

# Competition, facilitation or mediation via host? Patterns of infestation of small European mammals by two taxa of haematophagous arthropods

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**Abstract.** 1. We studied the effect of flea infestation on the pattern of tick (*Ixodes ricinus* and *Ixodes trianguliceps*) infestation on small mammals.

2. We asked (1) whether the probability of an individual host being infested by ticks was affected by its infestation of fleas (number of individuals and species) and (2) whether the abundance and prevalence of ticks in a host population was affected by the abundance, prevalence, level of aggregation, and species richness of fleas.

3. The probability of a host individual being infested by ticks was affected negatively by flea infestation. At the level of host populations, flea abundance and prevalence had a predominantly positive effect on tick infestation, whereas flea species richness had a negative effect on tick infestation.

4. The effect of flea infestation on tick infestation was generally greater in *I. ricinus* than in *I. trianguliceps*, but varied among host species.

5. It can be concluded that the effect of fleas on tick infestation of small mammals may be either negative or positive depending on the level of consideration and parameters involved. The results did not provide support for direct interactions between the two ectoparasite taxa, but suggested population and community dynamics and the defence system of the hosts as possible factors.

**Key words.** Abundance, fleas, ixodid ticks, probability of infestation, small mammals, species richness.

## Introduction

Interactions among species in a community may be either direct or indirect and either facilitative or competitive (Martin & Martin, 2001; Eskelinen, 2008). Moreover, positive and negative inter-specific effects may occur within the same community and among the same species either simultaneously or varying in time and space (see Callaway, 2007 for recent review). Obviously, the relative strength of facilitative or competitive interactions has important consequences for community organisation.

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Parasites present many advantages for studying community organisation. For example, numerous replicated samples in the majority of parasitological surveys may be obtained. In addition, several closely or distantly related parasite species are simultaneously present on a host (Combes, 2001; Poulin, 2007). Depending on the presence or absence of inter-specific interactions among parasite species sharing a host, both isolationist and interactive parasite communities have been distinguished (Holmes & Price, 1986). Parasite species in the former exploit different resources taken from the same host individual, whereas the latter comprise parasite species sharing the same trophic level (Poulin, 2007). Furthermore, parasites may compete not only for food but for space as well. The interactive communities do not necessarily include closely-related parasites, because parasites belonging to different taxa often have similar trophic and spatial niches. For example, the

vast majority of ectoparasitic arthropods exploit the same host resource, namely its blood, and often prefer the same area of a host's body, namely where blood is most readily available and where it is least accessible to the host's grooming (Jeffries & Lawton, 1984; Krasnov, 2008).

Recently, the number of parasite community studies increased sharply (Combes, 2001; Poulin, 2007). Many of these studies produced contradictory results and, consequently, the organization of these communities is still poorly understood. For example, there are numerous examples of negative effects that parasitic species exert on each other. Responses to these effects may be numerical (e.g. reduction in the size of infrapopulations of one or more competing species; Dezfuli *et al.*, 2001) or functional (e.g. change of infection site in response to the presence of a competitor; Friggens & Brown, 2005). However, positive inter-specific effects have also been reported (Krasnov *et al.*, 2005).

There may be several reasons behind contrasting patterns reported for different parasite communities. First, at the level of an individual host, the type of interactions may depend on immunosuppressive abilities of, at least, one of the interacting parasites. Indeed, parasites may compete for the same resource on the same host, not only with each other, but also with the host itself (Combes, 2001). Competition between a host and a parasite may lead to parasite-induced immunosuppression of a host which, in turn, may affect positively not only the immunosuppressing parasite, but also other co-occurring parasites (Cox, 2001). Consequently, competition among parasites may be mediated by competition with a shared competitor (host), so that the net result of interactions both between parasites and between each parasite and a host may be positive among-parasite effects, i.e. apparent facilitation (Levine, 1999). If none of the competitors causes immunosuppression, then the interactions between parasites may represent asymmetric competition (e.g. Hendrickson & Curtis, 2002). Second, inter-specific interactions among parasites within a host can be mediated via the host population or community as a result of an aggregative pattern of distribution of parasites among host individuals. Coexistence of competing species may be facilitated by reducing the overall intensity of competition via aggregated utilization of fragmented resources (aggregation model of coexistence) (e.g. Hartley & Shorrocks, 2002). In other words, the pattern of interactions between parasite species may depend on the scale being considered. In some cases, the type of parasite interactions occurring within an individual host may differ from the pattern occurring within a host population. In other cases, similar types of interactions found in individual hosts and in host populations may be caused by different mechanisms.

