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Is abundance a species attribute? An example with haematophagous ectoparasites

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Abstract Population density is a fundamental property of a species and yet it varies among populations of the same species. The variation comes from the interplay between intrinsic features of a species that tend to produce repeatable density values across all populations of the same species and extrinsic environmental factors that differ among localities and thus tend to produce spatial variation in density. Is inter-population variation in density too large for density to be considered a true species character? We addressed this question using data on abundance (number of parasites per individual host, i.e. equivalent to density) of fleas ectoparasitic on small mammals. The data included samples of 548 flea populations, representing 145 flea species and obtained from 48 different geographical regions. Abundances of the same flea species on the same host species, but in different regions, were more similar to each other than expected by chance, and varied significantly among flea species, with 46% of the variation among samples accounted by differences between flea species. Thus, estimates of abundance are repeatable within the same flea species. The same repeatability was also observed, but to a lesser extent, across flea genera, tribes and subfamilies. Independently of the identity of the flea species, abundance values recorded on the same host species, or in the same geographical region, also showed significant statistical repeatability, though not nearly as strong as that associated with abundance values from the same flea species. There were also no strong indications that regional differences in abiotic variables were an important determinant of variation in abundance of a given flea species on a given host species. Abundance thus appears to be a true species trait in fleas, although it varies somewhat within bounds set by species-specific life history traits.

Keywords Abundance · Fleas · Intraspecific variation · Repeatability · Species attribute

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Introduction

Understanding of the processes that determine the population density of organisms is a central question in ecology. It is commonly accepted that the density (abundance per unit area) of a species in a location results from the interplay between the intrinsic properties of that species (Hughes et al. 2000; Blackburn and

Gaston 2001; Lopez-Sepulcre and Kokko 2005) and the extrinsic, both biotic and abiotic, properties of the local habitat (Rosenzweig 1981; Morris 1987; Newton 1998). Consequently, because it results from interactions among a variety of factors, the predictability of the density level of any given species is often low, causing problems for conservationists and pest managers (e.g. Beissinger and Westphal 1998; Ludwig 1999; Fieberg and Ellner 2000). One of the likely reasons for this low predictability is the fact that the density of a species is determined simultaneously by extrinsic factors generating variation among populations of this species, and by intrinsic factors promoting among-population stability (= repeatability) in density.

Variability and repeatability of species density have been investigated mainly in free-living organisms (Begon et al. 2005). Parasites, in contrast, have received less attention. However, parasite populations represent convenient models to study intraspecific patterns of population parameters. In particular, this is because of the relative ease of obtaining replicated samples (e.g. host individuals, host populations or host species). Furthermore, the elucidation of spatial patterns of parasite population parameters is crucially important for epidemiology, veterinary medicine and pest management.

High intraspecific variation in the population parameters of parasites, such as their intensity of infestation, prevalence and abundance, is well documented. For example, the abundance of parasites is strongly dependent on the abundance of their host (see review in Anderson and May 1978; Arneberg et al. 1998; Tompkins et al. 2001), which, in turn, is spatially variable. This relationship has been documented in a variety of host–parasite systems (Grenfell and Dobson 1995). Moreover, the relationship between parasite and host abundance varies from being positive (e.g. Krasnov et al. 2002a) to being negative (e.g. Stanko et al. 2006) among different species of the same parasite taxa depending on species-specific reproductive rate and seasonality. In addition, the dependence of survival and, consequently, abundance of parasites on spatially variable abiotic factors has been reported for both endo- (Galaktionov 1996) and ectoparasites (Metzger and Rust 1997). However, in spite of the strong dependence of parasite population parameters on extrinsic factors and, therefore, the expected spatial variation of these parameters, species-specific features of parasites such as body size and egg production could constrain this variation (Poulin 1999). Indeed, Arneberg et al. (1997), studying nematodes parasitic in mammals, have demonstrated that intensity of infection as well as abundance were repeatable within nematode species,

i.e. were less variable within than among species, suggesting that the levels of intensity of infection and abundance are "true" attributes of a nematode species. The only other study of intraspecific variability versus stability of parasite population parameters was carried out on different taxa of metazoan parasite species of Canadian freshwater fishes (Poulin 2006). Again, prevalence, intensity of infection and abundance values from different populations of the same parasite species were more similar to each other, and more different from those of other species, than expected by chance alone. These results suggest that intensity of infestation and abundance are real characters of parasite species, supporting the view that the biological features of parasite species can potentially override local environmental conditions in driving parasite population dynamics.

