*), South America (*Scapteromys aquaticus* and *Oxymycterus rufus*) and west Siberia (*Apodemus agrarius*, *Microtus gregalis*, *Microtus oeconomus* and *Myodes rutilus*) using null models. We compared frequencies of co-occurrences of parasite species or higher taxa across host individuals with those expected by chance. When non-randomness of parasite co-occurrences was detected, positive but not negative co-occurrences of parasite species or higher taxa prevailed (except for a single sample of mesostigmate mites from *O. rufus*). Frequency of detection of non-randomness of parasite co-occurrences differed among parasite taxa, being higher in fleas and lower in mites and ticks. This frequency differed also among host species independent of parasite taxon, being highest in *Microtus* species and lowest in *O. rufus* and *S. aquaticus*. We concluded that the pattern of species co-occurrence in ectoparasite communities on rodent hosts is predominantly positive, depends on life history of parasites and may be affected to a great extent by life history of a host.

Studies of community organization in various taxa have revealed that communities of some organisms represent random assemblages, whereas communities of other organisms are characterized by one or another pattern of non-randomness (Diamond 1975, Patterson and Atmar 1986). A non-random pattern of species assemblage suggests that a community is structured by some deterministic processes, whereas a random assemblage of species suggests that a community is structured by stochastic processes. Whatever the considered pattern of non-randomness is, a central question asked when studying organization of communities is about frequency of species co-occurrence. Potential mechanisms that produce a pattern can be inferred only after establishment of whether empirical pattern deviates from those expected under random processes (Connor and Simberloff 1979, Hausdorf and Hennig 2007). For example, if species in a community co-occur more often than expected by chance, mechanisms behind this may be interspecific facilitation or shared preferences (Krasnov et al. 2006a). Such a community is expected to display positive co-occurrence and be aggregatively structured (Diamond 1975, Gotelli and Rohde 2002). If species in a community co-occur less frequently than expected by chance, this may be due to interspecific competition (Diamond 1975) or differential preferences (Pielou and Pielou 1968). Such a community is expected to display negative co-occurrence and be segregatively structured (Diamond 1975, Gotelli and Rohde 2002).

Null models represent one of the most effective ways of testing for patterns of species co-occurrence in a community (Gotelli 2000). In this approach, observed frequency of species co-occurrence in a natural community is compared with a set of simulated communities with randomly generated species assemblages. The null-model analysis itself, even if it reveals non-randomness in a community, cannot indicate the mechanism responsible for non-randomness (Rohde 2005).

Parasite communities are convenient models for studying community organization because of (a) the relative ease of obtaining replicated samples (e.g. host individuals), (b) the fact that most hosts are usually parasitized by several parasite species which often share a trophic level, and (c) discrete nature of boundaries of parasite communities. These features have led to a substantial increase in parasite community studies in the last decade (reviewed by Poulin 2007a). The majority of studies have dealt with parasite

communities in aquatic rather than in terrestrial hosts (but see Calvete et al. 2004) and with endo- rather than ectoparasites (but see Gotelli and Rohde 2002). Results of these studies were equivocal and demonstrated such great variability in patterns of structure among parasite communities that Poulin (2007b), in his seminal paper, concluded that most ecological patterns observed in communities of parasites are far from universal. Indeed, parasite communities appeared to fall along gradients (a) from being non-randomly (González and Poulin 2005) to randomly assembled (Gotelli and Rohde 2002) and (b) from being characterized by positive (Rohde et al. 1995, Krasnov et al. 2006a) to negative (Patrick 1991) species interactions.

One reason for lack of consistency in occurrence and/or pattern of community organization among parasites may be differences in various life history traits of taxa as well as among hosts harbouring them (Gotelli and McCabe 2002, Rohde 2005). However, to the best of our knowledge, no study has compared occurrence and pattern of community organization among different parasite taxa exploiting the same host species and/or among different host species harbouring the same parasite taxon. For example, only two studies have considered co-occurrence patterns in parasites of terrestrial hosts and these were restricted to a single parasite taxon (fleas in Krasnov et al. 2006a and streblid bat flies in Tello et al. 2008).

Gotelli and McCabe (2002), Gotelli and Rohde (2002) and Rohde (2005) suggested that level of vagility and/or dispersal ability may determine whether animals are subject to structuring mechanisms, such as competition and demonstrated that communities of large bodied and/or highly vagile taxa exhibit predominantly non-random structure, whereas communities of small bodied and/or weakly vagile taxa predominantly represent random assemblages. They argued that one of the reasons for this difference is that ecological niches in the latter are not saturated and their population densities are chronically low, so that interspecific interactions are weak and do not have much influence on community structure. Regarding parasites, the effect of vagility on occurrence of non-random pattern in community organization may be realized as differences between temporary and periodic ectoparasites (sensu Lehane 2005). Temporary ectoparasites are largely free-living and visit the host for long enough to take a blood meal (e.g. ixodid ticks and mosquitoes). Periodic ectoparasites spend considerably longer time on hosts than is required merely to obtain a blood meal but nevertheless spend a significant amount of time off-host (e.g. most fleas and mesostigmate mites). Obviously, temporary ectoparasites are more vagile than periodic ectoparasites. Consequently, non-randomness is expected to be found in communities of temporary ectoparasites rather than in those of periodic ectoparasites. Furthermore, vagility of a parasite may be mediated via features of host species such as mobility and/or dispersal distance. If a host species is highly mobile then chances for ectoparasite exchange between individual hosts and, consequently, for saturation of infracommunities are high. An infracommunity represents an assemblage of parasites belonging to different species exploiting the same host individual (see definition in Combes 2001 and Poulin 2007a). In other words, deterministic mechanisms are expected to act stronger on parasite communities of highly mobile than sedentary hosts.

