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Host community structure and infestation by ixodid ticks: repeatability, dilution effect and ecological specialization

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Abstract Abundance of a species in a location results from the interplay between the intrinsic properties of that species and the extrinsic properties, both biotic and abiotic, of the local habitat. Intrinsic factors promote among-population stability in abundance, whereas extrinsic factors generate variation among populations of a species. We studied (a) repeatability and (b) the effect of abundance and species richness of small mammals on the level of their infestation by larvae and nymphs of *Ixodes ricinus* (ecological generalist) and *Ixodes trianguliceps* (ecological specialist). We asked if tick infestation parameters are characteristic (=repeatable) for a particular host species or a particular stage of a particular tick species. We also asked how abundance and diversity of hosts affect the level of tick infestation on a particular host species. We predicted that the dilution effect (decrease in tick infestation levels with an increase of host abundance and/or species richness) will be better expressed in an ecological generalist, *I. ricinus*, than in an ecological specialist, *I. trianguliceps*. We found that (a) tick abundance, prevalence and aggregation were generally repeatable within tick species/stage; (b) tick abundance and prevalence, but not the aggregation level, were repeatable within host species; (c) the proportion of variance among samples explained by the differences between tick species and stages (as opposed to within-tick species and stage) was higher than that explained by the differences between host species (as opposed to within host species); and (d) the relationship between tick infestation parameters and host abundance and diversity revealed the dilution effect for *I. ricinus* but not for *I. trianguliceps*.

Introduction

Abundance of a species in a location results from the interplay between the intrinsic properties of that species and the extrinsic properties, both biotic and abiotic, of the local habitat. Intrinsic factors promote among-population stability (=repeatability) in abundance (e.g., Blackburn and Gaston 2001). Indeed, the level of abundance has been shown to be species-specific in many free-living (e.g., Begon et al. 2005) and parasitic (e.g., Arneberg et al. 1997; Poulin 2006; Krasnov et al. 2006a) organisms. Nevertheless, abundance is undoubtedly determined by characteristics of the habitat that a free-living species occupies (Morris 1987) or by the host that a parasitic species exploits (Krasnov et al. 2003, 2004). This is because extrinsic factors generate variation among populations of a species (e.g., Newton 1998).

Spatial distribution of a parasite is represented by a set of "islands" or patches (their host organisms). These "islands" can be more (e.g., individuals of the same species)

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or less (e.g., individuals belonging to different species) uniform. The abundance of the hosts and the species composition of host communities are crucial factors affecting distribution and abundance of parasites (e.g., Anderson and May 1978; Arneberg et al. 1998). In other words, abundance and distribution of parasites are strongly affected not only by the quality of the hosts (Krasnov et al. 2003, 2004) but also by their quantity and diversity (Arneberg et al. 1998). Although much theoretical effort has been dedicated to relationships between host abundance and community structure and parasite abundance and distribution (see review in Hudson et al. 2001), only few empirical studies have been done on a few host and parasite taxa (Haukisalmi and Henttonen 1990; Arneberg et al. 1998; Krasnov et al. 2002; Telfer et al. 2005; Stanko et al. 2006a).

Three main parameters describing infestation level of a host by a parasite are parasite abundance, prevalence and aggregation. Abundance is the mean number of parasites per individual host, whereas prevalence is the proportion of infested hosts. Occasionally, parasite abundance is evaluated as an intensity of infestation (=parasite load=parasite burden), which is the mean number of parasites per infested host. In addition, a general characteristic of parasite distribution is that most parasite individuals occur in a few host individuals, while most host individuals have only a few, if any, parasites (Anderson and May 1978; Poulin 1993; Shaw and Dobson 1995; Wilson et al. 2001). In other words, parasite distribution among host individuals is characterized by a high level of aggregation. Parasite aggregation among hosts is an almost universal phenomenon (Anderson and May 1978; May and Anderson 1978; Anderson and Gordon 1982; Shaw and Dobson 1995; Shaw et al. 1998).

Studies of the effect of host abundance and community structure on the abundance and distribution of parasites have provided contradictory results. For example, a positive correlation between parasite burden and host density was reported for helminth endoparasites of *Myodes glareolus* (Haukisalmi and Hentonnen 1990). In the Negev Desert, abundance of two flea species increased with an increase in the abundance of their host, *Dipodillus dasyurus* (Krasnov et al. 2002). These studies supported the predictions of epidemiological models (Anderson and May 1978; May and Anderson 1978; Dobson 1990). Positive relationships between abundance of the main host species and density of ticks were found by Ostfeld et al. (2001, 2006). It should be noted, however, that Ostfeld et al. (2001, 2006) estimated the density of questing rather than feeding tick larvae and nymphs. In contrast, ectoparasite loads on *Lacerta vivipara* correlated negatively with its abundance (Sorci et al. 1997). Relationships between flea abundance or prevalence and abundance of their mammalian hosts in central Europe appeared to be either negative or absent

(Stanko et al. 2006a). Increase in the diversity of the host community decreased the prevalence of *Bartonella* infection in its main host, *Apodemus sylvaticus* (Telfer et al. 2005). Negative relationships between parasite infestation parameters and host abundance and diversity can be viewed as a consequence of the dilution effect when a parasite population is spread over a larger number of host "patches".

The term "dilution effect" was initially introduced by Hamilton (1971) for predator–prey relationships and the situation when an increase in the number of individuals in a prey group leads to a decrease in an individual's probability to be attacked by a predator. Ostfeld and Keesing (2000a, b) redefined this term for host–parasite relationships and the situation occurring when high host diversity diluted the impact of the main reservoir of Lyme disease, *Peromyscus maniculatus*, so that its interactions with the main vector of the disease, a tick *Ixodes scapularis*, were reduced and the subsequent disease risk decreased. At present, this term is applied to a number of parasite species in a variety of hosts (e.g., Sasal 2003; Ratti et al. 2006). Furthermore, the term "dilution effect" was initially applied to the prevalence of the disease (Ostfeld and Keesing 2000a; Schmidt and Ostfeld 2001), but it can also be applied to the prevalence of the disease vector. Furthermore, given that prevalence in many parasites is positively correlated with their abundance (Morand and Guegan 2000; Simkova et al. 2002; Krasnov et al. 2002, 2005a, b, 2006b) and the degree of aggregation (Stanko et al. 2006a, b; but see Bagge et al. 2005), the dilution effect of parameters other than prevalence of infestation can be expected.

