VOL. 164, NO. 4 THE AMERICAN NATURALIST OCTOBER 2004

Ectoparasitic "Jacks-of-All-Trades": Relationship between Abundance and Host Specificity in Fleas (Siphonaptera) Parasitic on Small Mammals

Boris R. Krasnov,[1,*] Robert Poulin,[2,†] Georgy I. Shenbrot,[1,‡] David Mouillot,[3,§] and Irina S. Khokhlova[4,‖]

1. Ramon Science Center and Mitrani Department of Desert Ecology, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, P.O. Box 194, Mizpe Ramon 80600, Israel;
2. Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand;
3. Unité Mixte de Recherche, Centre National de la Recherche Scientifique, 5119 Ecosystemes Lagunaires, University of Montpellier II, CC093, FR-34095 Montpellier Cedex 5, France;
4. Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel

Submitted March 24, 2004; Accepted May 20, 2004;
Electronically published September 1, 2004

ABSTRACT: Animal species with larger local populations tend to be widespread across many localities, whereas species with smaller local populations occur in fewer localities. This pattern is well documented for free-living species and can be explained by the resource breadth hypothesis: the attributes that enable a species to exploit a diversity of resources allow it to attain a broad distribution and high local density. In contrast, for parasitic organisms, the trade-off hypothesis predicts that parasites exploiting many host species will achieve lower mean abundance on those hosts than more host-specific parasites because of the costs of adaptations against multiple defense systems. We test these alternative hypotheses with data on host specificity and abundance of fleas parasitic on small mammals from 20 different regions. Our analyses controlled for phylogenetic influences, differences in host body surface area, and sampling effort. In most regions, we found significant positive relationships between flea abundance and either the number of host species they exploited or the average taxonomic distance among those host species. This was true whether we used mean flea abundance or the maximum abundance they achieved on their optimal host. Although fleas tended to exploit more host species in regions with either larger number of available hosts or more taxonomically diverse host faunas, differences in host faunas between regions had no clear effect on the abundance–host specificity relationship. Overall, the results support the resource breadth hypothesis: fleas exploiting many host species or taxonomically unrelated hosts achieve higher abundance than specialist fleas. We conclude that generalist parasites achieve higher abundance because of a combination of resource availability and stability.

Keywords: abundance, host specificity, fleas, mammals.

An interspecific positive relationship between local abundance and occupancy is one of the most pervasive macroecological patterns (Gaston 2003). This pattern consists of the trend for species with larger local populations to be more widespread across many localities, whereas species with smaller local populations tend to occur in fewer localities. This correlation has been documented at a variety of scales, across various habitats, in different biogeographic regions, and for various taxa (Gaston 2003). It can be explained by a number of mechanisms that are not all mutually exclusive (see review in Gaston et al. 1997; Gaston 2003). One of the mechanisms explaining the positive local abundance–regional distribution relationship is based on interspecific variation in niche breadth; that is, this pattern may result from the ability of species with broader niches to attain higher local abundances and to have broader distribution (resource breadth hypothesis; Brown 1984, 1995). In other words, the same attributes that enable a species to exploit a diversity of environmental conditions and resources allow it to attain a broad distribution and high local density. Although the validity of this hypothesis has been questioned based on the results of studies of free-living taxa (Gaston et al. 1997; Gregory and Gaston 2000, but see Shenbrot et al. 1999), studies of parasitic animals often supported the resource breadth hypothesis. For example, Barger and Esch (2002) investigated

---

[*] Corresponding author; e-mail: krasnov@bgu.ac.il.

[†] E-mail: robert.poulin@stonebow.otago.ac.nz.

[‡] E-mail: shenbrot@bgu.ac.il.

[§] E-mail: mouillot@univ-montp2.fr.

[‖] E-mail: khokh@bgu.ac.il.

Am. Nat. 2004. Vol. 164, pp. 506–516.
0003-0147/2004/16404-40366$15.00.

a community of parasites of fish in streams of North Carolina and found that the number of host species infected by each parasite species was positively related to both frequency of occurrence among streams and average local abundance. However, data on nematodes parasitic in mammals demonstrate that both abundance and prevalence are independent of host specificity (Morand and Guegan 2000).

In sharp contrast with these findings, Poulin (1998) observed a negative relationship between the number of fish species used by 188 species of metazoan parasites and their average abundance in hosts. This apparent trade-off between the number of host species exploited and the abundance achieved by parasites in these hosts has been explained by the presumably high cost of parasite adaptations to multiple host defense mechanisms (trade-off hypothesis; Poulin 1998). Parasites that specialize to exploit a few hosts may attain greater abundance in these hosts than if they were exploiting a broader host spectrum and thus were forced to invest more in a wider range of adaptations against host defense mechanisms. Other living conditions such as microhabitat characteristics and food quality will also vary among host species, and parasites exploiting many host species may require further adaptations to cope with these variable conditions. Given that the abundance of a consumer in a habitat is considered as a measure of its efficiency of resource exploitation (Morris 1987), the trade-off hypothesis states that the broader the host spectrum of a parasite, the lower the efficiency of exploitation of any particular host.

The generality of this trade-off hypothesis needs to be tested. For example, it can be true mainly if a host assemblage is composed largely of phylogenetically distant species. In contrast, there is no need to invest more in evasive adaptations if a parasite exploits several closely related hosts because their defense mechanisms are probably similar. Consequently, if a host assemblage consists mainly of closely related hosts, there may be no trade-off between the number of host species used and the abundance of parasites in these hosts. The above considerations suggest that the abundance–host specificity relationship will vary with respect to the taxonomic composition of the assemblage of available hosts.