Here, we use null models (Gotelli 2000) to study patterns of species co-occurrences in infracommunities of several taxa of arthropod ectoparasites (mainly ixodid ticks, mesostigmate mites and fleas) harboured by rodent hosts on three continents, namely Africa (South Africa; *Rhabdomys pumilio*), South America (Argentina; *Oxymycterus rufus* and *Scapteromys aquaticus*) and Asia (west Siberia; *Apodemus agrarius*, *Microtus gregalis*, *Microtus oeconomus* and *Myodes rutilus*). We compared frequencies of co-occurrences of parasite species or higher taxa across host individuals (i.e. 'sites') with those expected by chance, i.e. derived from randomly assembled species by site matrices. Although some aspects of the algorithms suggested by Gotelli and Entsminger (2009) and Gotelli (2000) have been criticized (Sanderson 2000, Hausdorf and Hennig 2007), their good statistical properties have been demonstrated (Gotelli 2000, Gotelli and McCabe 2002). Following the hypothesis of Gotelli and McCabe (2002) and Rohde (2005) that non-randomness in organization of a community is related to level of vagility, we expected that non-random pattern of species co-occurrence in ticks will be found more frequently than in mites or fleas. We also expected that non-random patterns of parasite co-occurrence will be found more frequently in highly mobile hosts (e.g. *Apodemus agrarius*) than in territorially conservative hosts (e.g. *Microtus* voles).

Material and methods

Sampling of hosts and parasites

We used data on ectoparasites collected from bodies of common rodent hosts in South Africa, Argentina and west Siberia. In South Africa, sampling was carried out in eight localities in the Western Cape Province during 2003–2004. These localities included pristine lowland Fynbos/Renosterveld regions and adjacent agricultural areas. Each locality was sampled once over a period of 3–12 days. In Argentina, rodents were sampled in six localities of Buenos Aires province in 1990–1991, 1994–1996 and 2000–2001 during one-day trapping sessions (2–10 sessions per locality). Habitats of the study area were graminoid swamps, forested wetlands, frequently flooded scrublands and xeromorphic and riparian marshlands along river banks. In both South Africa and Argentina, rodents were captured using live-traps (80–180 traps per locality) arranged in lines or grids with 10 m distance between traps. In west Siberia, data were collected in deciduous forests in the vicinity of Novosibirsk during 1982–1987. Rodent sampling and parasite collections were carried out by the late A. K. Dobrotvorsky and transferred for further analyses to the Laboratory of Arthropod-Borne Viral Infections, Omsk Research Institute of Natural Foci Infections under the responsibility of one of the authors of this paper (NPKV). Rodents were captured using pitfall traps with drift fences arranged in 23 50 m-length lines (with 10 m distance between traps). Sampling was arranged into 19 monthly trapping sessions with traps being checked daily.

In all three regions, captured rodents were euthanized (with fluothane in South Africa and sulphur ether in Argentina and west Siberia), placed in an individual pre-marked plastic or cloth bag and transferred to a laboratory where each animal was systematically examined under a stereoscopic microscope using forceps to remove ectoparasites. All ectoparasites were removed, counted and identified to species level. In total, we used data on 3084 individual rodent hosts from which 38 223 individual ectoparasites belonging to six higher arthropod taxa were collected (Supplementary material Appendix 1). These higher taxa were ixodid ticks (Parasitiformes: Ixodida), mesostigmate mites (Parasitiformes: Mesostigmata), trombiculid mites (Acariformes: Prostigmata), lice (Insecta: Anoplura), fleas (Insecta: Siphonaptera) and staphylinid beetles (Insecta: Coleoptera). Staphylinids and trombiculids were recorded in Argentina only, whereas lice were collected in South Africa and Argentina only. Some ectoparasitic arthropods (trombiculid mites, staphylinid beetles, fleas) exploit their hosts during a single phase of their life cycles, whereas other ectoparasites (ticks, mites, lice) are parasitic during several life cycle phases. Consequently, we counted ticks as larvae, nymphs and imago, mesostigmate mites and lice as nymphs and imagoes, trombiculid mites only as larvae, and fleas and beetles only as imagoes. Detailed descriptions of study areas and sampling procedures may be found elsewhere (Dobrotvorsky 1992, Lareschi et al. 2007, Matthee et al. 2007).