Periodic (e.g. fleas) and temporary (e.g. tabanids) ectoparasites of terrestrial hosts may be much more strongly influenced by their off-host environment than both the endo- or permanent ectoparasites studied by Arneberg et al. (1997) and Poulin (2006). For example, survival and abundance of fleas are strongly affected by the microclimate of the host's nest/burrow (Krasnov et al. 2001, 2002b), host identity (Krasnov et al. 1998) and the total abundance and diversity of co-occurring flea species (Krasnov et al. 2005a). This suggests that the patterns reported by Arneberg et al. (1997) and Poulin (2006) may not be valid for terrestrial arthropod ectoparasites. However, another abundance-related parameter, the relationship between mean abundance and its variance, appears to be a true flea species character (Krasnov et al. 2006). This apparent contradiction can only be resolved by testing whether a key population parameter, such as abundance, of terrestrial periodic arthropod parasites, such as fleas, is a true species attribute or, alternatively, whether it is determined by extrinsic factors such as host species identity or the local environment.

The aim of this study was to test if the level of abundance of fleas parasitic on small mammals from 48 different geographic regions is species-specific or if it is determined mainly by host identity and/or parameters of the abiotic environment. We evaluated the repeatability of estimates of flea abundance across populations of the same flea species to determine if the abundance is repeatable within flea species; i.e. if the values of abundance are more similar among populations of the same flea species than among different flea species. We also tested the repeatability of flea abundance within host species and within regions. In addition, we searched for correlations between abiotic features of a region and flea population abundance,

separately for several flea species. Our prediction was that if population abundance is a spatially repeatable feature, then the effect of local climatic factors on abundance should be weak.

Methods

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Insectivora, Rodentia and Lagomorpha) in 48 different regions (see Electronic Supplementary Material, Table S1). These sources provided data on the number of individuals of a particular flea species found on a number of individuals of a particular host species. Mammal sampling as reported in the original sources was done either by live- or by snap-trapping, or by hunting. Most sources reported that mammals were examined immediately upon capture/kill. However, there was no information about the time lag between capture/kill and parasitological examination in some sources. Nevertheless, we assumed that this time lag was too short to allow fleas to leave the host body because the aim of all studies was a survey of ectoparasite assemblages. In addition, the sources that provided information of the time of mammal sampling reported that sampling covered either the entire spectrum of seasons or most parts of the year. This suggests that the effect of seasonality on flea abundance, and thus on the results of this study, was negligible (if any).

We cross-checked the species lists with the catalogues of Lewis and Lewis (1990) and Medvedev et al. (2005) to resolve cases of synonymy. Initially, we listed all flea–mammal combinations for each region. Then, we excluded those mammal species for which fewer than 15 individuals have been examined per region, because estimates of flea abundance could be inaccurate for such small samples. We included in the analysis only those flea species that were recorded on the same host species in at least two regions. The same flea species was often recorded from several different host species within and/or among regions. Abundance values for the same flea species but from several different host species are not comparable. Consequently, we focused on the principal host species for each flea species. The parasite's principal host is the host that supports the largest part of a parasite population. It should be noted, however, that in some cases a secondary host may have fewer parasites per host, but there might be greater numbers of the secondary hosts and, therefore, the secondary host may support the larger part of the parasite population. Nevertheless, the principal host is identified here either as the host species that supports a

given parasite species across the largest part of its geographic range, or as the host species on which the parasite attains its highest abundance (Dogiel et al. 1961; Poulin 2005). Indeed, a comparative analysis across 1,334 host–flea species associations demonstrated that the abundance of a particular flea species on its principal host species was on average more than twice that on its auxiliary hosts (Krasnov et al. 2004a).