The contradictory results in the studies of the relationships between the level of infestation of a parasite and host abundance and/or host diversity suggest that different parasite–host associations may be governed by different regulating mechanisms (Stanko et al. 2006a). For example, a positive relationship between the level of infestation and abundance of host "patches" (individuals and/or species) may arise from a greater probability that each parasite individual will contact a host when the number of hosts increases. However, if reproduction of a parasite cannot keep pace with, or does not depend on, the reproduction of hosts, then the dilution of a parasite population across an increasing host population (including hosts belonging to different species) can be expected. Furthermore, the effect of host abundance and community composition on the infestation level of a parasite may depend on the level of its ecological specialization. Indeed, specialist parasites that are able to exploit only a limited range of hosts, or can persist in only a limited range of habitats, are less likely to demonstrate a dilution effect in their infestation levels under an increase in the total abundance or number of species in a community of the hosts than host-opportunistic parasites are. The reason for this is that generalist parasites would be diluted across all

or most host individuals or species and/or in all or most habitats, whereas specialist parasite would be diluted across some of hosts and/or in some habitats only.

Here we studied (a) the repeatability and (b) the effect of abundance and species richness of small mammals on the level of their infestation by larval and nymphal ixodid ticks of two species. In the study area, these two ticks differ in their habitat specialization. *Ixodes ricinus* occupies a large variety of habitats [except those at elevations above 1,000 meters above sea level (m a.s.l.)], whereas *Ixodes trianguliceps* occurs in mountain and sub-mountain habitats only (Lichard 1965; Černý 1972; Pet'ko et al. 1991; but see Randolph 1975). Moreover, *I. ricinus* usually quest for their hosts outside their shelters and, thus, can persist under a variety of environmental conditions. In contrast, *I. trianguliceps* possesses a much narrower ecological specialization. All developmental stages of this species predominantly inhabit burrows and underground nests of their small mammalian hosts (Randolph 1975; Filippova 1977).

First, we asked if tick infestation parameters are characteristic (=repeatable) for a particular stage of a particular tick species. In other words, we asked if the values of infestation parameters within the same host species or across host species are more similar among samples of the same tick species/stage than among different tick species/stages. However, tick infestation parameters could be also characteristics of a particular host species. Consequently, we also asked if the values of infestation parameters (abundance, prevalence and aggregation) of the same tick/stage are more similar among samples taken from the same host species than among samples taken from different host species. Comparison of the proportion of the total variance explained by differences among host species or tick species/stages, as opposed to within-host species or within tick species/stages, would allow us to understand the relative importance of intrinsic tick species/stage properties, compared with extrinsic host properties, in determining the level of infestation.

Second, we asked how abundance and diversity of hosts affect the level of tick infestation on a particular host species. A decrease in the abundance, prevalence and/or aggregation of a tick with an increase in the total number of co-occurring host individuals and/or species would advocate the dilution effect. We predicted that the dilution effect (if any) would be better expressed in an ecological generalist, *I. ricinus*, than in an ecological specialist, *I. trianguliceps*.

Methods

Mammal sampling and tick collection

Ticks were collected from small mammals trapped between 1983 and 2001 in 18 locations across Slovakia (see details

in Pet'ko et al. 1991; Stanko 1996, 1998; Stanko et al. 2006b, 2007). Traps were deposited at each location following the same protocol (see Stanko 1996, 1998). Each trapping session (on average, 700 traps per session, ranging from 100 to 2,000 traps; 201,350 traps/nights in total) lasted 1–3 nights and totaled 90 sessions with, on average, seven sessions per location (from 1 to 32). A total of 14,368 individuals of 26 species of small mammals (rodents and soricomorphs) were trapped, from which larvae, nymphs and adults of three tick species (*I. ricinus*, *I. trianguliceps*, *Dermacentor reticulatus*) were collected. *D. reticulatus* was the rarest species (ten larvae and one nymph only were collected) and was not included in the analyses.

Data analysis

In the analyses we included only (a) samples where at least eight host individuals of a particular species were found to be infested with a particular stage of a particular tick species and (b) tick stage-host associations that occurred in no fewer than five trapping sessions. The cut-off values for the inclusion of data in the analyses were based on the assumption that the calculation of parameters of parasite abundance and community size could be inaccurate for small samples (Gregory and Woolhouse 1993). Analyses included 12,776 individual small mammals of five rodent species (*Apodemus agrarius*, *Apodemus flavicollis*, *Apodemus uralensis*, *Myodes glareolus*, and *Microtus arvalis*) and one soricomorph species (*Sorex araneus*), from which 10,918 larvae and 690 nymphs of *I. ricinus* and 1,235 larvae and 261 nymphs of *I. trianguliceps* were collected.

For each tick stage-host association within each trapping session we calculated mean abundance of a tick (mean number of ticks per individual host), its prevalence (percentage of infested individuals) and the level of tick aggregation. The latter was evaluated using the index of intraspecific aggregation, J, proposed by Ives (1988, 1991). This measure represents the proportional increase in the number of conspecific competitors experienced by a random individual relative to a random distribution. A zero value of J indicates random distribution of individuals, whereas, for example, $J=0.5$ indicates an increase of 50% in the number of conspecific competitors expected in a patch (=host individual) compared to a random distribution. For each trapping session we calculated the total number of individuals of all host species (ranging from 11 to 420) and total number of host species (ranging from 2 to 14). Prior to analysis all these variables were log-transformed except for prevalence, which was arcsin-transformed. Number of captured host individuals and species correlated positively with sampling effort (number of traps/nights per station) (after log-transformation $r^2 = 0.22$, $F_{1,90} = 24.8$ and $r^2 = 0.18$, $F_{1,90} = 19.2$, respectively, $p < 0.0001$ for both). To control for the

confounding effect of sampling effort, we substituted the original values of the number of captured host individuals and species with their residual deviations from regressions on the number of traps/nights after log-transformation.