Data organization

Data were organized as presence/absence matrices in which each row represented either a parasite species or a higher parasite taxon and each column represented an individual host. Presence/absence matrices were constructed for each of seven common host species and for each trapping session where at least four individuals of a given host were captured and at least two were infested. Thus, there were two groups of matrices for each host species. Matrices of one group (within-taxon matrices) represented presence/absence of different parasite species belonging to the same higher taxon (e.g. ticks, mesostigmate mites or fleas), whereas matrices of another group (among-taxa matrices) represented presence/absence of parasites belonging to a higher parasite taxon (ticks, mesostigmate mites, trombiculid mites, lice, fleas, or staphylinid beetles) but independent of parasite species. We included only parasite species for which at least 20 individuals were collected for the within-taxon matrices, whereas we included all parasite species for the among-taxa matrices. As a result, no within-taxon matrices were constructed for trombiculid mites, lice and beetles. Matrices for ticks were constructed for *R. pumilio* only, whereas matrices for mesostigmate mites and fleas were constructed for all host species except for fleas for *S. aquaticus*.

Recently, Hausdorf and Hennig (2007) proposed a method that can use a site by species abundance matrix as opposed to the typical incidence matrix. However, the use of analysis on presence/absence data, especially in application to parasite assemblages, seems to be more appropriate because (a) measurements of occurrences are more certain than measurements of abundances (Gotelli and McCabe 2002, Gotelli and Rohde 2002) and (b) parasite assemblages are composed of different, often distantly-related taxa that are characterized by substantially different species- and taxon-specific levels of abundance (Krasnov et al. 2006b, 2007, Korallo-Vinarskaya et al. 2009). As a result, a comparison between abundances of, for example, an imago of an ixodid tick (often several individuals per host) and an imago mesostigmate mite (often several dozens or even hundreds of individuals per host) is problematic. Furthermore, analyses of presence/absence and abundance data in studies of parasite community ecology have provided similar results (Haukisalmi and Henttonen 1993).

Data analysis

Analyses were carried out using the software EcoSim 7.72 (Gotelli and Entsminger 2009). We calculated two metrics of co-occurrence for each presence/absence matrix, following Gotelli and Rohde (2002). These metrics were the C-score (Stone and Roberts 1990) and the variance ratio (V-ratio; Schluter 1984). The C-score and V-ratio have been successfully applied to null model analyses of a variety of plant and animal assemblages, including those of parasites (Gotelli and McCabe 2002, Gotelli and Rohde 2002, Mouillot et al. 2005, Krasnov et al. 2006a, Tello et al. 2008). We used both indices because they are based on two different matrix structures, namely average co-occurrence and average covariance, respectively. They have also been shown to be statistically powerful and robust to minor changes in community structure (Gotelli 2000). Detailed descriptions of statistical properties and performance of these metrics can be found in Gotelli (2000) and Gotelli and Rohde (2002). In brief, C-score is the average number of checkerboard units that are found for each pair of species (Stone and Roberts 1990, Gotelli 2000), whereas the V-ratio is the ratio between variance in species richness and sum of variance in species occurrence (Schluter 1984, Gotelli 2000). Expected value of the ratio equals 1 if species are distributed independently. It is smaller or greater than 1 in the case of negative or positive covariance between species pairs, respectively (Gotelli 2000). A C-score larger than expected by chance [observed (O) > expected (E)] and V-ratio smaller than expected by chance (O < E) indicate negative co-occurrences (i.e. species are segregated). In contrast, C-score smaller than expected by chance (O < E) and V-ratio larger than expected by chance (O > E) indicate positive co-occurrences (i.e. species are aggregated) (Gotelli 2000, Gotelli and McCabe 2002, Gotelli and Rohde 2002).

We calculated observed indices for each presence/absence matrix and compared them with respective indices calculated for 5000 randomly assembled null matrices measuring the tail probability that each observed index is larger or smaller than expected by chance. Simulated matrices were assembled by Monte Carlo procedures using a fixed-equiprobable (FE) algorithm. The FE algorithm does not constrain number of parasite species or taxa that can be harboured by a host, suggesting that host individuals are equivalent in probability to support a particular number of parasite species. Earlier,

we demonstrated that, from the point of view of biological reality, the FE algorithm is most suitable for analysis of communities of ectoparasites of small mammals (Krasnov et al. 2006a). This is because it considers uninfested hosts as individuals that could be used by parasites, but, by chance, are not colonized (Gotelli and Rohde 2002), which is the case for small mammals and their arthropod ectoparasites (Krasnov et al. 2006c). Nevertheless, results of null model analysis may depend on whether uninfested hosts ('empty sites') are included in or excluded from the input matrices (Gotelli and Rohde 2002). In particular, inclusion or exclusion of 'empty sites' may affect values of V-ratio, but cannot affect values of C-score (see Gotelli and Entsminger 2009 for detailed explanations). We carried out null model analyses using V-ratio both including and excluding uninfested hosts. Results of these two runs of analyses were essentially the same (Krasnov et al. 2006a). Consequently, we present here only results of analyses where uninfested hosts were included. Results of null model analyses using V-ratio when uninfested hosts were excluded from input matrices are presented in the Supplementary material Appendix 2.