We used both these approaches. First, we identified the principal host as the host on which a flea occurred most frequently calculated across all regions from which this flea has been reported. Only records of the flea on the principal host were used in the analyses. Second, we identified the principal host as the mammal species on which the flea achieved its highest average abundance across all populations sampled. We then repeated all analyses using records of fleas on these principal hosts. This second run of the analyses provided the same results as the previous one. Consequently, in this paper we report only the results of analyses performed on the dataset where the principal host of a flea species was identified as the host on which a flea occurred most frequently across all regions inhabited by this flea. The principal host species for a flea genus, tribe, subfamily and family were identified in the same way. In total, we used data on 548 flea samples, representing 1,211,858 fleas of 145 species collected from 379,302 individual mammals of 48 species. In 108 of 145 flea species in the dataset, the principal host species identified by both methods was the same host species.

We used the mean number of fleas per individual host of a given species as a measure of flea abundance. Other measurements of infestation level, such as prevalence and intensity of flea infestation, were not available for most of the regions considered. To determine whether flea abundance is a true flea species attribute, i.e. a parameter that varies less among populations of the same flea species than among different flea species, we performed (1) correlation analyses between the values of flea abundance and (2) a repeatability analysis following that of Arneberg et al. (1997). In the former analysis, we correlated the lowest abundance recorded for a given flea species with all other values of abundance recorded in other regions for this species across all flea species. If abundances of the same flea species are consistent with each other across different regions, then a positive correlation is expected between the lowest value and other values of abundance.

In the repeatability analyses, we analysed the variation in flea abundance per host individual by a one-way ANOVA in which flea species was the independent factor, using only flea species for which at least two

samples were available. A significant effect of flea species would indicate that the abundance is repeatable within flea species, i.e. that abundance values for the same flea species from different geographic regions are more similar to each other than to values from other flea species. We estimated the proportion of the total variance originating from differences among flea species, as opposed to within species, following Sokal and Rohlf (1995). We first carried out the repeatability analysis using all flea species in the dataset. Then, we carried out the repeatability analysis across flea genera (48 genera), tribes (20 tribes), subfamilies (13 subfamilies) and families (4 families) to see if flea abundance is also a trait characteristic of higher order taxonomic ranks. To assess whether flea abundance is also determined by host identity or by a complex of environmental conditions, we performed the repeatability analyses using host species or region (as a proxy for geographic differences in a set of environmental conditions) instead of flea species as the single factor. A significant effect of host species or region would indicate that the flea abundances are repeatable within host species or region, respectively.

Finally, to understand the possible causes of geographic variation in flea abundance within a flea–host association, we calculated the parameters that characterised the abiotic environment for each region and for each of flea species with at least six different regional records on the same host species. Environmental parameters were latitude, mean surface annual temperature, mean surface air temperature in January, mean surface air temperature in July, mean annual precipitation and mean altitude. These variables were calculated for each region using 30′ grid data (Kineman et al. 2000). Because most of the variables were strongly correlated with each other ($r = -0.83$–0.95, $P < 0.001$ for all), we substituted them with the scores calculated from the principal component analysis of all these variables. The resulting two "environmental factors" explained 79.2% of the variance (56.4 and 22.8%, respectively) and their eigenvalues were 3.38 and 1.38, respectively. The first environmental factor (EF1) was strongly positively correlated with mean annual, mean July and mean January temperatures (factor loadings were 0.97, 0.78 and 0.90, respectively) and strongly negatively correlated with latitude (factor loading was -0.91), whereas the second environmental factor (EF2) was strongly positively correlated with mean altitude (factor loading was 0.76) and strongly negatively correlated with mean annual precipitation (factor loading was -0.80). For each flea species, we regressed measures of abundance on the principal host in a region against scores of these two principal compo-

nents using multiple stepwise (forward procedure) regression.