We studied the effect of fleas on the pattern of infestation of small mammals by larval, nymphal or adult ixodid ticks of two species, *Ixodes ricinus* and *Ixodes trianguliceps*. Fleas (Siphonaptera) are obligate holometabolous ectoparasites that generally occur on small- to medium-sized mammalian species. Their larvae are usually not parasitic but feed on organic matter in the nest or burrow of the host. In most species, pre-imaginal development is entirely off-host, whereas adults alternate between periods of occurring on the host body and in

its nest or burrow. In contrast, larvae, nymphs, and adults of the majority of ixodid ticks are haemophagous, spending most of their life in the natural habitats where they actively search for a host. Consequently, we considered fleas to be *preceding* parasites, and ticks to be *subsequent* parasites. In other words, we assumed that it is much more probable for an individual mammal to be initially infested by fleas and then attacked by ticks than vice versa.

We considered infestation of small mammals by ectoparasites of the two taxa at two levels. At the host individual level, we asked whether the probability of a host being infested by ticks depended on its infestation by fleas (number of individuals and species). At the level of host populations, we asked whether mean abundance and prevalence of ticks across conspecific cohabitating hosts were affected by the mean abundance, prevalence, and level of aggregation of fleas. We predicted that the relationships between tick infestation and flea abundance, prevalence and/or species richness would be positive at both levels. Fleas, especially at a high density, can suppress the immune response of a host (Khokhlova *et al.*, 2004), supposedly making it more prone to tick infestation. At the host population level, we predicted that the relationship between tick infestation and flea aggregation would be positive because, at a high flea aggregation, only a relatively small proportion of hosts would be expected to be infested by a high number of fleas and thus immunosuppressed.

## Materials and methods

### *Study area, mammal sampling, and parasite collection*

Mammals were sampled between 1983 and 2001 in 18 regions across Slovakia (see details in Stanko, 1998; Krasnov *et al.*, 2006a; Stanko *et al.*, 2002, 2007). Trapping sessions (on average, 700 traps per session, ranging from 100 to 2000 traps; 201 350 trap-nights in total) in the same region were carried out at different locations and were at least 6 months apart, thus avoiding pseudoreplications. A trapping session lasted one to three nights and totalled 90 sessions with, on average, seven (from 1 to 32) sessions per location. Trapped animals were sacrificed with sulphur ether, placed in individual cloth bags and transferred to a laboratory for parasitological examinations. A total of 14 368 individuals of 18 rodent and 8 soricomorph species were trapped, from which 30 flea species and 3 tick species were collected. For data analyses, we only included mammal species in which at least 150 individuals were captured. This resulted in 13 415 individual small mammals of five rodent and one soricomorph species that harboured 15 668 fleas of 19 species and 12 958 larvae, nymphs and adults of two tick species (see Supporting information, Tables S1 and S2).

### *Data analysis*

At the level of host individuals, we applied generalised linear models (GLM) with binomial distribution and logit-link function to test for the effect of flea infestation on the

probability of an individual mammal being infested by ticks, and searched for the best model using the Akaike's Information Criterion. This was done for each host species and each tick species separately, and only for sessions where at least one tick individual was found. A dependent dichotomous variable in these models was the occurrence of ticks (larvae, nymphs or adults) on an individual host, whereas the exploratory terms were the number of fleas and number of flea species collected from this host. Then, we further investigated the best models using logistic regressions with the quasi-Newton algorithm to evaluate how well flea-related variables predicted the probability of a host being infested by ticks.

At the level of host populations, we tested for the effect of flea infestation on the abundance and prevalence of *I. ricinus* or *I. trianguliceps* among co-occurring conspecific mammals. For these analyses, we selected only samples (= trapping sessions) where at least six host individuals of a particular species were captured and at least two individual ticks were collected. For each tick and host species within each trapping session, we calculated mean abundance of a tick (mean number of ticks per individual host) and its prevalence (percentage of infested individuals) and abundance, prevalence and aggregation of fleas. The level of flea aggregation was evaluated using the index of intra-specific aggregation, *J*, proposed by Ives (1988, 1991). Prior to analysis, all these variables were log- or log + 1-transformed except for prevalence which was arcsin-transformed. Then, we applied GLM with normal distribution and identity-link function and, again, searched for the best model using the Akaike's Information Criterion. Further investigation of the best significant models was done using stepwise multiple regressions (forward procedure).

To ensure independence of data points, we carried out a second run of each analysis in which we used the identity of a trapping session (time period and region) as a categorical variable. No effect of the trapping session identity was found in either analysis (see also Krasnov *et al.*, 2006b for justification of pooling the data across sampling periods and regions) and, consequently, we present only results of the first run.