To determine whether parameters of infestation are true attributes of either tick species and stage or host species, i.e., parameters that vary less among populations of the same tick species and stage or the host species than among different tick species and stages or different hosts, respectively, we performed repeatability analyses (Arneberg et al. 1997; Krasnov et al. 2005c, 2006a, b; Poulin 2006). First, we analyzed the variation in tick stage abundance, prevalence and the level of aggregation by one-way analyses of variance (ANOVAs) within and across host species, with tick species and stage as independent factor. A significant effect of tick species/stage would indicate that the abundance, prevalence or aggregation level is repeatable within tick species/stage, i.e., that values of infestation parameters of different tick species and stages for the same host or across all host species are more similar to each other than to values from other tick species and stages. Then, we carried out one-way ANOVAs with prevalence and the level of aggregation of each tick stage as dependent variables and host species as independent factor. In these analyses, the significance would show that values of infestation parameters for the same tick species and stage parasitic on different hosts are more similar to each other than to values from other host species. We estimated the proportion of the total variance explained by differences among tick species/stages or host species, as opposed to within tick species/stage or host species, respectively, following Sokal and Rohlf (1995).

In general, infestation parameters within host-tick species-stage association were strongly positively correlated with one another (Spearman rank correlation coefficients $\rho = 0.29$–0.97, $p < 0.05$ for all). There were only two exceptions from this trend: (a) aggregation levels of larval *I. trianguliceps* in *S. araneus* correlated negatively with their prevalence (Spearman rank correlation coefficient $\rho = -0.93$, $p < 0.05$), and (b) aggregation levels of nymphs of this tick in *A. agrarius* correlated negatively with their abundance and prevalence (Spearman rank correlation coefficient $\rho = -0.69$ and $\rho = -0.71$, respectively, $p < 0.05$ for both). Total number of host individuals and total number of host species in a trapping session correlated positively within host species (Spearman rank correlation coefficients $\rho = 0.35$–0.71, $p < 0.05$ for all). Consequently, we substituted the original values of both host and tick parameters with the scores calculated from principal component analyses of (a) three tick infestation variables (abundance, prevalence and level of aggregation) and (b) two host community variables (abundance and species richness) carried out separately for each host species and each tick

species and stage. As a result, two new variables (tick infestation variable and host community variable) were extracted.

To test for the effect of the host community structure on the pattern of tick infestation, we regressed the scores of the new tick infestation variable against the scores of the new host community variable separately for each host species and each tick species and stage. We avoided an inflated type I error by performing sequential Bonferroni adjustments of the significance level across all analyses. Significance was recorded at the adjusted level.

Results

A summary of the principal component analyses of tick infestation parameters and host community parameters is presented in Table 1. The two resulting variables explained 62–87% of the variance. The tick infestation variable correlated positively with mean abundance, prevalence and aggregation level of ticks for most host species and tick species and stages, except for the aggregation level of nymphal *I. trianguliceps* on *A. agrarius* and the prevalence of larval *I. trianguliceps* on *S. araneus*. The loadings of these factors into the resultant variables were negative. The host community variable correlated positively with both total number of host individuals and species and, thus, represented an increase in both total host abundance and diversity.

In four of six host species, as well as across all species, all three infestation parameters of a tick species/stage were also repeatable (Table 2; see Fig. 1 for an illustrative example of tick abundance in *A. flavicollis*). In other words, abundance, prevalence and aggregation level of each tick species/stage within each host and across all hosts had characteristic limits of variation. No within-tick species/stage repeatability of any infestation parameter was found in *M. arvalis*, whereas only prevalence was repeatable within tick species and stage in *S. araneus* (Table 2). In general, among-sample variation in tick abundance and level of aggregation was better explained by differences between tick species and stages than was the case for prevalence.

On the other hand, the repeatability analysis of the infestation parameters of two stages of two species of ticks demonstrated that mean abundance and prevalence of a particular stage of a particular tick can also be considered as a characteristic of a host species (Table 3, see Fig. 2 for an illustrative example of abundance of larval *I. ricinus*), except for nymphal *I. ricinus*. This means that estimates of tick abundance and prevalence were repeatable within the host species, i.e., were more similar to each other than

Table 1 Summary of principal component analyses of tick infestation parameters (*A* mean abundance, *P* prevalence, *J* aggregation level and host community parameters, *NI* total number of individuals, *SR* total number of species. Abbreviations of host species names are *AAGR A. agrarius*, *AFLA A. flavicollis*, *AURA A. uralensis*, *MGLA M. glareolus*, *MARV M. arvalis*, *SARA S. araneus*. Abbreviations of tick species and stages names are *IR-l* larval *I. ricinus*, *IR-n* nymphal *I. ricinus*, *IT-l* larval *I. trianguliceps*, *IT-n* nymphal *I. trianguliceps*. *E* eigenvalue, *%V* proportion of variance explained)

| Host | Tick/stage | Tick infestation variable | | | | | | Host community variable | | | |
| | | E | %V | Factor loading | | | | E | %V | Factor loading | |
				A	P	J				NI	SR
AAGR	IR-l	1.88	0.63	0.95	0.97	0.14		1.34	0.67	0.83	0.82
	IR-n	2.00	0.67	0.92	0.86	0.58		1.37	0.68	0.81	0.83
	IT-l	2.10	0.71	0.98	0.88	0.60		1.1	0.55	0.74	0.80
	IT-n	2.58	0.86	0.98	0.95	−0.84		1.29	0.65	0.79	0.80
AFLA	IR-l	1.93	0.64	0.94	0.97	0.30		1.39	0.70	0.81	0.82
	IR-n	2.13	0.80	0.95	0.87	0.67		1.50	0.75	0.87	0.89
	IT-l	2.00	0.69	0.95	0.90	0.53		1.21	0.61	0.77	0.86
	IT-n	1.88	0.63	0.97	0.97	0.40		1.06	0.53	0.75	0.73
AURA	IR-l	1.89	0.63	0.98	0.92	0.30		1.37	0.68	0.77	0.84
	IR-n	2.05	0.68	0.98	0.94	0.44		1.16	0.68	0.76	0.79
MGLA	IR-l	1.92	0.64	0.97	0.97	0.28		1.24	0.63	0.80	0.85
	IR-n	1.87	0.62	0.97	0.96	0.25		1.18	0.59	0.77	0.73
	IT-l	2.16	0.72	0.98	0.91	0.60		1.23	0.61	0.77	0.79
	IT-n	2.21	0.74	0.96	0.94	0.63		1.21	0.60	0.79	0.78
MARV	IR-l	1.87	0.62	0.95	0.88	0.43		1.63	0.81	0.90	0.92
	IR-n	2.57	0.86	0.93	0.98	0.85		1.31	0.66	0.81	0.83
	IT-l	2.62	0.87	0.99	0.95	0.86		1.80	0.90	0.90	0.95
SARA	IR-l	2.21	0.73	0.95	0.96	0.58		1.59	0.79	0.89	0.89
	IT-l	1.93	0.65	0.53	−0.82	0.98		1.96	0.96	0.99	0.95