Results

Each of the 145 flea species in the dataset was recorded from 2 to 18 regions. Twenty-four species were found on the same host species in at least six regions (see Electronic Supplementary Material, Table S2).

A strong positive correlation was found between the lowest abundances and all other abundance values across flea species ($r = 0.67$, $P < 0.0001$). In other words, different fleas demonstrated a relatively narrow range of abundances when exploiting the same host species in different regions (Fig. 1).

The repeatability analysis for the 145 flea species recorded in least two regions demonstrated that mean flea abundance per host individual can be considered as a flea species character (Fig. 2a). Abundances of the same flea species on the same host species are more similar to each other than expected by chance, and vary significantly among flea species ($F_{144,403} = 4.2$, $P < 0.0001$), with 45.9% of the variation among samples accounted by differences between flea species. Thus, estimates of abundance are repeatable within the same flea species. Furthermore, flea abundances on the same host species were also repeatable across flea genera, tribes and subfamilies, but were not repeatable across flea families (Table 1). In addition, the percentage of the variation among samples accounted by differences among flea taxa, as opposed to within-taxa, was lower for genera compared to species, for tribes compared to genera and for subfamilies compared to tribes (Table 1).
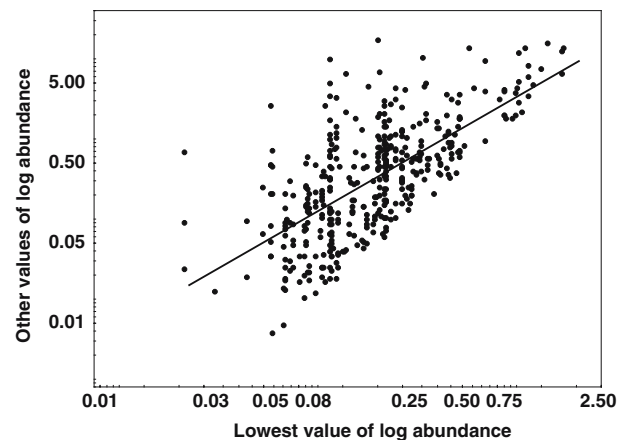

Fig. 1 Relationship between the lowest abundance and other abundance values on the same host species, for 145 flea species recorded in at least two regions. *Values at tick marks* are back-transformed
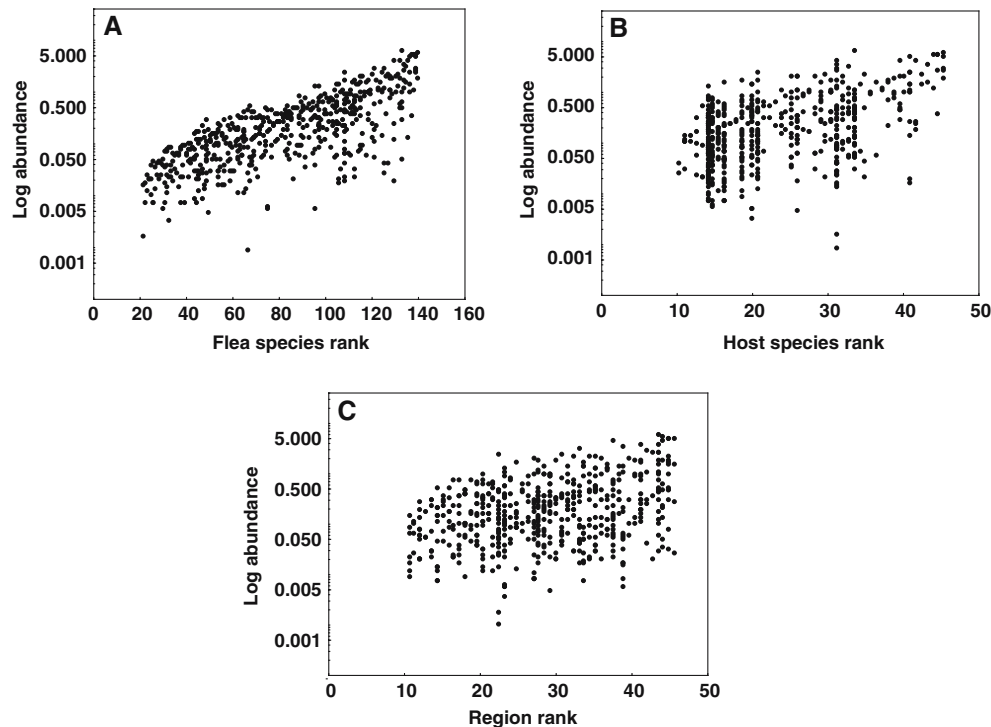
Fig. 2 **a** Rank plot of flea abundance. The 145 flea species recorded in at least two regions are ranked according to their mean log-transformed abundance values, with rank 1 given to the species with the lowest mean abundance; all sample estimates are plotted for each species. If variation is small within compared to between flea species, we expect the points to fall in a region of the plot stretching from the *lower left* to the *upper right corner*, with few or no points in either the *upper left* or *lower right corner*. **b** Rank plot of flea abundance across 48 host species. **c** Rank plot of flea abundance across 48 regions. *Values at tick marks* of *y*-axis are back-transformed