## Results

The best models explaining variance in the probability of a host individual being infested by *I. ricinus* or *I. trianguliceps* as an abundance and diversity of fleas, are presented in Table 1. The probability of a host individual being infested by *I. ricinus* depended on either flea number or flea diversity on all host species except *S. araneus*, whereas the probability of a host individual being infested by *I. trianguliceps* depended on flea infestation in two out of four host species, which harboured this tick (Table 1). Logistic regression analyses showed that the probability of a host being infested by ticks increased with a decrease in either flea number or species richness (Table 1).

The best models explaining variance in mean abundance and prevalence of *I. ricinus* within a host population demonstrated the effect of flea-related variables in all host species, whereas a significant effect of flea-related variables on mean abundance and prevalence of *I. trianguliceps* was found in *M. glareolus*

**Table 1.** The best models explaining variance in the probability of a host individual being infested by *Ixodes ricinus* (IR) or *I. trianguliceps* (IT) as affected by number of fleas (FN) and number of flea species (FS) collected from a host, and a summary of logistic regressions of the probability [Logit(p)] of a host individual being infested by these ticks according to these best models.

Tick	Host	AIC	LR $\chi^2$	Equation	Final loss	$\chi^2$
IR	Aa	2836.5	64.4***	1.15–0.41 FS	1357.0	60.7***
	Af	4685.7	69.4***	0.61–0.32 FS	2232.1	69.3***
	Au	878.2	18.0***	1.38–0.48 FS	424.7	15.2***
	Mg	1766.7	20.4***	0.79–0.10FN	840.1	21.1***
	Ma	294.8	18.1***	2.59–0.59 FS	220.6	18.7***
	Sa	162.4	0.5 <sup>ns</sup>	—	—	—
	IT	277.6	0.7 <sup>ns</sup>	—	—	—
IT	Af	1472.6	1.1 <sup>ns</sup>	—	—	—
	Mg	1332.6	10.0**	1.52–0.18 FS	654.1	10.0**
	Sa	66.8	6.7*	2.28–0.13FN	40.4	4.1*

AIC, Akaike's Information Criterion; LR, likelihood ratio.

\*\*\* $P < 0.0001$ ; \*\* $P < 0.001$ ; \* $P < 0.05$ ; ns-non-significant.

Names of host species are: Aa (*Apodemus agrarius*), Af (*Apodemus flavicollis*), Au (*Apodemus uralensis*), Mg (*Myodes glareolus*), Ma (*Microtus arvalis*) and Sa (*Sorex araneus*).

and *S. araneus* only (Table 2). The effect of flea abundance and prevalence on tick infestation was positive in all cases when this effect was significant (Table 2) (see illustrative example with abundance of *I. ricinus* and abundance of fleas on *A. agrarius* in Fig. 1). In contrast, the effect of flea species richness on tick infestation parameters was consistently negative when it was significant (Table 2) (see illustrative example with prevalence of *I. ricinus* and species richness of fleas on *M. glareolus* in Fig. 2). A significant effect of the level of flea aggregation was found only for mean abundance of *I. trianguliceps* on *M. glareolus*. The number of ticks decreased with an increase in flea aggregation on this host (Table 2).

## Discussion

The probability of a host individual being infested by ticks was affected negatively by flea infestation, which was in sharp contrast to our prediction. We also found that, at the level of host populations, flea abundance and prevalence had a predominantly positive effect on tick infestation, which is in agreement with our predictions. However, flea species richness had an opposite effect. The two tick species differed in their responses to host infestation by fleas; the effect of flea infestation was generally greater in *I. ricinus* than in *I. trianguliceps*. Although *I. ricinus* was, in general, more common than *I. trianguliceps*, this difference was related mainly to the size of host spectrum and mean abundance but not prevalence (see Supporting information, Tables S1 and S2). Consequently, between-tick differences in the majority of patterns found in this study were likely associated with between-tick ecological differences (see below) rather than resulting from a lack of statistical power because of a relatively low abundance of *I. trianguliceps*.