expected by chance. In contrast, the aggregation level of a tick species/stage appeared not to be characteristic of a host species and varied randomly among host species. Nevertheless, the proportion of variation in tick abundance and prevalence among samples accounted for difference between host species was relatively low (Table 3).

Regression analyses between tick infestation variable and host community variable demonstrated that whenever tick infestation parameters (abundance, prevalence and aggregation level) were affected by host abundance and diversity, the relationship between tick infestation variable and host community variable conformed to dilution effect (Table 4). In other words, tick abundance, prevalence and/or aggregation level either decreased with an increase in the numbers of host individuals and species in a community or did not depend on host abundance and diversity. The only exception was aggregation level of the nymphal *I. trianguliceps* in *A. agrarius*, which increased with an increase in host abundance and diversity (negative loading of aggregation level into the tick infestation variable, see Table 1). The occurrence of the dilution effect of host abundance and diversity on tick infestation differed among tick as well as among host species. This effect was found for (a) *I. ricinus*,

but not *I. trianguliceps*; and (b) *I. ricinus* parasitic on three *Apodemus* species and *M. glareolus*, but not on *M. arvalis* and *S. araneus*.

Discussion

This study demonstrated that tick abundance and prevalence were generally repeatable within both tick species/ stage and host species, whereas aggregation level was repeatable within tick species/stage, but not within host species. However, the proportion of variation among samples that accounted for differences between tick species and stages was higher than that which accounted for differences between host species. Finally, relationship between tick infestation parameters and host abundance and diversity revealed the dilution effect for *I. ricinus* but not *I. trianguliceps*. The latter result supported our prediction.

Repeatability of infestation parameters within tick species/stage implies that some species-specific and/or stage-specific life history traits determine the limits of abundance, prevalence and aggregation. Similar patterns for abundance were found for nematodes (Arneberg et al. 1997) and fleas
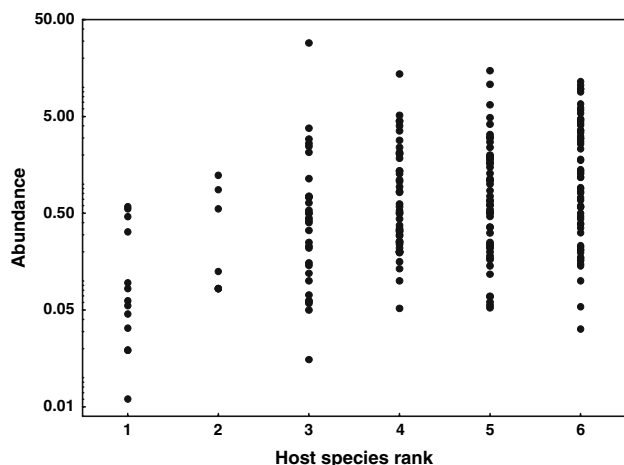
Fig. 1 Rank plot of abundance (log-scale) of different tick species/stages in *A. flavicollis*. Tick species/stages are ranked according to the log-transformed values of their abundance, with rank 1 given to the species/stage with the lowest mean abundance; all sample estimates are plotted for each species/stage. *Each datapoint* represents abundance value calculated for a particular tick species/stage on a particular host species in a particular sample. If variation is small within, compared with between, species/stages, we expect the points to fall in a region of the plot stretching from the *lower left corner* to the *upper right corner*, with few or no points in either the *upper left corner* or *lower right corner*. Tick species/stages ranked are: *1* nymphal *I. trianguliceps*, *2* larval *I. trianguliceps*, *3* nymphal *I. ricinus* and *4* larval *I. ricinus*

Table 2 Summary of repeatability analyses of abundance, prevalence and aggregation level among tick species and stages within host species (within-host species ANOVAs with tick species and stage as an independent variable). See Table 1 for abbreviations of host species names. *%V* Proportion of the variation among samples accounted for by differences between tick species and stages

| Host	Infestation parameter	F	df	p	$\%V$
AAGR	Abundance	17.6	3, 105	<0.00001	28.7
	Prevalence	10.8	3, 105	<0.00001	4.2
	Aggregation level	12.1	3, 105	<0.00001	33.4
AFLA	Abundance	37.9	3, 152	<0.00001	41.8
	Prevalence	31.7	3, 152	<0.00001	8.9
	Aggregation level	6.9	3,152	<0.0001	13.8
AURA	Abundance	8.5	1, 42	<0.005	19.3
	Prevalence	4.5	1, 42	<0.004	2.0
	Aggregation level	6.1	1, 42	<0.01	21.7
MGLA	Abundance	32.1	3, 125	<0.00001	24.9
	Prevalence	24.4	3, 125	<0.00001	3.7
	Aggregation level	3.0	3, 125	<0.02	6.0
MARV	Abundance	1.7	2, 21	0.2	–
	Prevalence	2.0	2, 21	0.14	–
	Aggregation level	1.0	2, 21	0.32	–
SARA	Abundance	1.5	1, 10	0.25	–
	Prevalence	5.5	1, 10	<0.01	2.4
	Aggregation level	0.1	1, 10	0.8	–
All	Abundance	73.3	3, 470	<0.0001	24.1
	Prevalence	50.9	3, 470	<0.0001	3.7
	Aggregation level	20.3	3, 470	<0.0001	15.3
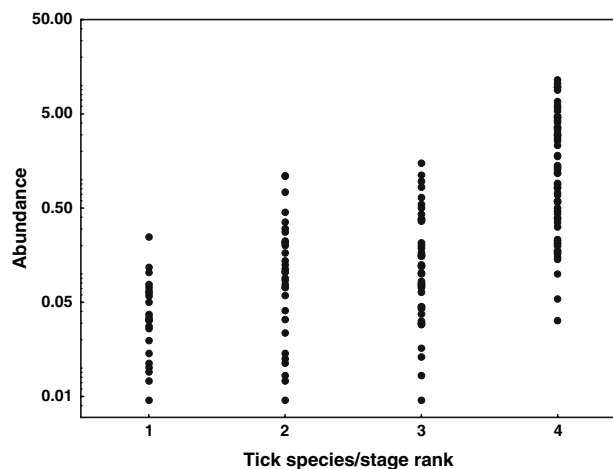
Fig. 2 Rank plot of abundance (log-scale) of larval *I. ricinus* on different hosts. See Fig. 1 for explanations. Host species ranked are: *1 M. arvalis*, *2 S. araneus*, *3 A. uralensis*, *4 M. glareolus*, *5 A. agrarius* and *6 A. flavicollis*