To understand whether non-random ectoparasite community organization occurs more often in some parasite taxa or host species than in others, we counted how many times the C-score and V-ratio detected non-randomness of parasite co-occurrence for each host species and within and among parasite taxa. Then, we used these counts to evaluate combined rate of detection of non-randomness events within a parasite taxon or host species using meta-analyses. Combined rate of detection of non-randomness was calculated using rates of detection of non-randomness for each ectoparasite taxon (or for higher taxa) in each host weighted by number of presence/absence matrices. Fixed effects and random effects models produced similar results. Here, we report results of analyses that used the fixed effects model (results of the meta-analyses using random effects model are presented in the Supplementary material Appendix 3). All meta-analyses were carried out using Comprehensive Meta-Analysis 2.2 (Biostat Inc., Englewood, NJ).

To further compare results across parasite taxa and host species, we calculated the standardized effect size (SES) for each matrix we analyzed (i.e. for each host species and for each trapping session). SES measures number of standard deviations that the observed index is above or below the mean index of simulated matrices (see details in Gotelli and McCabe 2002). The null hypothesis is that average SES across a set of presence/absence matrices is zero. To test this null hypothesis we used one-sample t-tests to determine whether SES for each index, host species and either parasite taxon or all parasite taxa did not differ from zero. Assuming a normal distribution of deviations, approximately 95% of the observed SES values are expected to fall between -2.0 and 2.0 (i.e. ± 1.96 Z). Then, we used one-way ANCOVA to test for difference in average SES among parasite taxa (ticks, mites and fleas) across and within host species (except for *S. aquaticus*; there were not enough data on ticks and fleas for this host) or among host species across parasite taxa and within parasite taxon (except for ticks; diverse assemblages of these parasites were found on *R. pumilio* only). Because matrix size (number of rows times number of columns) may affect statistical power of the analysis (Gotelli and McCabe 2002), it was included as a covariate.

Results

Co-occurrence metrics calculated for real data did not differ significantly from the metrics calculated for simulated matrices in some samples, but the observed indices differed significantly from the null expectations in other samples (Table 1). Indices for fleas in all hosts detected non-randomness for the majority of samples (among hosts; 75–86% for C-score and 79–86% for V-ratio). In contrast, the proportion of samples where indices for mites and higher taxa indicated non-randomness in parasite co-occurrence varied among host species, being the highest in *M. gregalis*, *M. oeconomus* and *R. pumilio* (C-score – 50–81%; V-ratio – 50–61% for mites and C-score – 75–81%; the V-ratio – 61–81% for higher taxa) and the lowest in *O. rufus* (C-score – 20%; V-ratio – 20% for mites and C-score – 50%; V-ratio – 33% for higher taxa). Importantly, in all cases when significant non-randomness was detected, values of C-scores were significantly larger than expected by chance and values of V-ratios were significantly smaller than expected by chance (except for a single matrix for mites in *O. rufus*) (Table 1).

Results of meta-analyses also demonstrated that non-randomness in parasite co-occurrences was consistently detected for fleas, but much less so for mites or higher taxa (Table 2, see Fig. 1 for illustrative example with C-score). Combined rate of detection of non-randomness was detected in one third to half of matrices for mites

Table 1. Summary of null model analyses of co-occurrence of parasite species or higher taxa for seven host species using C-score/V-ratio. Uninfested hosts were included in input matrices. O = E – number of samples for which the observed value of index did not differ significantly than that expected by chance ($p > 0.05$); O < E – number of samples for which the observed value of index was significantly less than that expected by chance ($p < 0.05$); O > E – number of samples for which the observed value of index was significantly greater than that expected by chance ($p < 0.05$).

Host	Parasite	O = E	O < E	O > E
A. agrarius	mites	11/8	3/-	-/6
	fleas	3/3	11/-	-/11
	higher taxa	6/7	8/-	-/7
M. gregalis	mites	3/7	12/-	-/11
	fleas	3/3	15/-	-/15
	higher taxa	4/5	14/-	-/13
M. oeconomus	mites	8/7	8/-	-/9
	fleas	2/2	14/-	-/14
	higher taxa	3/3	13/-	-/13
M. rutilus	mites	13/13	4/-	-/4
	fleas	3/3	16/-	-/16
	higher taxa	9/9	10/-	-/10
O. rufus	mites	12/13	2/1	1/2
	fleas	1/1	6/-	-/6
	higher taxa	12/14	6/-	-/4
R. pumilio	ticks	3/3	5/-	-/5
	mites	3/4	5/-	-/4
	fleas	2/1	6/-	-/7
	higher taxa	2/2	6/-	-/6
S. aquaticus	mites	19/18	5/-	-/6
	higher taxa	14/14	10/-	-/10

Table 2. Summary of meta-analyses of rate of detection of non-randomness in organization of ectoparasite communities in seven host species using fixed effects model. A – within ectoparasite taxon among hosts, B – among ectoparasite taxa within host. *p <0.05, ns – non-significant. Z – combined Z-scores, I^2 – heterogeneity statistics.