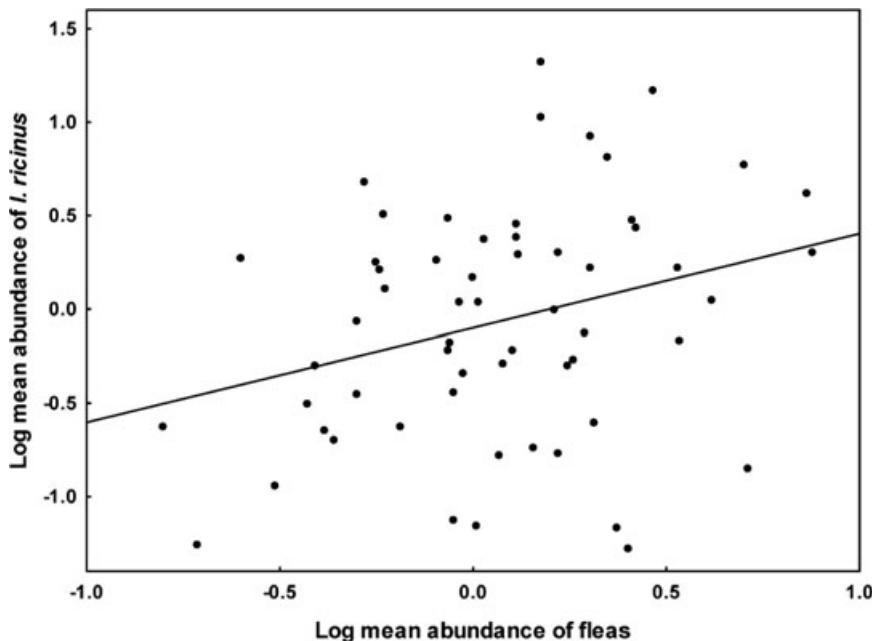
**Table 2.** The best models explaining variance in mean abundance (MA) and prevalence (P) of *Ixodes ricinus* (IR) or *I. trianguliceps* (IT) as affected by mean abundance (FA), prevalence (FP), species richness (FSR) and aggregation level (FJ) of fleas within a host population and summary of multiple regressions of tick variables according to these best models.

Tick	Host	Tick variable	AIC	LR $\chi^2$	Equation	$r^2$	$F_{df}$
IR	Aa	MA	88.0	5.2*	$-0.47 + 0.30FP$	0.10	5.3 <sub>1,50</sub> *
		P	40.8	2.1 <sup>ns</sup>	—	—	—
	Af	MA	106.2	11.7**	$0.37FP - 0.31FSR$	0.18	6.2 <sub>2,56</sub> **
		P	53.9	15.5***	$0.72 + 0.42FP - 0.35FSR$	0.23	8.4 <sub>2,56</sub> ***
	Au	MA	44.6	4.3*	$0.41FA$	0.16	4.3 <sub>1,23</sub> *
		P	15.2	4.2 <sup>ns</sup>	—	—	—
	Mg	MA	66.4	5.2*	$-0.33FSR$	0.10	5.2 <sub>1,45</sub> *
		P	9.7	9.1***	$-0.33FSR$	0.18	9.6 <sub>1,45</sub> **
	Ma	MA	7.6	12.8*	$1.55FA - 1.01FP - 0.62FJ - 1.18FSR$	0.76	3.2 <sub>4,4</sub> <sup>ns</sup>
		P	-17.3	13.1**	$0.76FP - 0.49FSR$	0.77	9.8 <sub>2,6</sub> **
IT	Sa	MA	30.4	7.1*	$0.44FP$	0.20	3.4 <sub>2,13</sub> <sup>ns</sup>
		P	12.6	5.3*	$0.57FA$	0.33	6.9 <sub>1,14</sub> *
	Aa	MA	-1.4	7.0*	$-0.66 + 0.62FA + 0.52FSR$	0.54	3.6 <sub>2,6</sub> <sup>ns</sup>
		P	-13.2	7.6*	$0.78 - 1.21FP$	0.66	3.9 <sub>2,6</sub> <sup>ns</sup>
	Af	MA	27.7	0.7 <sup>ns</sup>	—	—	—
		P	-24.1	2.6 <sup>ns</sup>	—	—	—
		MA	25.5	5.7*	$-0.45FJ$	0.20	5.9 <sub>1,23</sub> *
	Mg	MA	-27.5	3.2 <sup>ns</sup>	—	—	—
		P	6.5	3.7 <sup>ns</sup>	—	—	—
	Sa	MA	-4.6	24.9***	$0.80FP$	0.64	16.1 <sub>1,9</sub> **

AIC, Akaike's Information Criterion; LR, likelihood ratio. Only significant standardised coefficients are shown.

\*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$ ; ns-non-significant.