In addition, the trade-off hypothesis and resource breadth hypothesis make different predictions about the differences in local abundances between parasites with different host specificity (niche breadth). The trade-off hypothesis predicts that adaptations required by host-opportunistic parasites to overcome host defense systems may occur at the expense of the parasites' ability to attain high abundances in these hosts. A "jack-of-all-trades" parasite therefore would be a "master of none," and its abundance even in an optimal host species should be lower than that of a host-specific parasite in the same host, all else being equal. The resource breadth hypothesis suggests that a jack-of-all-trades parasite will be a "master of all" (Brown 1995) and will attain high abundance in all or the majority of its host species. Consequently, the abundance of host-opportunistic parasites, at least in their optimal hosts, will be higher or equal to that of host-specific parasites in the same hosts, all else being equal. Testing the relationship between parasite abundance and host specificity is thus a powerful way to investigate the evolution of ecological specialization in general and host specificity in parasites in particular, a subject of much research over the past 2 decades (Futuyma and Moreno 1988; Ward 1992; Thompson 1994).

The aims of this study were, first, to assess the interspecific relationship between mean abundance and host specificity among flea species parasitic on small mammals and, second, to compare maximal abundances between flea species with different level of host specificity within the same geographic region. We used published data on the abundance and host occurrences of fleas (Siphonaptera) from 20 distinct regions. Fleas are parasites of higher vertebrates and are most abundant and diverse on small mammals. They usually alternate between periods when they occur on the host body and periods when they occur in their hosts' burrows or nests. In most cases, preimaginal development is entirely off-host. The larvae are not usually parasitic. Flea species vary in their degree of host specificity ranging from highly host-specific to host-opportunistic (Marshall 1981).

To avoid the potentially confounding effect of phylogenetic relationships among flea species (Felsenstein 1985; Harvey and Pagel 1991) and to obtain independent data points for comparisons across species, we used the method of phylogenetically independent contrasts (Felsenstein 1985). In addition, rather than taking the mere number of host species used by a flea as a measure of host specificity, we also applied a measure of host specificity that takes into account the taxonomic or phylogenetic affinities of the various hosts (Poulin and Mouillot 2003). This measure places the emphasis on the taxonomic distance between hosts used by a flea rather than on their number, providing a different and complementary perspective on host specificity, one that truly focuses on the specialization of the flea for its host habitat.

Methods

Data were obtained from published surveys that reported flea distribution and abundance on small mammals in 20 different Holarctic regions (table 1). These sources provided data on a number of individuals of a particular flea species found on a number of individuals of a particular

Table 1: Data on small mammals and fleas in 20 regions

Region	Number of flea species (number of examined individuals)	Number of host species (number of examined individuals)	Source
Northern New Mexico	34 (23,975)	29 (876)	Morlan 1955
Idaho	31 (10,853)	15 (3,921)	Allred 1968
California	17 (2,256)	9 (1,547)	Davis et al. 2002
North Kyrgyzstan	37 (2,743)	16 (5,008)	Shwartz et al. 1958
Turkmenistan	42 (530,973)	18 (236,668)	Zagniborodova 1960
Kustanai region, northwestern Kazakhstan	19 (988)	17 (195)	Reshetnikova 1959
Tarbagatai region, eastern Kazakhstan	37 (1,549)	23 (338)	Mikulin 1958
Pavlodar region, eastern Kazakhstan	14 (277)	16 (74)	Sineltschikov 1956
Akmolinsk region, northern Kazakhstan	26 (2,104)	19 (307)	Mikulin 1959*b*
Moyynkum Desert, Kazakhstan	32 (35,748)	18 (69,426)	Popova 1967
Eastern Balkhash Desert, Kazakhstan	39 (143)	22 (506)	Mikulin 1959*a*
Dzhungarskyi Alatau, Kazakhstan	23 (5,253)	15 (5,230)	Burdelova 1996
Selenga region, central Siberia	13 (1,045)	9 (1,948)	Pauller et al. 1966
Altai Mountains	10 (2,011)	24 (1,501)	Sapegina et al. 1981
Tuva	28 (11,669)	13 (3,145)	Letov et al. 1966
Mongolia	23 (15,569)	9 (1,740)	Vasiliev 1966
Slovakia	21 (10,975)	20 (9,968)	Stanko et al. 2002
Khabarovsk region, southern Russian Far East	20 (3,301)	9 (6,635)	Koshkin 1966
North Asian Far East	16 (1,424)	15 (1,670)	Yudin et al. 1976
Negev Desert, Israel	11 (4,774)	13 (1,223)	Krasnov et al. 1997 and unpublished data

host species. No detailed survey that includes all the relevant information was found for regions outside the Holarctic. Flea species with cosmopolitan distributions (e.g., *Xenopsylla cheopis*) were omitted from the analysis. Single findings of a flea species on a host species or in a region were considered accidental and were not included in the analysis. In total, we used data on 234 flea species found on 152 mammalian species.

For each species of flea, two measures of abundance and two measures of host specificity were used. Measures of abundance were mean number of fleas per host individual and maximal number of fleas per host individual. Both measures were calculated across all of a flea's host species. To avoid the potential confounding effects of host sampling effort (number of individuals examined) and host body size, the residuals of the regressions of both measures against number of host individuals and cumulative body surface area of hosts were used. Following Walsberg and Wolf (1995), body surface area of a host species was estimated from host body mass (g) as $10 \times (\text{body mass})^{0.667}$. Data on mean body mass were obtained either from original sources or from Silva and Downing (1995).