	Index	Parasite	Host	Event rate	95% limits	Z	I^2
A	C-score	mites		0.36	0.26–0.47	−2.44*	69.90
		fleas		0.83	0.73–0.89	5.28*	0.00
		higher taxa		0.56	0.46–0.65	1.17^{ns}	55.48
	V-ratio	mites		0.40	0.31–0.50	−1.95*	53.85
		fleas		0.84	0.75–0.91	5.44*	0.00
		higher taxa		0.53	0.39–0.70	0.66^{ns}	61.29
B	C-score		*A. agrarius*	0.53	0.36–0.69	0.35^{ns}	75.37
			M. gregalis	0.80	0.67–0.89	3.97*	0.00
			M. oeconomus	0.70	0.54–0.82	2.44*	66.2
			M. rutilus	0.53	0.38–0.65	0.35^{ns}	82.24
			O. rufus	0.34	0.19–0.53	-1.68^{ns}	72.8
			R. pumilio	0.68	0.50–0.82	2.00*	0.00
			S. aquaticus	0.32	0.20–0.47	−2.32*	7.00
	V-ratio		*A. agrarius*	0.56	0.40–0.70	0.68^{ns}	47.35
			M. gregalis	0.71	0.57–0.84	2.92*	6.00
			M. oeconomus	0.73	0.57–0.84	2.80*	53.49
			M. rutilus	0.53	0.38–0.65	0.35^{ns}	82.24
			O. rufus	0.27	0.14–0.45	−2.43*	71.94
			R. pumilio	0.69	0.5–0.83	1.97*	0.00
			S. aquaticus	0.34	0.22–0.48	−2.15*	32.23

and higher taxa (Fig. 1a, 1c), but more than 80% of matrices for fleas (Fig. 1b). Moreover, independent of parasite taxon, meta-analyses demonstrated that ectoparasite communities of some host species (*M. gregalis*, *M. oeconomus* and *R. pumilio*) consistently demonstrated non-randomness, whereas this was not the case for other host species (Table 2).

Average SES values for both indices are presented in Fig. 2. For the majority sets of matrices, average SES values differed significantly from zero ($t = -2.13$–-8.49 for C-score and $t = 2.70$–7.95 for V-ratio; $p < 0.05$ for all), except for ticks in *R. pumilio* and mites in *O. rufus* ($t = -2.26$–0.70 for C-score and $t = 0.76$–2.18 for V-ratio; $p > 0.05$ for all). Furthermore, SES values for C-score were either lower or approximately equal to −2.0 for fleas, whereas they were higher than −2.0 for ticks, mites (except in *M. gregalis*) and higher taxa (except in *M. gregalis* and *M. oeconomus*). Analogously, SES values for V-ratio were higher or approximately equal than 2.0 for fleas in all hosts, mites in *M. gregalis* and higher taxa in *M. gregalis* and *M. oeconomus* and lower than 2.0 for the rest of host-parasite associations.

Results of ANCOVAs with marix size as a covariate of effect of parasite taxon and host species on SES of C-score and V-ratio are presented in Table 3. SES differed significantly (a) among taxonomic groups of parasites when analyzed across host species and (b) among host species when analyzed across parasite taxa. Within a host species, SES also differed significantly among taxonomic groups of parasites (except for V-ratio for parasites of *M. gregalis* and both indices for parasites of *R. pumilio*). When analyzed within parasite taxon, SES for fleas and higher taxa, but not mites differed significantly among host species.

Discussion

Results of this study demonstrated that (a) when non-randomness of parasite co-occurrences was detected, it typically indicated positive but not negative co-occurrences of parasite species or higher taxa (except for a single sample of mesostigmate mites from *O. rufus*); (b) frequency of detection of non-randomness of parasite co-occurrences differed among parasite taxa, being higher in fleas and lower in mites and ticks; and (c) frequency of detection of non-randomness of parasite co-occurrences differed also among host species independent of parasite taxon, being highest in *Microtus* species. In particular, this suggests that organization of parasite communities is affected by an interplay between parasite and host life histories. Effect of parasite life history explains differences in community organization between parasites of different taxa exploiting the same host. Effect of host life history explains differences in community organization of the same parasites exploiting different hosts (Mouillot et al. 2005).

Why do ectoparasite species co-occur positively?

Null model analyses of co-occurrences of ectoparasites belonging to different taxa, exploiting different hosts in different habitats and located on different continents consistently demonstrated positive co-occurrence of ectoparasitic arthropods on individual small mammals and thus support earlier results (Krasnov et al. 2006a, Tello et al. 2008). Positive co-occurrence of species in parasite communities has also been reported for intestinal helminths in birds (Bush and Holmes 1986) and ectoparasites of marine and freshwater fish (Morand et al. 1999, but see Gotelli and Rohde 2002, Mouillot et al. 2005).