Table 1 Summary of the repeatability analyses (ANOVAs) of flea abundance across flea taxa of different ranks

Taxonomic rank	F	df	P	% variance occurring among taxa
Species	4.2	144,403	<0.0001	45.9
Genus	5.3	55,368	<0.0001	36.8
Tribe	6.8	19,228	<0.0001	32.3
Subfamily	6.7	12,176	<0.0001	30.5
Family	1.2	4,151	0.32	0.5

Table 2 Summary of the repeatability analyses (ANOVAs) of flea abundance across host species and regions

Effect	F	df	P	% variance occurring among host species or regions
Host species	4.5	47,500	<0.0001	24.1
Regions	2.6	47,500	<0.0001	12.7

The repeatability analyses using host species and regions instead of flea species as the main factor demonstrated significant repeatability of flea abundance independent of flea species both among host species and among regions (Table 2). However, the proportions of the variance accounted by differences among host species and among regions, as opposed to within-host and within-region, respectively, were lower than that accounted by differences among flea species, being 24.1 and 12.7%, respectively (Table 2; Fig. 2b, c).

Despite a significant, albeit weak, repeatability of flea abundances across regions, in 19 of 24 flea species that were recorded on the same host in at least six regions, no correlation was found between abundance and either of the two environmental composite factors (r^2=0.07–0.61, F=0.1–3.6, n=6–18; P>0.05 for all). However, in the other five species there was a correlation between abundance and one of the environmental composites (Table 3). The abundance of *Amalaraeus penicilliger* correlated with scores of EF2, increasing with an increase in the mean altitude and a decrease in the mean annual precipitation of a region. The abundance of the remaining four species correlated with scores of EF1 (increase in air temperature and decrease of latitude) (Table 3). However, the direction of this correlation varied among species, being either positive or negative (Table 3).

Table 3 Summary of multiple regression analyses (forward procedure) of flea abundance against environmental factors EF1 and EF2 (see text for explanations)

Species	r^2	F	n	Regression coefficient	
				EF1	EF2
Amalaraeus penicilliger	0.33	5.5	13	–	0.49
Amphipsylla schelkovnikovi	0.87	10.1	6	−1.52	–
Hystrichopsylla talpae	0.49	5.9	9	−0.54	–
Megabothris turbidus	0.57	9.2	9	1.1	–
Peromyscopsylla silvatica	0.65	5.5	6	−0.75	–

All regressions are significant, $P<0.05$

Discussion

The results of this study demonstrate that patterns found for mammalian endoparasites (Arneberg et al. 1997) and parasites of fish (Poulin 2006) are also valid for mammalian ectoparasites (at least for those included in this analysis) despite their greater sensitivity to external factors. Flea abundance appeared to be repeatable among populations of the same species exploiting the same host, albeit it varied to some degree and, thus, can be considered as a true flea species character. Furthermore, abundance can also be considered as an attribute characteristic of a flea genus, tribe or subfamily, but not family. In addition, flea abundance can be viewed to a lesser extent as a property of a host species and a property of a region. In other words, some host species and some locations are characterised by higher flea abundance than other hosts or locations.