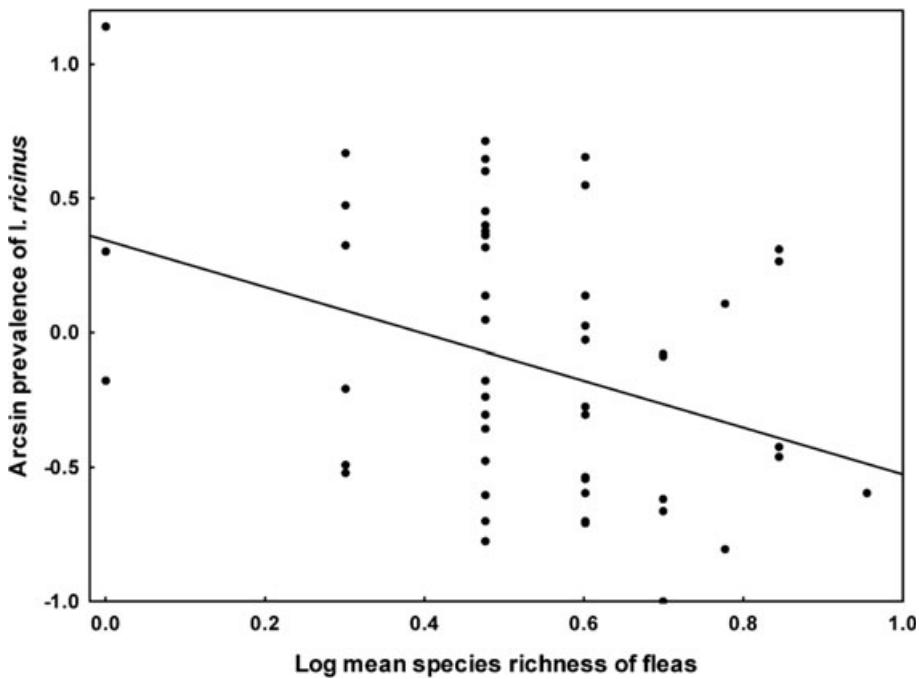
See Table 1 for abbreviations of host species names.



**Fig. 1.** Relationship between mean abundance of *Ixodes ricinus* and mean abundance of fleas across populations of *Apodemus agrarius*.

In general, the probability of an individual host infested by fleas to be infested also by ticks was lower than that of a flea-free host or a host that harboured only a few flea individuals or species. In other words, hosts already exploited by fleas were less attractive to ticks. This may suggest competition between

fleas and ticks. Ticks evade this competition by avoiding hosts harbouring fleas. However, ticks have to be able to assess the infestation status of a potential host (flea-free, low flea-infested and high flea-infested) for such a scenario to be feasible. It is known, that host selection by ticks can be pheromone mediated



**Fig. 2.** Relationship between prevalence of *Ixodes ricinus* and mean species richness of fleas across populations of *Myodes glareolus*.

(Norval *et al.*, 1989) with pheromones allowing unfed ticks to discriminate between hosts on which these parasites have fed successfully (suitable hosts) and those on which they have not (potentially unsuitable hosts). It is not known whether such pheromones occur in fleas. However, even if fleas are able to emit such pheromones, the adequate responses to pheromones between parasites of different subphyla (i.e. Chelicerata and Hexapoda) are highly unlikely. Nevertheless, ticks respond to host-produced kairomonal cues (Carroll & Schmidtmann, 1996). Therefore, ticks would be able to distinguish between, for example, flea-infested and flea-free hosts if flea parasitism modified the chemistry of host-produced substances. However, this explanation is highly speculative and remains to be studied.

Another possible explanation for the negative relationship between flea parasitism and the probability of a host being infested by ticks, may be associated with differences in mobility among individuals with different levels of flea infestation. A sit-and-wait strategy of ixodids causes highly mobile hosts to be more likely victims of their attacks (e.g. Aristova & Okulova, 1976). Small mammals heavily infested with fleas are generally less mobile than low-infested or uninfested individuals (Krasnov *et al.*, 2002). This is because the former are usually represented by resident individuals possessing permanent home ranges with well-developed burrows or nests, whereas the latter are transient individuals that have no individual home ranges (Gliwicz, 1992). These homeless individuals are not usually putative hosts for fleas, because they do not possess burrows that are necessary for flea reproduction and development of pre-imaginal stages, although they can take part in flea transmission (Janion, 1968). Thus, the association between higher mobility

and lack of permanent burrow/nest may result in the association between a higher probability of tick infestation and low infestation by fleas.

In host populations, mean abundance or prevalence of ticks was, in general, positively related to mean abundance or prevalence of fleas in these hosts. This positive relationship between flea and tick infestation may be a manifestation of similar independent responses of ticks and fleas to some other factor such as, for example, host abundance and species richness. Indeed, in our study area, abundance and prevalence of both fleas and ticks were generally negatively associated with abundance and/or species richness of small mammals in a location (Stanko *et al.*, 2006; Krasnov *et al.*, 2007). In other words, abundance of fleas and ticks decreased with an increase in number of host patches (Hamilton, 1971; Ostfeld & Keesing, 2000). In fleas, the reason behind this decrease may be the lower rate of flea reproduction and transmission compared with the rate of reproduction and dispersal of hosts (Stanko *et al.*, 2006). The mechanism underlying the decrease in abundance of ticks seems to differ from that of fleas. Ixodid ticks attacking small mammals are represented mainly by larvae and nymphs (at least, in *I. ricinus*) which do not reproduce and, thus, their number at a location during a year can only decrease (Randolph & Rogers, 1997) or stay stable. In contrast, hosts can both reproduce and immigrate into that location. As a result, when host populations and/or a host community grow, approximately the same number of larvae or nymphs is distributed across a greater number of host individuals decreasing thus both abundance and prevalence of ticks.