(Krasnov et al. 2006a) parasitic on mammals and across and within six main taxa of fish parasites (Poulin 2006). In contrast, inter-population within-species variation in prevalence among parasite species appeared to be either high (Poulin 2006) or even random (Arneberg et al. 1997). Patterns of among-population within-parasite species variation in aggregation level have been studied only for fleas on small mammals, and aggregation level in these parasites appeared to be a species-specific attribute (Krasnov et al. 2006b). The explanation of higher inter-population variation in prevalence of a parasite species, as opposed to that in abundance, is related to the fact that prevalence is determined by the encounter rate between host individuals and parasites. This rate is strongly affected by processes acting outside the host, such as, for example, the survival of free-living stages, and, therefore, may strongly depend on local environmental conditions (Poulin 2006).

Repeatability of infestation parameters within-tick species/stage suggests that each of these parameters has some pre-defined species-stage-specific lower and upper limits. In the case of ticks, lower limits of abundance can be affected by the species-specific and stage-specific time necessary for a blood meal, whereas upper limits of abundance can be determined by species-specific reproductive outputs, mortality rates and abilities of larval and nymphal ticks to cope with crowding. For example, egg production by an engorged female *I. trianguliceps* was estimated to be

between 1,000 and 2,000 (Randolph 1975) or even as low as 350–500 (Filippova 1977), whereas an engorged female *I. ricinus* produces 3,000–5,000 eggs (e.g., Honzáková et al. 1975). As a result, abundance of larval *I. ricinus* in

Table 3 Summary of repeatability analyses of abundance, prevalence and aggregation level of tick species and stages among host species (ANOVAs with host species as an independent variable). See Table 1 for abbreviations of tick species and names of stages. %V Proportion of the variation among samples accounted for by differences between host species

Tick species and stage	Infestation parameter	F	df	p	%V
IR-l	Abundance	8.2	5, 204	<0.0001	11.5
	Prevalence	5.0	5, 204	<0.0001	2.12
	Aggregation level	1.1	5, 204	0.34	–
IR-n	Abundance	1.4	4, 127	0.25	–
	Prevalence	1.9	4, 127	0.12	–
	Aggregation level	0.4	4, 127	0.81	–
IT-l	Abundance	5.0	4, 77	<0.001	10.4
	Prevalence	6.1	4, 77	<0.0001	0.9
	Aggregation level	0.7	4, 77	0.55	–
IT-n	Abundance	6.9	2, 47	<0.0001	10.3
	Prevalence	6.4	2, 47	<0.002	0.2
	Aggregation level	1.1	2, 47	0.32	–

Table 4 Summary of regression analyses of a tick infestation variable against a host community variable (see text for explanations). See Table 1 for abbreviations of host species and tick stage and species names

Tick species and stage	Host	r^2	df	F	p	Slope
IR-l	AAGR	0.27	1,51	17.8	<0.0001	−0.54
	AFLA	0.21	1,59	16.0	<0.0001	−0.42
	AURA	0.16	1,20	5.2	<0.003	−0.31
	MGLA	0.25	1,45	15.4	<0.001	−0.48
	MARV	0.13	1,11	1.7	0.22	
	SARA	0.25	1,3	1.0	0.38	
IR-n	AAGR	0.36	1,39	22.4	<0.0001	−0.60
	AFLA	0.42	1,39	28.2	<0.0001	−0.65
	AURA	0.33	1,11	9.4	<0.01	−0.48
	MGLA	0.14	1,28	4.7	<0.01	−0.38
	MARV	0.02	1,5	0.1	0.77	
IT-l	AAGR	0.26	1,8	2.4	0.12	
	AFLA	0.006	1,30	0.2	0.66	
	MGLA	0.004	1,27	0.4	0.91	
	SARA	0.38	1,3	1.9	0.26	
IT-n	AAGR	0.01	1,3	0.1	0.84	
	AFLA	0.09	1,20	1.5	0.12	
	MGLA	0.02	1,21	0.5	0.49	

our study area was six-times higher than that of larval *I. trianguliceps* (on average, across all host species, 1.94 ± 0.48 vs 0.29 ± 0.05, respectively). In spite of its dependence on local factors (Poulin 2006), prevalence appeared to be also repeatable within tick species/stages, although to a lower degree than abundance. Species-stage-specific level of prevalence can also be explained by species-stage-specific reproductive output and mortality level. For example, low fecundity of *I. trianguliceps* seems to be compensated by low mortality of its larvae, because they inhabit mainly burrows and underground nests of their small mammalian hosts (Filippova 1977). As a result, although prevalence of larval *I. ricinus* was twice as high as that of *I. trianguliceps* (0.33 ± 0.03 vs 0.14 ± 0.02, respectively), the difference between prevalences of their nymphs was much less (0.09 ± 0.01 vs 0.06 ± 0.01, respectively).