Measures of host specificity were the number of mammalian species on which the flea species were found, corrected for sampling effort (residuals of the regression against number of hosts examined), and the specificity index, S_{TD}, and its variance, VarS_{TD} (Poulin and Mouillot 2003). The index S_{TD} measures the average taxonomic distinctness of all host species used by a parasite species. When these host species are placed within a taxonomic hierarchy, the average taxonomic distinctness is simply the mean number of steps up the hierarchy that must be taken to reach a taxon common to two host species, computed across all possible pairs of host species. For any given host species pair, the number of steps corresponds to half the path length connecting two species in the taxonomic tree, with equal step lengths of 1 being postulated between each level in the taxonomic hierarchy. The greater the taxonomic distinctness between host species, the higher the number of steps needed and the higher the value of the index S_{TD}; thus it is actually inversely proportional to specificity. A high index value means that, on average, the hosts of a flea species are not closely related. Taxonomic distinctness is used as a surrogate for genetic or phylogenetic distances among hosts; although the latter measures would provide a better representation of the overall differences between hosts, data are not yet available for all mammalian host taxa included in the present analyses. Using the taxonomic classification of Wilson and Reeder (1993), all mammal species included here were fitted into a taxonomic structure with five hierarchical levels above species, that is, genus, subfamily, family, order, and class (Mammalia). We restricted our use of taxonomic levels to these basic ones because they are the only ones available for all mammalian taxa included here. The maximum value that the index S_{TD} can take (when all hosts belong to different orders) is thus 5, and its lowest value (when all hosts are congeners) is 1. However, since the index cannot be computed for parasites exploiting a single host species, we assigned a S_{TD} value of 0 to these flea species to reflect their strict host specificity. The variance in S_{TD}, VarS_{TD}, provides information on any asymmetries in the taxonomic distribution of host species (Poulin and Mouillot 2003); it can only be computed when a parasite exploits three or more host species (it always equals 0 with two host species). In addition, we calculated for each region the mean number of host species on which a flea species was found and the mean index of host specificity (S_{TD}) and its variance (VarS_{TD}), across all flea species in the region.

To control for the effects of flea phylogeny, we used the method of independent contrasts (Felsenstein 1985). The phylogenetic trees for fleas were based on the taxonomy used in Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971), Traub et al. (1983), and the cladistic tree of flea families of Medvedev (1998). To compute independent contrasts, we used the PDAP:PDTREE module (Garland et al. 1993; Midford et al. 2003) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2004). We standardized each contrast as suggested by Garland et al. (1992). To test for the relationship between flea host specificity and either mean or maximal abundance within regions, we regressed standardized contrasts in log-transformed measures of host specificity against standardized contrasts in log-transformed measures of abundance using major axis regressions forced through the origin (Pagel 1992; Garland et al. 1993).

Results

The mean number of host species exploited by a flea species ranged from 2.3 in North Kyrgyzstan to 12.6 in the Altai Mountains, whereas the maximal host number used by a flea within a region varied from four (*Amalaraeus penicilliger*, *Megabothris calcarifer*, and *Megabothris rectangulatus*, Selenga) to 22 (*Neopsylla mana*, Altai Mountains). The index S_{TD} ranged in most regions from 0 to 2.99–4.33 (Negev Desert–North Asian Far East and Dzhungarskyi Alatau) and only attained the highest value of 5 in the Kustanai region (one flea species), Tuva (two flea species), and Mongolia (two flea species). The variety of collection techniques used to sample mammals in the different regions may be in part responsible for the differences in host specificity across regions. In the analyses across all flea species, the mean number of hosts per flea species differed significantly among regions (ANOVA of the number of host species controlled for sampling effort, $F = 6.30$, $P < .0001$). The same was true for S_{TD} ($F = 2.27$, $P < .001$) and VarS_{TD} ($F = 6.78$, $P < .00001$).

The three measures of host specificity were interrelated to some extent. Across all fleas pooled over all 20 regions, coefficients of correlation between the number of host species exploited by a flea species and either the index S_{TD} or its variance VarS_{TD} were 0.31 and 0.34, respectively ($P < .05$), whereas the coefficient of correlation between S_{TD} and VarS_{TD} was 0.46 ($P < .05$). The latter result suggests that, in general, fleas with high S_{TD} values tend to include one or very few host species from a higher taxon (i.e., order) completely unrelated to that comprising most of the host species, a phenomenon that increases the variance in S_{TD}.

The mean number of host species exploited by a flea species was found to be positively correlated with both the mean and maximal abundances of fleas per host in 16 of 20 regions (table 2; an example for Mongolia is shown in fig. 1). No significant correlation between number of host species and mean flea abundance was found in flea assemblages of Akmolinsk, Pavlodar, Khabarovsk, and New Mexico, whereas number of host species was not correlated with maximal parasite abundance in the flea assemblages of Pavlodar, Khabarovsk, California, and New Mexico (table 2). Mean and maximal abundance of flea per host significantly increased with an increase in the index S_{TD} in 13 and 14 out of 20 regions, respectively (table 2; an example for Mongolia is shown in fig. 2). No correlation between mean flea abundance and S_{TD} was found in Akmolinsk, Pavlodar, Altai Mountains, Khabarovsk, Negev Desert, California, and New Mexico, whereas maximal flea abundance also did not correlate with S_{TD} in all these regions except for Akmolinsk. In contrast, neither abundance measure correlated with VarS_{TD} in any region except for Dzhungarskyi Alatau and Altai Mountains, where mean abundance significantly increased with an increase in VarS_{TD} (table 2).