Repeatability of abundance within flea species implies that some species-specific life history traits determine the limits of abundance. Lower limits of flea abundance can be affected by species-specific mating systems and/or the relationship between mating and blood feeding, whereas upper limits of abundance can be determined by species-specific reproductive outputs, generation times, preferences for blood-sucking on a specific body part of a host and/or the ability of both imago and larvae to withstand crowding. Indeed, some flea species can mate without a bloodmeal (e.g. *Nosopsyllus fasciatus*; Iqbal and Humphries 1974), whereas in other species an unfed male is unable to inseminate a female (e.g. *Ctenocephalides felis*; Dean and Meola 1997 and *Leptopsylla segnis*; Krampitz 1980). The necessity to feed prior to mating may possibly increase the number of fleas on a host body at any given time. For example, on *Mus musculus*, the average abundance of *L. segnis* is higher than that of *N. fasciatus* (0.75±0.31 vs 0.04±0.01 fleas per individual host). Flea species also differ in the number of mating events necessary to lay viable eggs (Hsu and Wu 2000), which can affect their mean abundance.

Another species-specific mating pattern related to the abundance of fleas on a host is the time that fleas spend either on or off the host body and mating on or off the host ("body" versus "nest" fleas; see Ioff 1941; Smit 1962; Marshall 1981; Vatschenok 1988). As a result, all else being equal, abundance of the "body" fleas should be higher than that of the "nest" fleas. Indeed, the mean abundance of the "body" flea, *Citellophilus tesquorum*, was higher than that of the "nest" flea, *Neopsylla setosa*, on the same host, *Spermophilus undulatus* (2.41±0.60 vs 0.43±0.08 fleas per individual host). Nevertheless, sampling of "nest" fleas from host bodies appeared to be just as reliable for the evaluation of flea abundance as sampling from host nests (Krasnov et al. 2004b).

Flea fecundity varies drastically among flea species (Marshall 1981; Vatschenok 1988; Krasnov et al. 2002c). For example, two fleas characteristic of *M. musculus*, *Nosopsyllus mokrzeckyi* and *L. segnis*, demonstrate sharp differences in fecundity (1–2 clutches per day with 2–3 eggs per clutch versus 2–3 clutches per day with 4 eggs per clutch, respectively; Kosminskyi 1965). This difference in fecundity is paralleled by a difference in mean abundance (0.14±0.08 vs 0.75±0.31, respectively). As flea species also vary in their generation time (Marshall 1981; Vatschenok 1988), variation in frequency and size of clutches undoubtedly causes variation in the lifetime fecundity (Marshall 1981) which, in turn, may be manifested by interspecific variation in mean abundance. Some fleas prefer to take a bloodmeal from a specific area on a host body (Linsdale and Davis 1956; Hsu et al. 2002), whereas other species are distributed evenly over it (Marshall 1981). Site-specific fleas might be more prone to crowding compared with less site-specific species and, thus, may achieve lower abundance. Finally, species-specific levels of intraspecific competition for food could also determine the mean abundance of a flea species, although there are no empirical data supporting this explanation.

Repeatability of flea abundance within flea genera, tribes and subfamilies suggests that limits of abundance as well as intrinsic properties of fleas that determine these limits are phylogenetically constrained. In other words, a relatively narrow, species-specific range of inter-population variation in abundance is the result, at least in part, of natural selection. Consequently, the observed range of abundance for a given flea species has not only evolved for some particular ecological reason, but it seems also to be nested within the flea

phylogeny and, thus, it can be inherited by descent. This advocates the necessity of using phylogenetic information in comparative analyses of abundance (e.g. Stanko et al. 2002; Gaston and Blackburn 2003).