The results of our study demonstrate that the level of aggregation is characteristic for a particular stage of a particular tick. Parasites face a trade-off between being too aggregated and being too random (Anderson and Gordon 1982; Shaw and Dobson 1995). For example, a parasite could be lost due to high mortality of heavily infected hosts if the level of aggregation is too high. Consequently, there should be an optimal level of aggregation of a parasite that may depend on demographic factors such as intrinsic birth and death rates and mobility. Birth rate and mortality, as well as mobility, differ among larval and nymphal *I. ricinus* and *I. trianguliceps* (Filippova 1977). As a result, different species/stages demonstrate characteristic aggregation levels, as was the case with fleas (Krasnov et al. 2006b).

This study showed that infestation parameters are properties of a tick species/stage. Moreover, species-specific and stage-specific limits are more characteristic for tick abundance and aggregation level than for prevalence. Furthermore, infestation levels appear to be less characteristic for host species than for tick/stage, as indicated by (a) a low proportion of variation in abundance and prevalence among samples accounting for difference among host species as opposed to within host species; (b) a lack of within-host repeatability of the aggregation level of all tick species and stages; and (c) random variation of all infestation parameters of nymphal *I. ricinus* among host species. In particular, the cause of the lack of repeatability of the aggregation level of larval ticks may be the pattern of larval acquisition by host individuals. Tick larvae arise as "a package" from one large egg mass (Randolph and Steele 1985). As a result, a host which, by chance, encounters an egg mass will likely become heavily infested with larvae, whereas a host which, by chance, evades egg masses will likely harbor few, if any, larvae. Tick nymphs co-feed with tick larvae on the same host individuals (Randolph et al. 1996, 1999) and, therefore, the random among-host variation of the level of their aggregation can arise due to the random among-host variation of the aggregation level of larvae.

Nevertheless, it is suggested that some host species are characterized by higher infection levels, by any parasite species, than are other host species (Poulin 2006). Arneberg

et al. (1997) found the repeatability of the intensity and abundance of nematodes within mammalian hosts, although the repeatability among host species was weaker than that observed among parasite species. Poulin and Mouritsen (2003) reported significant, albeit weak, repeatability of the prevalence of larval trematodes within snail species. Relatively weak repeatability of prevalence, but not abundance, of various parasites was found among fish species by Poulin (2006). The repeatability of flea abundance within the same host species was reported by Krasnov et al. (2006a). Again, the repeatability of this parameter within the host species was weaker than that within flea species. These studies clearly demonstrated that, although the identity of the host species has a certain effect, the infestation parameters are mainly properties of parasite species and not of host species.

The results of our study, together with earlier observations, show that abundance and aggregation and, to a lesser degree, prevalence of infestation by metazoan parasites are real parasite species characters. However, these parameters are somewhat variable. Indeed, the proportion of variance in abundance, prevalence and aggregation level among samples accounted for difference among, as opposed to within, tick species and stages appeared to be rather low. It attained about 24% and 15% for abundance and aggregation level, respectively, but was as low as 4–5% for prevalence. This means that extrinsic factors strongly affect tick species-specific and stage-specific infestation parameters. The results of this study suggest that abundance and diversity of hosts may play the major role, at least for *I. ricinus*.

In general, abundance, prevalence and aggregation of larval and nymphal *I. ricinus* decreased with an increase in total number of host individuals and species in a location. Thus, larvae and nymphs were diluted with an increased number of host patches. Furthermore, because neither larvae nor nymphs are able to reproduce, and, thus, their numbers in a location during a year can only decrease (due to relatively high mortality; see Randolph 1979; Brown 1988; Randolph and Rogers 1997) or, sometimes, stay stable. In addition, self-dispersal abilities of tick larvae and nymphs are limited (Filippova 1977), although new larvae and/or nymphs can be introduced to a location by dispersing animals (see, e.g., Estrada-Peña et al. 2006). In contrast, hosts can both reproduce and immigrate into that location. As a result, when host populations and/or host communities grow, approximately the same number of larvae or nymphs is distributed across greater numbers of host individuals. Consequently, (a) the number of ticks per individual host (=abundance) decreases; (b) a higher proportion of individual hosts stays tick-free (i.e., prevalence decreases); and (c) the number of heavily infested hosts (e.g., aggregation level) decreases (although not in all cases; see also Bagge et al. 2005).

As we predicted, the dilution effect was manifested in *I. ricinus* but not in *I. trianguliceps*. This can stem from the difference between these species in the level of ecological specialization. Larvae, nymphs and imago of *I. trianguliceps* inhabit mainly burrows and underground nests of the hosts (Randolph 1975; Filippova 1977), whereas *I. ricinus* quest for their hosts outside their shelters. Therefore, an increase in the number of host species and/or species in a location would not affect *I. trianguliceps* because the growth of a host population and/or community would not generally increase the number and diversity of small mammalian inhabitants per burrow (e.g., Gliwicz 1992).

The manifestation of the dilution effect in *I. ricinus* parasitic on *Apodemus* species and *M. glareolus*, but not on *M. arvalis* and *S. araneus*, requires an explanation. The main ecological difference between these two groups of species is that the latter either live in well-constructed burrows (*M. arvalis*) or rarely visit "open" habitats (*S. araneus*; see Dolgov 1985), whereas the former prefer above-ground nests. As a result, infestation of *M. arvalis* and *S. araneus* by *I. ricinus* (which quests for hosts in "open" habitats) in our study area was relatively low at all times (e.g., mean abundances of larval *I. ricinus* on *M. arvalis* and *S. araneus* were 0.2 and 0.07, respectively, compared with 0.4–1.0 for the remaining host species).

Earlier studies of the relationships between host abundance and diversity and their infestation by various ixodid species suggest that our results may represent a local manifestation of a more general pattern. For example, abundances of a generalist tick *Ixodes scapularis* on *Peromyscus leucopus* were found to be lowest in the years of highest host densities (Ostfeld et al. 1996). Prevalence of nymphal *I. scapularis* on *P. leucopus* appeared to be lower in small vs large forest fragments in an agricultural landscape (Wilder and Meikle 2004), i.e., in those patches where *P. leucopus* density is usually higher (Anderson et al. 2003). In contrast, a study of questing behavior of *Ixodes spinipalpis*, using sentinel laboratory mice, demonstrated no relationship between overall availability of sentinel animals and the rate of their infestation by larval or nymphal ticks (Burkot et al. 2001). *Ixodes spinipalpis* is a nidicolous species that is considered to be more host-specific than, for example *I. ricinus* and *I. scapularis* (Burkot et al. 2001) and, thus, it seems to be an ecological equivalent of *I. trianguliceps*.