Discussion

The results of this study demonstrated positive correlations between the breadth of the host range and local abundance of fleas in most of the studied regions. These two parameters were not interrelated in the other regions, and no trade-off between host range size and local abundance was found in any region. Thus it appears that, in general, host-opportunistic flea species are also the ones that attain higher local densities. Consequently, the pattern found in this study provides support for the resource breadth hypothesis (Brown 1984, 1995) but not for the trade-off hypothesis (Poulin 1998). Moreover, Poulin (1999) found a positive correlation between the number of exploited host species and local abundance in helminth parasites of

Table 2: Coefficients of correlation

	Mean abundance			Maximal abundance		
Region	NHS	S_{TD}	VarS_{TD}	NHS	S_{TD}	VarS_{TD}
New Mexico	.04 NS	−.08 NS	−.47 NS	.08 NS	−.01 NS	−.40 NS
Idaho	.62***	.39**	.31 NS	.72***	.43**	.24 NS
California	.46**	.37 NS	.30 NS	.32 NS	.29 NS	.47 NS
North Kyrgyzstan	.48**	.32*	.45 NS	.43**	.41**	.39 NS
Turkmenistan	.46**	.42**	.002 NS	.69***	.56***	.19 NS
Kustanai	.59**	.52*	−.15 NS	.68**	.58**	−.3 NS
Tarbagatai	.35*	.46**	.01 NS	.48**	.55***	.05 NS
Pavlodar	.11 NS	−.39 NS	.007 NS	.29 NS	−.33 NS	.20 NS
Akmolinsk	.32 NS	.19 NS	.07 NS	.64***	.44*	.24 NS
Moyynkum	.52**	.43**	.22 NS	.46**	.38*	.31 NS
Eastern Balkhash	.54***	.39**	.19 NS	.65***	.49**	.28 NS
Dzhungarskyi Alatau	.80***	.49**	.57*	.75***	.43**	.41 NS
Selenga	.62****	.59*	.43 NS	.73**	.64*	.33 NS
Altai Mountains	.75**	.04 NS	.70*	.66**	.04 NS	.59 NS
Tuva	.42*	.39*	.31 NS	.53**	.45**	.37 NS
Mongolia	.86***	.60**	.14 NS	.88***	.61**	.12 NS
Slovakia	.48**	.59**	.42 NS	.54**	.63**	.47 NS
Khabarovsk	−.17 NS	.15 NS	.42 NS	.08 NS	.21 NS	.39 NS
North Asian Far East	.56**	.51*	.49 NS	.66**	.54**	.45 NS
Negev Desert	.60*	.07 NS	−.09 NS	.65**	.10 NS	.06 NS

Note: Coefficients of correlation (r) between two measures of abundance (mean and maximal abundance per host individual controlled for sampling effort and area of host body surface) and three measures of host specificity (NHS = number of host species; S_{TD} = index of specificity; VarS_{TD} = its variance; NS = not significant) for fleas in 20 regions, calculated using independent contrasts.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

birds (supporting the resource breadth hypothesis). However, when these same data were reanalyzed using the index S_{TD}, the observed pattern was opposite to that obtained when using the number of host species as a measure of host specificity, indicating a potential trade-off (Poulin and Mouillot, 2004). In this study, both measures of host specificity, that is, the number of host species and S_{TD}, demonstrated the same pattern. This suggests that some features of flea species that allow them to attain high densities in a host also allow them to exploit more host species from a wider range of taxa. However, despite the fact that these features, whatever they are, allow an increase in the taxonomic diversity of the host range, the features are usually not associated with a greater taxonomic complexity of this range as suggested by the lack of correlation between local abundances and VarS_{TD} (except for two regions). In other words, the taxonomic diversity of the hosts of fleas with high abundances and many host species is usually not characterized by an uneven distribution of host species among higher taxa. Still, our results demonstrate that siphonapteran "jacks-of-all-trades" appear to be also masters of most if not all of them.

We did not distinguish between truly parasitic associations and nonparasitic associations such as phoresy because no distinction between these was made in the original sources. Ectoparasites sometimes use vertebrate hosts merely for phoretic dispersal and sometimes just for feeding, even though they are unable to reproduce on those hosts. It is conceivable that a high proportion of phoretic associations could have influenced our results, but it is unlikely that this would be enough to generate the strong and consistent patterns we observed. In addition, most fleas never use their hosts solely for dispersal (Marshall 1981).

Two main arguments that can explain why resource generalists are expected to have higher local abundances than resource specialists (Hughes 2000). First, the total amount of resources available to a generalist may be greater than resources available to a specialist. Indeed, for most fleas in each region, host-specific fleas exploited a subset of the hosts that are exploited also by host-opportunistic fleas. For example, in North Kyrgyzstan, *Apodemus uralensis* is the only host species of the highly specific *Ctenophthalmus golovi*, but it is also exploited by the host-opportunistic fleas *Amphipsylla rossica*, *Amphipsylla anceps*, *Frontopsylla ornata*, *Neopsylla teratura*, and *Neopsylla pleskei*. Second,