In addition, the low probability of a flea-infested individual being infested by ticks does not necessarily mean that it can

never happen. It is possible that interactions between fleas and ticks start only after a host has been infested by both and could be mediated via the host immune system. Saliva of all blood-feeding arthropods contains potent immunogens which cause energetically demanding immune responses of the host (Wikle, 1996; Lochmiller & Deerenberg, 2000). Moreover, the effectiveness of energy allocation to immune defence decreases as the diversity of attack types increases (Taylor *et al.*, 1998), so that the optimal strategy may be to tolerate damage (Jokela *et al.*, 2000). It is conceivable that a host subjected to attacks from multiple parasite species is forced to give up its defence and to surrender (e.g. Raberg *et al.*, 2006). In addition, the efficiency of a host behavioural defence may also deteriorate under a high number or high diversity of parasites (e.g. Hinkle *et al.*, 1998). Therefore, the pattern observed at the level of host populations may arise because of apparent facilitation between flea and tick species via suppression of host immune or behavioural defences. Another way for a host behavioural defence to mediate inter-specific competitive interactions between ectoparasites, is to negatively affect density of both competitors and thus decrease the severity of competition (Waage & Davies, 1986; Bush & Malenke, 2008; see also below).

An effect of flea aggregation on tick infestation was found in *I. trianguliceps* (its mean abundance) on *M. glareolus* only. Mean abundance of ticks was lower in populations with a higher level of flea aggregation, i.e. in populations where fleas were concentrated on a few individuals only, which was in contrast to our prediction. However, most hosts harboured only a few, if any, fleas and thus, had a higher probability to be infested by ticks (see above). The higher probability of tick infestation may, in turn, be associated with a higher number of ticks attacking an individual because (1) tick larvae arise as a package from one large egg mass and remain on the same host (Randolph & Steele, 1985) and (2) aggregation pheromone may attract unfed ticks to a host already being parasitised (Norval *et al.*, 1989). It remains to be studied why the relationship between flea aggregation and tick infestation has not been found in other host species.

The negative effect of flea species richness on tick infestation may also be explained by the mediating effect of host density. In our study area, host density was shown to have a major positive influence on the richness of flea communities of small mammals, both among host species and among populations (Stanko *et al.*, 2002). Host density, in turn, correlates negatively with tick abundance (Krasnov *et al.*, 2007; see above). Moreover, in our earlier study, we found the negative relationship between tick abundance and host density to be characteristic for *I. ricinus*, but not for *I. trianguliceps*. In this study, the negative effect of flea species richness on tick abundance was also found in *I. ricinus* only, supporting the above explanation.

The effect of flea infestation on the probability of a host being infested by ticks was manifested in *I. trianguliceps* less so than in *I. ricinus*, and was found in only two out of four host species. This between-tick species difference may be related to the difference in their natural histories. While *I. ricinus* usually quests for hosts outside their shelters, all developmental

stages of *I. trianguliceps* inhabit burrows and underground nests of their hosts and quest for hosts there (Randolph, 1975). Consequently, an individual tick encounters only a limited number of hosts, so low selectivity, at least in terms of host individuals, would be a beneficial strategy. The differential effect of flea-related variables on occurrence, abundance and/or prevalence of the two ticks may also be related to a host-specific response of a tick. For example, feeding success of larval *I. ricinus* was affected by host species and differed between the hosts *M. glareolus* and *Apodemus sylvaticus* (Nilsson & Lundqvist, 1978). Furthermore, tick behaviour also appeared to be host dependent, in particular for larval movements on a host body. More larvae demonstrated fast and directional movements to the head of a host (favourable site of attachment) on *A. sylvaticus* than on *M. glareolus*, whereas only a few ticks moved at all on *S. araneus* (Nilsson & Lundqvist, 1978).