The positive pattern of ectoparasite co-occurrence found in this and other studies is likely mediated via the host and may arise due to two main, not mutually exclusive reasons. First, some host individuals may represent better patches for any parasite species than other host individuals. Heterogeneity among host individuals in their suitability for parasites is a ubiquitous phenomenon, one of the

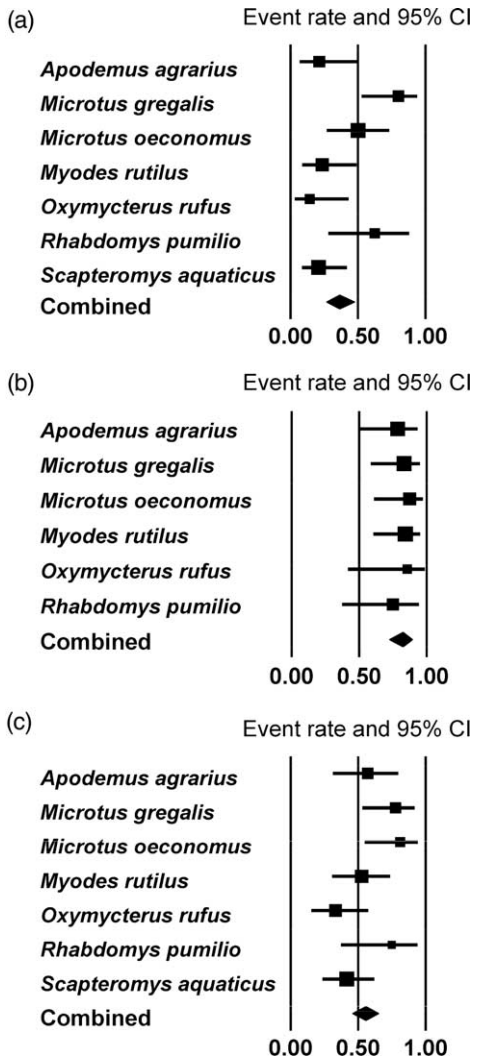

Figure 1. Forest plots for meta-analyses of rate of detection of non-randomness in the organization of ectoparasite communities of seven host species using the C-score. (a) mites, (b) fleas, (c) higher ectoparasite taxa, CI = confidence limits (horizontal lines). The size of squares is proportional to sample size (number of analyzed matrices). Middle vertical line is where number of matrices for which the non-randomness was detected is equal to number of matrices for which the non-randomness was not detected.

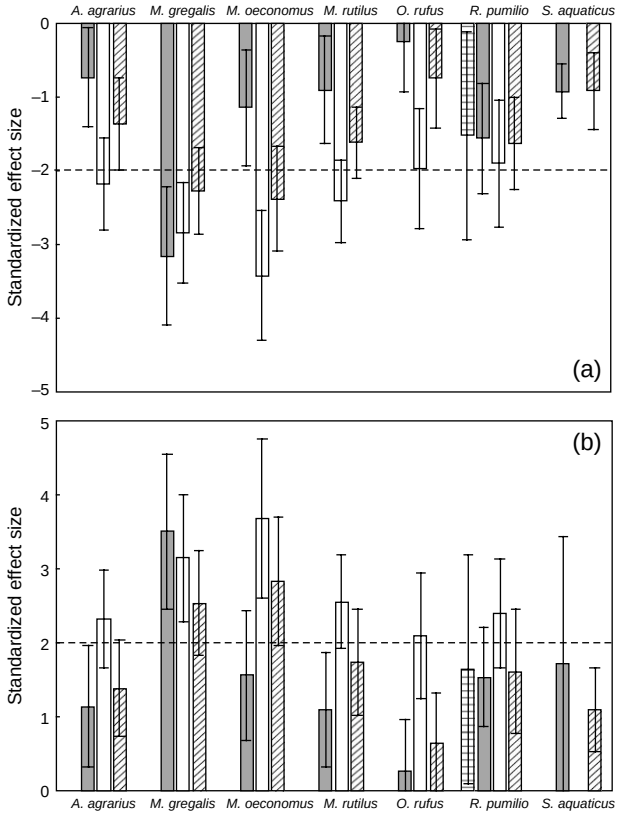

Figure 2. Standardized effect sizes (mean ± 1.96 SE) for C-score (a) and V-ratio (b) for different parasite taxa and different host species. Horizontally hatched bars – ticks, gray bars – mites, white bars – fleas, diagonally hatched bars – higher taxa. Dashed lines denote standardized effect sizes of −2.0 and 2.0 which are approximately 5% significance level for C-score and V-ratio, respectively, assuming a normal distribution of deviations (i.e. ±1.96 Z).