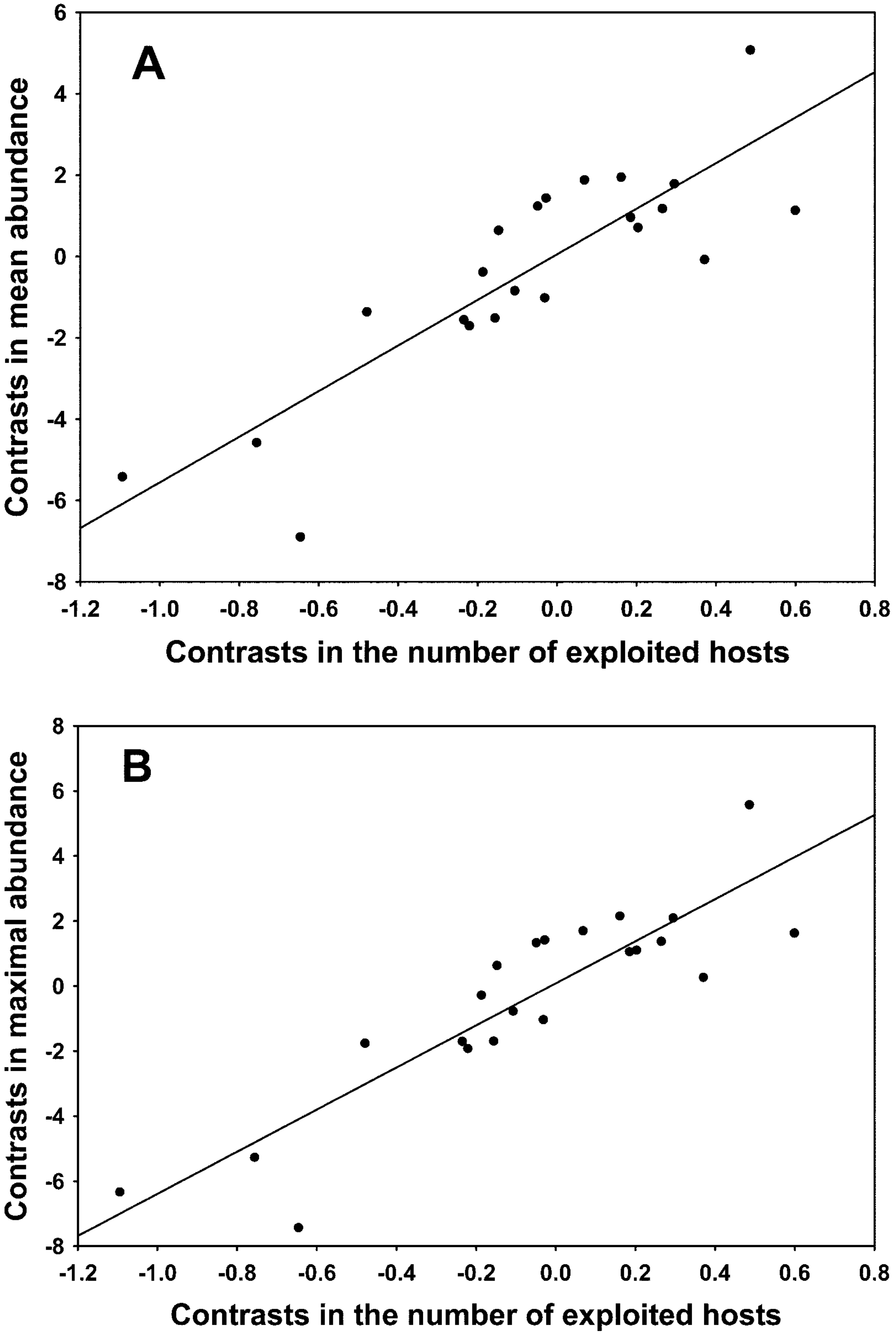

Figure 1: Relationship between the number of host species and mean (*A*) or maximal (*B*) abundance of fleas per host individual (controlled for sampling effort and area of host body surface) among flea species from Mongolia using phylogenetically independent contrasts.