The repeatability of flea abundance within the same host species demonstrates that this parameter can be also seen as a property of the host. Indeed, some host species always harbour more fleas than other host species (Krasnov et al. 1998). Furthermore, Arneberg et al. (1997) reported the abundance of nematodes to be repeatable within mammalian species. In other words, independently of nematode species, some mammal species have many nematodes per individual, whereas other mammals have only a few nematodes per individual. However, the repeatability of nematode abundance among host species was weaker than that among nematode species (18% of the variation in abundance associated with differences among host species versus 36% associated with differences among nematode species; Arneberg et al. 1997). The results of our study provided a very similar ratio between percentages of the variation of flea abundance associated with differences among host species and among flea species (21.4% vs 45.9%, respectively).

The repeatability of flea abundance within host species suggests that some host properties constrain to some extent the number of fleas harboured by an individual. These constraints can be related to processes on the host body that affect adult fleas and/or to processes within a host burrow or nest that affect pre-imaginal fleas. The abundance of adult fleas can be limited by host body features, host immune defence and host anti-parasitic behaviour. Host body size can determine the number of parasites per host, as more space is available for multiple parasite individuals on larger hosts (e.g. Morand and Guégan 2000, but see Krasnov et al. 2005a). Host species also differ in the level of their immune and behavioural defence against parasites (Klein and Nelson 1998; Mooring et al. 2000). A host species with lower immunocompetence and/or a more limited ability to self-groom can be exploited by a higher number of fleas than a host species with higher immunocompetence and/or higher self-grooming efficiency, all else being equal. In addition, the fecundity of fleas depends on which host species they exploit (e.g. Krasnov et al. 2002c, 2004c) which might, in turn, determine host-specific levels of flea abundance.

Species-specific differences in sheltering behaviour and burrow/nest structure (depth, length of tunnels, nest composition, defecation in or outside burrow, etc.) can determine the amount of organic matter in the burrow/nest substrate (food for flea larvae) as well as burrow microclimate (Kucheruk 1983). The amount of organic matter and microclimatic parameters affect flea abundance (Krasnov et al. 2001, 2005b) which is likely reflected in among-host differences in the abundance of adult fleas.

Burrow structure can differ not only among host species but also within host species although among different locations (Shenbrot et al. 2002). On the other hand, burrows of different host species in the same location can be characterised by similar microclimate conditions due to the same macroclimate (Kucheruk 1983). This can lead to among-location differences (as opposed to within-location similarities among host species) in flea abundance and, together with among-location climatic differences, can, at least partly, explain the repeatability of within-region flea abundances found in this study. However, the lack of a clear relationship between flea abundance on a given host species and regional climatic parameters found for most species in this study suggests that abiotic characteristics of a location play only a minor role in the observed pattern of within-region repeatability of flea abundance. From the point of view of each flea species, the biotic components of a location include not only the host species but also the co-occurring assemblage of other flea species. Recently, we demonstrated that the abundance of a given flea species (1) correlates positively with the total abundance of all other co-occurring flea species in the community and (2) correlates negatively with the diversity of the flea community (Krasnov et al. 2005a). The latter is also related to the diversity of host species in a location (Krasnov et al. 2004d). Consequently, the repeatability of flea abundance within regions as opposed to among regions can be explained by among-region differences in a set of biotic and abiotic factors. Nevertheless, only a small portion (12.7%) of population variation in abundance was associated with among-region differences.

In conclusion, our results suggest that the abundance of a flea species parasitic on a small mammalian host, although variable within some limits, is (1) a true species character, (2) to some extent is determined by host species identity and (3) to a small extent is affected by local biotic and abiotic conditions. This supports the ideas of Arneberg et al. (1997) and Poulin (2006) that the biological attributes of parasite species are primary determinants of parasite dynamics compared with characteristics of hosts and of the local environment.

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