consequences of which is aggregated distribution of conspecific parasites among host individuals (Shaw and Dobson 1995, Combes 2001, Poulin 2007a). In general, the reason for higher suitability of a host individual for parasites is that either its encounters with parasites are more frequent or parasites can extract resources from the host more easily (Combes 2001) or both. Given that (a) many ectoparasitic arthropods spend substantial time in the off-host environment; (b) trophic requirements of many ectoparasitic arthropods are essentially the same, i.e. host blood; and (c) anti-parasitic defences (grooming behaviour and immune response) may be similarly effective against various parasites (McTier et al. 1981), it is clear that a host highly suitable for ectoparasites belonging to one particular taxon is likely to be also suitable to ectoparasites belonging to another taxon. For example, in many mammals the mobility of males is higher and their immunocompetence is lower than those of females (Olsen and Kovacs 1996). Consequently, chances to encounter a greater diversity of parasites are higher and/or immune defence is less effective in males when compared to females of the same host species. As a result, males usually harbour more diverse assemblages of different ectoparasites than females (Schalk and Forbs 1997). Heterogeneity in body condition of hosts may be another reason behind unequal suitability for any parasite. Indeed, maintenance of a competent immune system may be more energetically costly (Sheldon and Verhulst 1996), and the tradeoff between advantages of resistance against parasites and its cost can be critical for host individuals that face energy limitations. Therefore, energy deprived hosts may be less resistant and, thus, represent better patches for multiple parasites (Alzaga et al. 2008).

Second, the immunosuppressive effect of ectoparasites on their mammalian hosts is well known (for rodents parasitized by: ixodid ticks – Wikel 1982, fleas – Khokhlova et al. 2004a). Suppression of the host's immune system by one ectoparasite may facilitate exploitation of this host by another ectoparasite (Krasnov et al. 2005). Furthermore, multiple attacks of different parasites may further weaken defence abilities of a host (Bush and Holmes 1986,

Khokhlova et al. 2004b). Mounting different types of immune response is more costly than mounting one specific type of response, so that effectiveness of overall defence decreases with an increase in the diversity of parasite attacks and a host subjected to attacks from multiple parasite species is forced to lessen its defence efforts (Jokela et al. 2000). This may result in positive co-occurrence of ectoparasites within an infracommunity.

Assemblages of the same ectoparasites on the same hosts appeared to be structured at some times and/or locations, whereas they appeared to be randomly assembled at other times and/or locations. This suggests that some temporally or spatially variable factors are responsible for variable expressions of community organization. These factors can be related to host density and parasite abundance (Krasnov et al. 2006a). Reasons for temporal and/or spatial variability of ectoparasite community organization remain to be further studied.

Why does frequency of parasite co-occurrence vary among parasite taxa?

Frequency of detection of non-randomness in organization of assemblages differed among ectoparasite taxa. As predicted, frequency of detection of non-randomness was low in mites, but contrary to our predictions, it was high in fleas and low in ticks. This difference could be caused by differences in life history characteristics of ectoparasites not related to vagility and/or dispersal ability. All fleas are obligate haematophages and feed exclusively on host blood. In contrast, interspecific variation in ecology and feeding modes of mesostigmate mites is enormous, ranging from predation to ecto- and endoparasitism (reviewed by Radovsky 1985). Moreover, ectoparasitic mites include both facultative and obligatory haemato- and/or lymphophages. Among the latter, there are species that solely feed on host's blood and species that feed on both host's blood and small arthropods. Similar to fleas, ixodid ticks are also obligate haematophages. Fleas, however, are more tightly associated with their hosts as they alternate between periods when they occur on the host body and when they occur in its burrow or nest. Ticks, on the other hand, stay on the body of the host only to accomplish a blood meal (once during each developmental stage) and usually quest for their hosts in the open off-host environment, attacking a host when it passes close by. Thus, lower frequency of detection of non-randomness in tick and mite assemblages may be caused by relatively lower dependence of mites on the host as a food source and random distribution of ticks in the off-host environment.

Results of this study and those of Gotelli and McCabe (2002) and Gotelli and Rohde (2002) allow us to compare deviations from randomness in communities among different taxonomic groups, including both free-living and parasitic animals (Rohde 2005). Absolute average SES values for C-score for presence-absence matrices were higher for bats, birds, non-chiropteran mammals and ants and lower for non-ant invertebrates, reptiles/amphibians and ectoparasites of fish. Among parasites included in the present study, absolute average SES value for flea matrices (2.5) was somewhat lower than that for non-chiropteran mammals (3.1) and similar to that for ants (2.6), whereas SES values for tick and mite matrices (1.8 and 1.2, respectively) were either somewhat higher or similar, respectively, to that for reptiles/amphibians (1.3) and were much higher than that for fish ectoparasites (0.3). This does not fit well to the idea of Rohde (2005) that degree of non-random organization of a community is positively correlated with vagility of a taxon of interest. Indeed, although abilities of fleas to actively disperse are undoubtedly higher than those of mites, they do not seem to be higher than those of ticks (Krasnov 2008).

Why does frequency of parasite co-occurrence vary among host species?