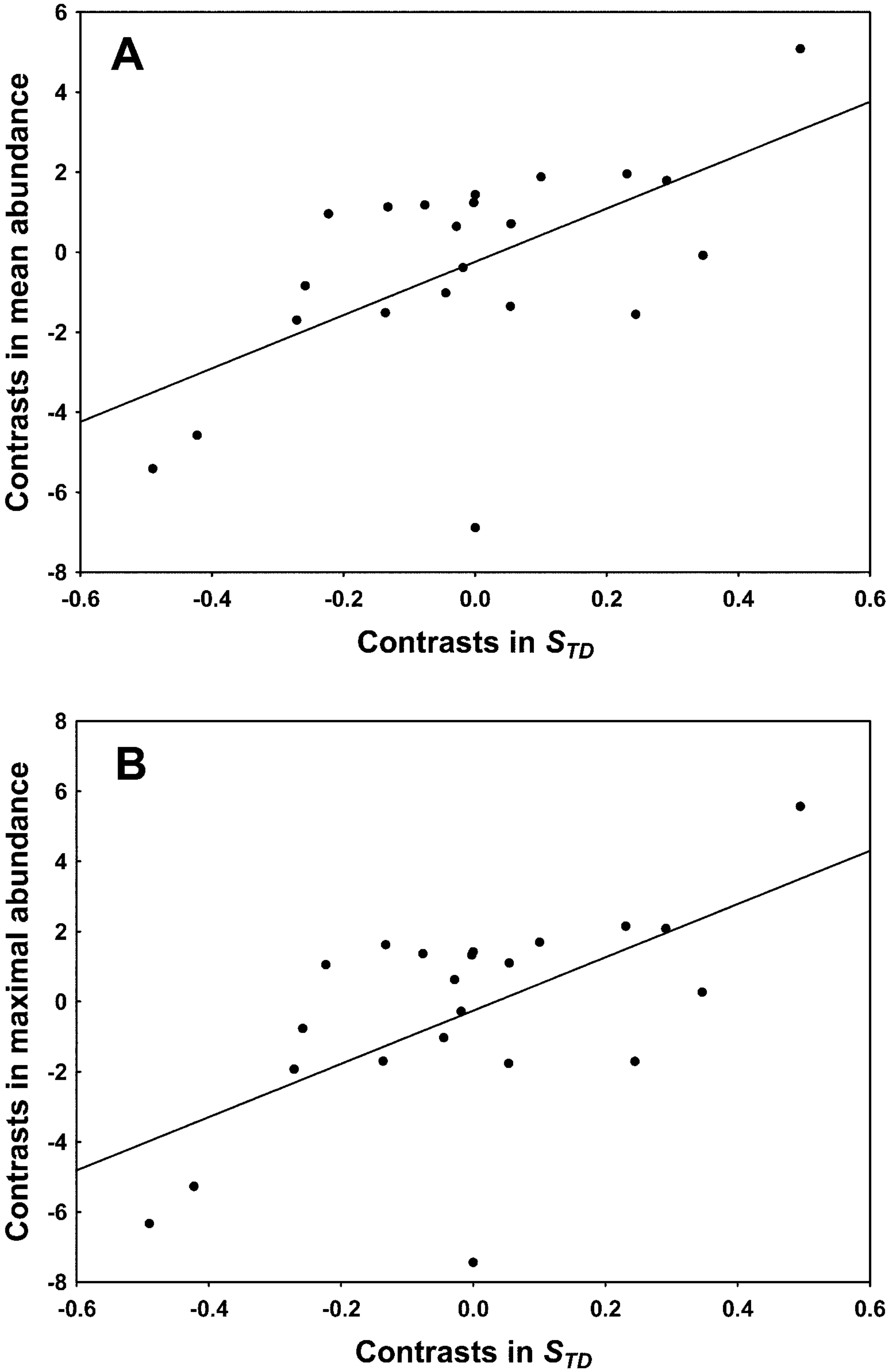

Figure 2: Relationship between the index of host specificity, S_{TD}, and mean (*A*) or maximal (*B*) abundance of fleas per host individual (controlled for sampling effort and area of host body surface) among flea species from Mongolia using phylogenetically independent contrasts.

the ability of a generalist to maintain higher local abundances may be related to lower variability in the total amount of resources available to them (MacArthur 1955). For example, a highly host-specific flea may suffer from a high risk of population crash if the population of its single host species decreases sharply in a given year; in contrast, if one or a few hosts of a host-opportunistic flea undergo drastic population decrease, even going locally extinct, this flea can easily survive on other host species. However, evidence in support of this hypothesis in hematophagous periodic ectoparasites (such as fleas) is extremely scarce. Nevertheless, year-to-year variation in the mean abundance of the host-opportunistic *Ctenophthalmus turbidus* and *Ctenophthalmus uncinatus* (17 and 15 host species, respectively), did not depend on density fluctuations of their hosts, whereas the opposite was true for the host-specific *Paleopsylla soricis* (85% of individuals were recovered from a single host species; Nazarova 1981). Moreover, the relationships between abundance and resource variability reported for other taxa are contradictory. They ranged from positive (Root and Capuccino 1992) to negative associations (Redfearn and Pimm 1988), via no pattern at all (Lewis 1977).

Within-region comparisons of maximal abundance of fleas with different degree of host specificity also supported the resource breadth hypothesis. The abundance of a species in a habitat reflects the extent to which conditions in that habitat meet the multiple Hutchinsonian niche requirements of a species (Brown 1995) and therefore can be considered as a measure of habitat suitability for that species. Although the whole host range of a host-opportunistic parasite can be quite broad, not all host species within this range are equally suitable for this parasite (Prasad 1969). Consequently, the host in which the abundance of a host-opportunistic flea is the highest can be regarded as an optimal host species. Our results demonstrated that host-opportunistic fleas attained higher abundances than host-specialist fleas even when we took into account the optimal hosts only (i.e., when using maximal instead of mean abundance). Again, this rejects the idea that a jack-of-all-trades is master of none. Furthermore, the positive trend between local abundance and host specificity held even in regions where the number of mammalian host species that can potentially be exploited was relatively low (California, Selenga, and Mongolia).

The absence of the negative trend between local flea abundance and their ability to exploit many hosts species as predicted by the trade-off hypothesis (Poulin 1998) does not, however, mean that host-opportunistic fleas are not faced with the problem of the necessity to develop multiple adaptations to evade multiple host defense systems. However, in the case of fleas, this trade-off can be counterbalanced by another trade-off related to the nonparasitic life style of flea larvae. As mentioned above, flea larvae occur in the burrows of their mammalian host and feed on all kinds of organic matter. Differences among host species in burrow conditions (microclimate and organic content of the substrate) are presumably less pronounced (especially within a region) than differences among those hosts in defense means. The larvae can, therefore, survive similarly in burrows of different host species. In addition, mammals of different species often visit each other's burrows (Kucheruck 1983). Larvae of fleas that exploit multiple hosts can thus achieve broader spatial distribution, and consequently, the imago upon emergence has a higher probability of successfully attacking a host individual. The cost of adaptations against the defense system of a new host species can therefore be compensated by the higher success of newly emerged imago in attacking an appropriate host.

Alternatively, the absence of any abundance-specificity trade-off in fleas can be related to cross-resistance of a host against closely related ectoparasites (McTier et al. 1981) because of the similarity of salivary components within an ectoparasite taxon (Mans et al. 2002). A host can develop defense mechanisms that are equally effective against multiple ectoparasite species, including those that it did not previously meet. A flea species that colonizes a new host can thus encounter immune responses with which it is already familiar (from its previous hosts). As a result, it may not decrease its exploitation success and could even attain relatively high average abundance on this new host.

A variety of relationships between local abundance and niche breadth has been reported for different free-living and parasite taxa (Inkinen 1994; Gregory and Gaston 2000). Poulin and Mouillot (2004) studied the relationship between the taxonomic diversity of the host species used by parasites and their average abundance in those hosts in different helminth taxa and found that this relationship was negative in nematodes and positive in trematodes. These various relationships between abundance and niche breadth in different animals suggest that jacks-of-all-trades belonging to different taxa behave differently, possibly depending on their life-history characteristics.

Sometimes, a positive correlation between local abundance and niche breadth in a free-living taxon is attributed to sampling bias simply because niche breadth (e.g., number of habitats used) of species with low abundances could be systematically underestimated (Wright 1991). Given that, if a host individual is examined carefully enough, the recovery of fleas from host individuals is assumed to be exhaustive, and thus, erroneous records of the absence of a parasite from the host individual are very unlikely. However, sampling bias of parasites can stem from the overdispersion pattern of their distribution among host individuals (most parasite individuals of a given species are found in a few hosts, whereas most hosts support few or no parasites of that species; Krasnov et al. 2002, for fleas). This can be overcome by extensive surveys of host individuals (Krasnov et al. 2002), as was the case in most of the studied regions. However, the undersampling of both generalist and specialist parasites because of limited sample size of host individuals can mask any relationship between local abundance and distribution or host specificity, as may have been the case in Pavlodar and Akmolinsk (averages 4.6 and 16.1 examined individuals per host species, respectively). Reasons for the absence of a relationship between abundance and host specificity in fleas from Khabarovsk and New Mexico are less clear. Perhaps the explanation for Khabarovsk was the mixture of data on hosts from natural habitats and from human settlements (Koshkin 1966).