It should be noted, however, that, in some cases, a positive relationship between tick density and host abundance has also been reported (e.g., Daniels et al. 1993). However, in many studies, the density of ticks was measured via questing rather than feeding individuals, i.e., using a methodological approach that is not appropriate for the question at hand. Nevertheless, the results of studies of the relationships between tick infestation levels and host abundance and diversity are often contradictory (e.g., Adler et al. 1992

vs Ostfeld et al. 1996). This is because host abundance and diversity are, undoubtedly, not the only factors that may influence the infestation parameters of pre-imaginal ticks. Ticks stay on their hosts only long enough to take a blood meal and do not depend on hosts for shelter. Therefore, they are subject to the effects of the external environment (e.g., Estrada-Peña et al. 2004). As a result, their infestation parameters can be affected by environmental factors (e.g., Estrada-Peña 2001), either directly or via the influence on their questing behavior (Perret et al. 2000).

References

Adler GH, Telford SR, Wilson ML, Spielman A (1992) Vegetation structure influences the burden of immature *Ixodes dammini* on its main host, *Peromyscus leucopus*. Parasitology 105:105–110

Anderson RM, Gordon DM (1982) Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortality. Parasitology 85:373–398

Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions. I. Regulatory processes. J Anim Ecol 47:219–247

Anderson CS, Cady AB, Meikle DB (2003) Effects of vegetation structure and edge habitat on the density and distribution of white-footed mice (*Peromyscus leucopus*) in small and large forest patches. Can J Zool 81:897–904

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

Arneberg P, Skorping A, Grenfell B, Read AF (1998) Host densities as determinants of abundance in parasite communities. Proc R Soc Lond B 265:1283–1289

Bagge AM, Sasal P, Valtonen ET, Karvonen A (2005) Infracommunity level aggregation in the monogenean communities of crucian carp (*Carassius carassius*). Parasitology 131:367–372

Begon M, Townsend CR, Harper JL (2005) Ecology: from individuals to ecosystems, 4th edn. Blackwell, London

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

Brown B (1988) Highlights of contemporary research on host immune responses to ticks. Vet Parasitol 28:321–334

Burkot TR, Maupin GO, Schneider BS, Denatale C, Happ CM, Rutherford JS, Zeidner NS (2001) Use of a sentinel host system to study the questing behavior of *Ixodes spinipalpis* and its role in the transmission of *Borrelia bissettii*, human granulocytic ehrlichiosis, and *Babesia microti*. Am J Trop Med Hyg 65:293–299

Černý V (1972) The tick fauna of the Czechoslovakia. Folia Parasitol 19:87–92

Daniels TJ, Fish D, Schwartz I (1993) Reduced abundance of *Ixodes scapularis* (Acari, Ixodidae) and Lyme disease risk by deer exclusion. J Med Entomol 30:1043–1049

Dobson AP (1990) Models for multi-species host-communities. In: Esch GW, Bush AO, Aho JM (eds) Parasite communities: patterns and processes. Chapman and Hall, London, pp 260–288

Dolgov VA (1985) *Sorex* shrews of the Old World. Moscow University Press, Moscow (in Russian)

Estrada-Peña A (2001) Distribution, abundance, and habitat preferences of *Ixodes ricinus* (Acari: Ixodidae) in Northern Spain. J Med Entomol 38:361–370

Estrada-Peña A, Guglielmone AA, Mangold AJ (2004) The distribution and ecological "preferences" of the tick *Amblyomma cajennense* (Acari: Ixodidae), an ectoparasite of humans and other mammals in the Americas. Ann Trop Med Parasitol 98:283–292

Estrada-Peña A, Quilez J, del Cacho E, Acedo CS (2006) A framework to map abundance of tick metapopulations. Ecol Model 193:663–674

Filippova NA (1977) Ixodid ticks of subfamily Ixodinae. Fauna USSR. Arachnids, vol 4 (2) (114). Nauka, Leningrad (in Russian)

Gliwicz J (1992) Patterns of dispersal in non-cyclic populations of small rodents. In: Stenseth NC, Lidicker WZ (eds) Animal dispersal. Small mammals as a model. Chapman and Hall, London, pp 147–159

Gregory RD, Woolhouse ME (1993) Quantification of parasite aggregation: a simulation study. Acta Tropica 54:131–139

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Haukisalmi V, Henttonen H (1990) The impact of climatic factors and host density on the long-term population dynamics of vole helminths. Oecologia 83:309–315

Honzáková E, Olejníček J, Černý V, Daniel M, Dusbábek F (1975) Relationships between number of eggs deposited and body of engorged *Ixodes ricinus* female. Folia Parasitol 22:37–43

Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) (2001) The ecology of wildlife diseases. Oxford University Press, Oxford

Ives AR (1988) Aggregation and the coexistence of competitors. Ann Zool Fenn 25:75–88

Ives AR (1991) Aggregation and coexistence in a carrion fly community. Ecol Monogr 61:75–94

Krasnov BR, Khokhlova IS, Shenbrot GI (2002) The effect of host density on ectoparasite distribution: an example with a desert rodent parasitized by fleas. Ecology 83:164–175

Krasnov BR, Khokhlova IS, Shenbrot GI (2003) Density-dependent host selection in ectoparasites: an application of isodar theory to fleas parasitizing rodents. Oecologia 134:365–373

Krasnov BR, Khokhlova IS, Burdelova NV, Mirzoyan NS, Degen AA (2004) 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, Morand S, Khokhlova IS, Shenbrot GI, Hawlena H (2005a) Abundance and distribution of fleas on desert rodents: linking Taylor's power law to ecological specialization and epidemiology. Parasitology 131:825–837

Krasnov BR, Stanko M, Miklisova D, Morand S (2005b) Distribution of fleas (Siphonaptera) among small mammals: mean abundance predicts prevalence via simple epidemiological model. Int J Parasitol 35:1097–1101