Host species in this study differed in their manifestation of ectoparasites patterns. For example, the effect of fleas on the probability of a host individual being infested by *I. ricinus* was found in all rodents, but not in a soricomorph, whereas the effect of fleas on the probability of a host individual being infested by *I. trianguliceps* was found in one of three rodent species and a soricomorph species. This difference may be related to the aforementioned mediating effect of host defence on ectoparasite competition (Bush & Malenke, 2008). Host species differ in their ability to defend themselves against ectoparasites via anti-parasitic grooming (Nikitina & Nikolaeva, 1979, 1981; Krasnov, 2008) and may, consequently, differ in the mediating effect of this behavioural defence on ectoparasite competition.

In conclusion, the effect of fleas on tick infestation of small mammalian hosts was either negative or positive, depending on the level of consideration and parameters involved. Results of this study did not provide support for direct interactions between the two ectoparasite taxa, but suggested, instead, the mediating role of population and community dynamics and the defence system of the host.

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## References

- Aristova, V.A. & Okulova, M.N. (1976) Influence of the mobility of small forest mammals on their infestation with larvae and nymphs of ixodid ticks. *Fauna and Ecology of Rodents*, **13**, 88–100 (in Russian).

- Bush, S.E. & Malenke, J.R. (2008) Host defence mediates interspecific competition in ectoparasites. *Journal of Animal Ecology*, **77**, 558–564.
- Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer-Verlag, Dordrecht, The Netherlands.
- Carroll, J.F. & Schmidtmann, E.T. (1996) Dispersal of blacklegged tick (Acaris: Ixodidae) at the woods–pasture interface. *Journal of Medical Entomology*, **33**, 554–558.
- Combes, C. (2001) *Parasitism. The Ecology and Evolution of Intimate Interactions*. University of Chicago Press, Chicago.
- Cox, F.E.G. (2001) Concomitant infections, parasites and immune responses. *Parasitology*, **122**, S23–S38.
- Dezfuli, B.S., Giari, L. & Poulin, R. (2001) Costs of intraspecific and interspecific host sharing in acanthocephalan cystacanths. *Parasitology*, **122**, 483–489.
- Eskelinen, A. (2008) Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *Journal of Ecology*, **96**, 155–165.
- Friggins, M.M. & Brown, J.H. (2005) Niche partitioning in the cestode communities of two elasmobranchs. *Oikos*, **108**, 76–84.
- Gliwicz, J. (1992) Patterns of dispersal in non-cyclic populations of small rodents. *Animal Dispersal: Small Mammals as a Model* (ed. by N.C. Stenseth and W.Z. Lidicker), pp. 147–159. Chapman and Hall, London.
- Hamilton, W.D. (1971) Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.
- Hartley, S. & Shorrocks, B. (2002) A general framework for the aggregation model of coexistence. *Journal of Animal Ecology*, **71**, 651–662.
- Hendrickson, M.A. & Curtis, L.A. (2002) Infrapopulation sizes of co-occurring trematodes in the snail *Ilyanassa obsoleta*. *Journal of Parasitology*, **88**, 884–889.
- Hinkle, N.C., Koehler, P.G. & Patterson, R.S. (1998) Host grooming efficiency for regulation of cat flea (Siphonaptera: Pulicidae) populations. *Journal of Medical Entomology*, **35**, 266–269.
- Holmes, J.C. & Price, P.W. (1986) Communities of parasites. *Community Ecology: Patterns and Processes* (ed. by J. Kikkawa and D.J. Anderson), pp. 187–213. Blackwell Scientific Publishing, New York.
- Ives, A.R. (1988) Aggregation and the coexistence of competitors. *Annales Zoologici Fennici*, **25**, 75–88.
- Ives, A.R. (1991) Aggregation and coexistence in a carrion fly community. *Ecological Monographs*, **61**, 75–94.
- Janion, S.M. (1968) Certain host-parasite relationships between rodents (Muridae) and fleas (Aphaniptera). *Ekologia Polska*, **16**, 561–606.
- Jeffries, M.M. & Lawton, J.H. (1984) Enemy-free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.
- Jokela, J., Schmid-Hempel, P. & Rigby, M.C. (2000) Dr. Pangloss restrained by the Red Queen—steps towards a unified defence theory. *Oikos*, **89**, 267–274.
- Khokhlova, I.S., Spinu, M., Krasnov, B.R. & Degen, A.A. (2004) Immune response to fleas in a wild desert rodent: effect of parasite species, parasite burden, sex of host and host parasitological experience. *Journal of Experimental Biology*, **207**, 2725–2733.
- Krasnov, B.R. (2008) *Functional and Evolutionary Ecology of Fleas: A Model for Ecological Parasitology*. Cambridge University Press, Cambridge.