In addition, in some regions the results obtained when using either the number of hosts or the index S_{TD} as measures of host specificity varied, with sometimes only one of the two measures generating a relationship between abundance and host specificity. The cause of these discrepancies may be that these measures reflect different aspects of host specificity. For example, a flea species that exploits many hosts may have a low value of S_{TD} (if all these hosts are congeners) or vice versa. Indeed, in the Altai Mountains, the S_{TD} value of *Neopsylla mana* was only slightly higher than that of *Frontopsylla elata* (3.77 vs. 3.40, respectively), although *N. mana* exploited twice as many host species (22 vs. 11, respectively). In California, *Aetheca wagneri* and *Oropsylla montana* each parasitized four rodent species. However, their S_{TD} values were evaluated as 1.5 and 3.33, respectively. *Aetheca wagneri* had a relatively low S_{TD} value because all its hosts belonged to the same subfamily and three of them were congeners. *Oropsylla montana* had a relatively high S_{TD} value because all of its four hosts belonged to different genera from two families. Nevertheless, the general agreement between the results obtained using either the number of host species or S_{TD} indicates that both aspects of host specificity co-vary positively with abundance. A flea that adds taxonomically distant host species to its repertoire is therefore not doing so at a cost to its abundance but because its generalist strategy allows it both high abundance and an expanding host range.

Acknowledgments

We thank two anonymous referees for their helpful comments on an earlier version of this article. B.R.K. and G.I.S. received financial support during this study from the Ministry of Science and Technology of Israel. R.P. is supported by a James Cook Research Fellowship from the Royal Society of New Zealand. This is publication 164 of the Ramon Science Center and 425 of the Mitrani Department of Desert Ecology.

Literature Cited

Allred, D. M. 1968. Fleas of the National Reactor Testing Station. Great Basin Naturalist 28:73–87.

Barger, M. A., and G. W. Esch. 2002. Host specificity and the distribution-abundance relationship in a community of parasites infecting fishes in streams of North Carolina. Journal of Parasitology 88:446–453.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124: 255–279.

———. 1995. Macroecology. University of Chicago Press, Chicago.

Burdelova, N. V. 1996. Flea fauna of some small mammals in Dzhungarskyi Alatau. Pages 119–20 *in* L. A. Burdelov, ed. Proceedings of the conference: ecological aspects of epidemiology and epizootology of plague and other dangerous diseases. Almaty, Kazakhstan. [In Russian.]

Davis, R. M., R. T. Smith, M. B. Madon, and E. Sitko-Cleugh. 2002. Flea, rodent and plague ecology at Chichupate campground, Ventura County, California. Journal of Vector Ecology 27:107–127.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics 19:207–233.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford.

Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1997. Interspecific abundance-range size relationships: an appraisal of mechanisms. Journal of Animal Ecology 66: 579–601.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18–32.

Garland, T., Jr., A. W. C. Dickerman, M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265–292.

Gregory, R. D., and K. J. Gaston. 2000. Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. Oikos 88: 512–526.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hopkins, G. H. E., and M. Rothschild. 1953. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. 1. Tungidae and Pulicidae. Trustees of the British Museum (Natural History), London.

———. 1956. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. 2. Coptopsyllidae, Vermipsyllidae, Stephanocircidae, Iscnopsyllidae, Hypsophthalmidae and Xiphiopsyllidae. Trustees of the British Museum (Natural History), London.

———. 1962. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. 3. Hystrichopsyllidae. Trustees of the British Museum (Natural History), London.

———. 1966. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. 4. Hystrichopsyllidae. Trustees of the British Museum (Natural History), London.

———. 1971. An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History). Vol. 5. Leptopsyllidae and Ancistropsyllidae. Trustees of the British Museum (Natural History), London.

Hughes, J. B. 2000. The scale of resource specialization and the distribution and abundance of lycaenid butterflies. Oecologia (Berlin) 123:375–383.

Inkinen, P. 1994. Distribution and abundance in British noctuid moths revisited. Annales Zoologici Fennici 31: 235–243.

Koshkin, S. M. 1966. Materials on flea fauna in Sovetskaya Gavan. Proceedings of the Irkutsk State Scientific Anti-Plague Institute of Siberia and Far East 26:242–248. [In Russian.]

Krasnov, B. R., G. I. Shenbrot, S. G. Medvedev, V. S. Vatschenok, and I. S. Khokhlova. 1997. Host-habitat relation as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. Parasitology 114:159–173.

Krasnov, B. R., I. S. Khokhlova, and G. I. Shenbrot. 2002. The effect of host density on ectoparasite distribution: an example with a desert rodent parasitized by fleas. Ecology 83:164–175.

Kucheruk, V. V. 1983. Mammal burrows: their structure, topology and use. Fauna and Ecology of Rodents 15:5–54. [In Russian.]

Letov, G. S., N. D. Emelyanova, G. I. Letova, and A. D. Sulimov. 1966. Rodents and their ectoparasites in the settlements of Tuva. Proceedings of the Irkutsk State Scientific Anti-Plague Institute of Siberia and Far East 26:270–276. [In Russian.]

Lewis, W. M., Jr. 1977. Ecological significance of the shapes of abundance-frequency distributions for coexisting phytoplankton species. Ecology 58:850–859.

MacArthur, R. H. 1955. Fluctuations in animal populations, and a measure of community stability. Ecology 36:533–536.