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

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

Krasnov BR, Stanko M, Miklisova D, Morand S (2006b) Host specificity, parasite community size and the relation between abundance and its variance. Evol Ecol 20:75–91

Lichard M (1965) Notes on the occurrence and ecology of tick *Ixodes trianguliceps* Birula, 1895. Biologia (Bratislava) 20:348–358 (in Slovak)

May RM, Anderson RM (1978) Regulation and stability of host-parasite population interactions. II. Destabilizing processes. J Anim Ecol 47:455–461

Morand S, Guegan J-F (2000) Distribution and abundance of parasite nematodes: ecological specialization, phylogenetic constraints or simply epidemiology? Oikos 88:563–573

Morris DW (1987) Ecological scale and habitat use. Ecology 68:362–369

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

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

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

Ostfeld RS, Miller MC, Hazler KR (1996) Causes and consequences of tick (*Ixodes scapularis*) burdens on white-footed mice (*Peromyscus leucopus*). J Mammal 77:266–273

Ostfeld RS, Schauber EM, Canham CD, Keesing F, Jones CG, Wolff JO (2001) Effects of acorn production and rodent abundance on abundance and *Borrelia burgdorferi*-infection prevalence of nymphal *Ixodes scapularis* ticks. Vector Borne Zoonotic Dis 1:55–63

Ostfeld RS, Canham CD, Oggenfuss K, Winchcombe RJ, Keesing F (2006) Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. PLOS Biol 4:e145

Perret JL, Guigoz E, Rais O, Gern L (2000) Influence of saturation deficit and temperature on *Ixodes ricinus* tick questing activity in a Lyme borreliosis-endemic area (Switzerland). Parasitol Res 86:554–557

Pet'ko B, Černý V, Jurášek V (1991) Parasite–host relationships of the tick *Ixodes trianguliceps* Bir. and coincidence of its ecological niches with those of *Ixodes ricinus* (L.). In: Dusbábek F, Bukva V (eds) Modern acarology. Academia, Prague, pp 455–460

Poulin R (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. Int J Parasitol 23:937–944

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

Poulin R, Mouritsen KN (2003) Large-scale determinants of trematode infections in intertidal gastropods. Mar Ecol Prog Ser 254:187–198

Randolph SE (1975) Patterns of the distribution of the tick *Ixodes trianguliceps* Birula on its host. J Anim Ecol 44:451–474

Randolph SE (1979) Population regulation in ticks: the role of acquired resistance in natural and unnatural hosts. Parasitology 79:141–156

Randolph SE, Rogers DJ (1997) A generic population model for the African tick *Rhipicephalus appendiculatus*. Parasitology 115:265–279

Randolph SE, Steele GM (1985) An experimental evaluation of conventional control measures against the sheep tick, *Ixodes ricinus* (L.) (Acari, Ixodidae). 2. The dynamics of the tick-host interaction. Bull Entomol Res 75:501–518

Randolph SE, Gern L, Nutall PA (1996) Co-feeding ticks: epidemiological significance for tick-borne pathogen transmission. Parasitol Today 12:472–479

Randolph SE, Miklisova D, Lysy J, Rogers DJ, Labuda M (1999) Incidence from coincidence: patterns of tick infestation on rodents facilitate transmission of tick-borne encephalitis virus. Parasitology 118:177–186

Ratti O, Ojanen U, Helle P (2006) Increasing group size dilutes black fly attack rate in Black Grouse. Ornis Fennica 83:86–90

Sasal P (2003) Experimental test of the influence of the size of shoals and density of fish on parasite infections. Coral Reefs 22:241–246

Schmidt KA, Ostfeld RS (2001) Biodiversity and dilution effect in disease ecology. Ecology 83:609–619

Shaw DJ, Dobson AP (1995) Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111:S111–S127

Shaw DJ, Grenfell BT, Dobson AP (1998) Patterns of macroparasite aggregation in wildlife host populations. Parasitology 117:597–610

Simkova A, Kadlec D, Gelnar M, Morand S (2002) Abundance-prevalence relationship of gill congeneric ectoparasites: testing the core satellite hypothesis and ecological specialization. Parasitol Res 88:682–686

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

Sorci G, Defraipont M, Clobert J (1997) Host density and ectoparasite avoidance in the common lizard (*Lacerta vivipara*). Oecologia 11:183–188

Stanko M (1996) Ectoparasites of small mammals (Insectivora, Rodentia) of the Ondava downstream (East Slovakian Lowland). 3. Ticks (Ixodida). Natura Carpatica 37:151–160 (in Slovak)

Stanko M (1998) Ectoparasites of small mammals (Insectivora, Rodentia) of the Natural nature reserve Latoricky luh (East Slovakian Lowland). 1. Fleas (Siphonaptera) and ticks (Ixodida). Natura Carpatica 39:111–120 (in Slovak)

Stanko M, Krasnov BR, Morand S (2006a) Relationship between host density and parasite distribution: inferring regulating mechanisms from census data. J Anim Ecol 75:575–583

Stanko M, Fričová J, Miklisová D, Mošanský L (2006b) Host-parasite relationships among parasitic arthropods and common vole (*Microtus arvalis*, Rodentia) in lowland ecosystems of Slovakia. In: Buczek A, Blaszak C (eds) Arthropods: epidemiological importance. Koliber, Lublin, pp 89–97

Stanko M, Krasnov BR, Miklisova D, Morand S (2007) Simple epidemiological model predicts the relationships between prevalence and abundance in ixodid ticks. Parasitology 134:59–68

Telfer S, Bown KJ, Sekules R, Begon I, Hayden T, Birtles R (2005) Disruption of a host-parasite system following the introduction of an exotic host species. Parasitology 130:661–668

Wilder SM, Meikle DB (2004) Prevalence of deer ticks (*Ixodes scapularis*) on white-footed mice (*Peromyscus leucopus*) in forest fragments. J Mammal 85:1015–1018

Wilson K, Bjørnstad ON, Dobson AP, Merler S, Poglaen G, Randolph SE, Read AF, Skorping A (2001) Heterogeneities in macroparasite infections: patterns and processes. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) The ecology of wildlife diseases. Oxford University Press, Oxford, pp 6–44