- Krasnov, B.R., Khokhlova, I.S. & Shenbrot, G.I. (2002) The effect of host density on ectoparasite distribution: an example with a desert rodent parasitized by fleas. *Ecology*, **83**, 164–175.
- Krasnov, B.R., Mouillot, D., Shenbrot, G.I., Khokhlova, I.S. & Poulin, R. (2005) Abundance patterns and coexistence processes in communities of fleas parasitic on small mammals. *Ecography*, **28**, 453–464.
- Krasnov, B.R., Stanko, M., Miklisova, D. & Morand, S. (2006a) Habitat variation in species composition of flea assemblages on small mammals in central Europe. *Ecological Research*, **21**, 460–469.
- Krasnov, B.R., Stanko, M. & Morand, S. (2006b) Age-dependent flea (Siphonaptera) parasitism in rodents: a host's life history matters. *Journal of Parasitology*, **92**, 242–248.
- Krasnov, B.R., Stanko, M. & Morand, S. (2007) Host community structure and infestation by ixodid ticks: repeatability, dilution effect and ecological specialization. *Oecologia*, **154**, 185–194.
- Levine, J.M. (1999) Indirect facilitation: evidence and predictions from a riparian community. *Ecology*, **80**, 1762–1769.
- Lochmiller, R.L. & Deerenberg, C. (2000) Trade-offs in the evolutionary immunology: just what is the cost of immunity. *Oikos*, **88**, 87–98.
- Martin, P.R. & Martin, T.E. (2001) Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology*, **82**, 189–206.
- Nikitina, N.A. & Nikolaeva, G. (1979) Study of the ability of some rodents to get rid of fleas. *Zoologicheskiy Zhurnal*, **58**, 931–933 (in Russian).
- Nikitina, N.A. & Nikolaeva, G. (1981) Ability of rodents to clean themselves of specific and non-specific fleas. *Zoologicheskiy Zhurnal*, **60**, 165–167 (in Russian).
- Nilsson, A. & Lundqvist, L. (1978) Host selection and movements of *Ixodes ricinus* (Acaris) larvae on small mammals. *Oikos*, **31**, 313–322.
- Norval, R.A., Andrew, H.R. & Yunker, C.E. (1989) Pheromone-mediation of host-selection in bont ticks (*Amblyomma hebraeum koch*). *Science*, **243**, 364–365.
- Ostfeld, R.S. & Keesing, F. (2000) The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Canadian Journal of Zoology*, **78**, 2061–2078.
- Poulin, R. (2007) *Evolutionary Ecology of Parasites: From Individuals to Communities*, 2nd edn. Princeton University Press, Princeton, New Jersey.
- Raberg, L., Roode, J.C., Bell, A.S., Stamou, P., Gray, D. & Read, A.F. (2006) The role of immune-mediated apparent competition in genetically diverse malaria infections. *American Naturalist*, **168**, 41–53.
- Randolph, S.E. (1975) Patterns of the distribution of the tick *Ixodes trianguliceps* Birula on its host. *Journal of Animal Ecology*, **44**, 451–474.
- Randolph, S.E. & Rogers, D.J. (1997) A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology*, **115**, 265–279.
- Randolph, S.E. & Steele, G.M. (1985) An experimental evaluation of conventional control measures against the sheep tick, *Ixodes ricinus* (L.) (Acaris, Ixodidae). 2. The dynamics of the tick-host interaction. *Bulletin of Entomological Research*, **75**, 501–518.
- 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., Miklisova, D., Gouy de Bellocq, J. & Morand, S. (2002) Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia*, **131**, 289–295.
- Stanko, M., Krasnov, B.R. & Morand, S. (2006) Relationship between host abundance and parasite distribution: inferring regulating

- mechanisms from census data. *Journal of Animal Ecology*, **75**, 575–583.
- Stanko, M., Krasnov, B.R., Miklisova, D. & Morand, S. (2007) Simple epidemiological model predicts the relationships between prevalence and abundance in ixodid ticks. *Parasitology*, **134**, 59–68.
- Taylor, L.H., Mackinnon, M.J. & Read, A.F. (1998) Virulence of mixed-clone and single-clone infections of the rodent malaria *Plasmodium chabaudi*. *Evolution*, **52**, 583–591.
- Waage, J.K. & Davies, C.R. (1986) Host-mediated competition in a bloodsucking insect community. *Journal of Animal Ecology*, **55**, 171–180.
- Wikl, S.K. (ed.) (1996) *The Immunology of Host-Ectoparasitic Arthropod Relationships*. Centre for Agricultural Bioscience International, Wallingford, Connecticut.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

Two tables describing data on parasites and small mammals used in the analyses.

Table S1. Data on small mammals and ectoparasites included in the analyses.

Table S2. Summary data on the infestation of six host species by fleas and ticks.

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