Ectoparasites may disperse using their hosts as vehicles, so degree of community non-randomness was expected to differ among hosts with different mobility (Rohde 2005). Although this difference was found in our study, results did not support our predictions. Absolute SES values for C-score across parasite taxa on a host were higher for relatively sedentary *Microtus* hosts (2.3–2.8) and lower for mobile hosts such as *A. agrarius* (1.4).

Nevertheless, our results showed that parasite assemblages in some host species were consistently non-random,

Table 3. Summary of one-way ANCOVAs (with matrix sizes as covariates) of effect of parasite taxon within host species (ticks, mites and fleas) and host species within parasite taxon (mites, fleas and higher taxa) on the average standardized effect size (SES) of C-score and V-ratio. The effect of a covariate (matrix size) was significant ($p < 0.05$ for all) except for SES of both indices in *A. agrarius*, *M. oeconomus*, *O. rufus* and *R. pumilio* ($p > 0.21$ for all).

Effect	Parasite taxon or host species	DF	C-score		V-ratio	
			F (DF)	p	F (DF)	p
Parasite taxon	*A. agrarius*	2,25	12.2	<0.001	7.6	<0.01
	M. gregalis	1,33	4.6	<0.05	1.2	0.27
	M. oeconomus	1,29	20.1	<0.001	12.8	<0.001
	M. rutilus	1,33	15.0	<0.001	13.5	<0.001
	O. rufus	1,19	5.5	<0.05	6.2	<0.05
	R. pumilio	2,20	0.1	0.9	0.6	0.5
	all hosts	3,314	5.6	<0.001	6.2	<0.001
Host species	mites	6,104	1.1	0.4	1.7	0.1
	fleas	5,75	2.6	<0.05	2.8	<0.05
	higher taxa	6,109	3.3	<0.01	2.7	<0.05
	all taxa	6,311	20.2	<0.001	17.3	<0.001

whereas this was not the case in other host species. Frequency of detection of non-randomness of flea and mite assemblages appeared to be highest in *M. gregalis* and *M. oeconomus*, lowest in *O. rufus* and *S. aquaticus* and intermediate in *A. agrarius*, *M. rutilus* and *R. pumilio* (Fig. 2). It is possible that architecture and relative stability of host shelters play some role in community organization of those ectoparasites that depend strongly on host's burrow/nest (fleas and mites). Deep and long-lasting burrows with a constant microclimate are likely to be better habitats than shallow and short-lived shelters for any flea and mite species. As a result, an individual host living in a long-lasting burrow may have higher chances to be infested by a variety of parasites than a host living in an ephemeral burrow or above-ground nest. Indeed, both *M. gregalis* and *M. oeconomus* possess deep and complex burrow systems that function for many years (Gromov and Polyakov 1992), whereas solitary *M. rutilus* live in above-ground nests and shallow burrows which they often abandon to build new ones (Nikitina 1980a). Frequent abandonment of shelters (burrows and above-ground nests) has been reported also for *A. agrarius* (Nikitina 1980b) and *R. pumilio* (Schradin and Pillay 2006). *Scapteromys aquatucis* and *O. rufus* do not construct burrows and prefer to hide under vegetation which may be exposed to frequent flooding and subsequent abandoning (Kravetz 1973).

Community organization of ectoparasites may also be affected by social structure of their hosts. Host group-living can facilitate exchange of ectoparasites and thus lead to more frequent co-occurrence of different parasites on the same host individual. Both *M. gregalis* and *M. oeconomus* are highly social and live in groups (Gromov and Polyakov 1992), whereas *M. rutilis*, *S. aquatucis* and *O. rufus* are solitary (Kravetz 1973, Nikitina 1980a). *Apodemus agrarius* and *R. pumilio* have been shown to vary in degree of sociality from being solitary to group-living (Nikitina 1980b, Schradin and Pillay 2005).

A host is a habitat for parasites, providing them with a place to live, forage and mate (Kuris et al. 1980). Translating our result of the effect of host species on parasite community organization for free-living species, we may expect patterns of species co-occurrence in free-living communities to vary among habitats. Studies that involved comparison of species co-occurrence patterns among communities from different habitats are scarce. Nevertheless, the habitat effect on community organization was found for fish in southern France (Céréghino et al. 2005) and chameleons in Africa (Luiselli 2006), although it has not been found for snakes in Brazil (França and Araújo 2007).

In conclusion, our study demonstrated that pattern of species co-occurrence in ectoparasite communities on rodent hosts is typically positive. This pattern may depend on the life history of the parasites and may be affected, to a great extent, by the life history of the host.

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Supplementary material (available online as Appendix O17902 at <www.oikos.ekol.lu.se/appendix>). Appendix 1. Data on rodents and their ectoparasites included in the analyses. Appendix 2. Summary of null model analyses of the co-occurrence of parasite species or higher taxa in individuals of seven host species using V-ratio. Uninfested hosts were excluded from input matrice. Appendix 3. Summary of meta-analyses of the rate of detection of non-randomness in the organization of ectoparasite communities in seven host species using random effects.