Maddison, W. P., and D. R. Maddison. 2004. Mesquite: a modular system for evolutionary analysis. Version 1.01. http://mesquiteproject.org.

Mans, B. J., A. I. Louw, and A. W. H. Neitz. 2002. Evolution of hematophagy in ticks: common origins for blood coagulation and platelet aggregation inhibitors from soft ticks of the genus *Ornithodoros*. Molecular Biology and Evolution 19:1695–1705.

Marshall, A. G. 1981. The ecology of ectoparasite insects. Academic Press, London.

McTier, T. L., J. E. George, and S. N. Bennet. 1981. Resistance and cross-resistance of guinea pigs to *Dermacentor andersoni* Stiles, *D. variabilis* (Say), *Amblyomma americanum* (Linnaeus) and *Ixodes capularis* (Say). Journal of Parasitology 67:813–822.

Medvedev, S. G. 1998. Classification of fleas (order Siphonaptera) and its theoretical foundations. Entomological Review 78:511–521.

Midford, P. E., T. Garland, Jr., and W. P. Maddison. 2003. PDAP:PDTREE package for Mesquite. Version 1.00. http://mesquiteproject.org/pdap_mesquite/index.html.

Mikulin, M. A. 1958. Data on fleas of the Middle Asia and Kazakhstan. V. Fleas of the Tarbagatai. Proceedings of the Middle Asian Scientific Anti-Plague Institute 4:227–240. [In Russian.]

———. 1959*a*. Data on fleas of the Middle Asia and Kazakhstan. VIII. Fleas of the Akmolinsk region. Proceedings of the Middle Asian Scientific Anti-Plague Institute 5:237–245. [In Russian.]

———. 1959*b*. Data on fleas of the Middle Asia and Kazakhstan. X. Fleas of the eastern Balkhash desert, Trans-Alakul desert and Sungorian Gates. Proceedings of the Middle Asian Scientific Anti-Plague Institute 6:205–220. [In Russian.]

Morand, S., and J.-F. Guegan. 2000. Distribution and abundance of parasite nematodes: ecological specialisation, phylogenetic constraint or simply epidemiology? Oikos 88:563–573.

Morlan, H. B. 1955. Mammal fleas of Santa Fe County, New Mexico. Texas Reports of Biology and Medicine 13:93–125.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362–369.

Nazarova, I. V. 1981. Fleas of the Volga-Kama region. Nauk, Moscow. [In Russian.]

Pagel, M. D. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology 156:431–442.

Pauller, O. F., N. I. Elshanskaya, and I. V. Shvetsova. 1966. Ecological and faunistical review of mammalian and bird ectoparasites in the tularemia focus of the Selenga River delta. Proceedings of the Irkutsk State Scientific

Anti-Plague Institute of Siberia and Far East 26:322–332. [In Russian.]

Popova, A. S. 1967. Flea fauna of the Moyynkum desert. Pages 402–406 *in* B. K. Fenyuk, ed. Rodents and their ectoparasites. Saratov University Press, Saratov. [In Russian.]

Poulin, R. 1998. Large-scale patterns of host use by parasites of freshwater fishes. Ecology Letters 1:118–128.

———. 1999. The intra- and interspecific relationships between abundance and distribution in helminth parasites of birds. Journal of Animal Ecology 68:719–725.

Poulin, R., and D. Mouillot. 2003. Parasite specialization from a phylogenetic perspective: a new index of host specificity. Parasitology 126:473–480.

———. 2004. The relationship between specialization and local abundance: the case of helminth parasites of birds. Oecologia (Berlin) 140:372–378.

Prasad, R. S. 1969. Influence of host on fecundity of the Indian rat flea, *Xenopsylla cheopis* (Roths.). Journal of Medical Entomology 6:443–447.

Redfearn, A., and S. L. Pimm. 1988. Population variability and polyphagy in herbivorous insect communities. Ecological Monographs 58:39–55.

Reshetnikova, P. I. 1959. Flea fauna of the Kustanai region. Proceedings of the Middle Asian Scientific Anti-Plague Institute 6:261–265. [In Russian.]

Root, R. B., and N. Capuccino. 1992. Patterns in population change and the organization of the insect community associated with goldenrod. Ecological Monographs 62:393–420.

Sapegina, V. F., I. V. Lukyanova, and B. N. Fomin. 1981. Fleas of small mammals in northern foothills of the Altai Mountains and the upper Ob River region. Pages 167–176 *in* A. A. Maximov, ed. Biological problems of natural nidi. Nauka, Siberian Branch, Novosibirsk. [In Russian.]

Shenbrot, G. I., B. R. Krasnov, and K. A. Rogovin. 1999. Spatial ecology of desert rodent communities. Springer, Berlin.

Shwartz, E. A., E. L. Berendiaeva, and R. V. Grebenuk. 1958. Fleas of rodents of the Frunze region. Proceedings of the Middle Asian Scientific Anti-Plague Institute 4: 255–261. [In Russian.]

Silva, M., and J. A. Downing. 1995. CRC handbook of mammalian body masses. CRC, Boca Raton, Fla.

Sineltschikov, V. A. 1956. Study of flea fauna of the Pavlodar region. Proceedings of the Middle Asian Scientific Anti-Plague Institute 2:147–153. [In Russian.]

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

Thompson, J. N. 1994. The coevolutionary process. University of Chicago Press, Chicago.

Traub, R., M. Rothschild, and J. F. Haddow. 1983. The Ceratophyllidae: key to the genera and host relationships. Academic Press, London.

Vasiliev, G. I. 1966. On ectoparasites and their hosts in relation to the plague epizootic in Bajan-Khongor aimak (Mongolian People Republic). Proceedings of the Irkutsk State Scientific Anti-Plague Institute of Siberia and Far East 26:277–281. [In Russian.]

Walsberg, G. E., and B. O. Wolf. 1995. Effects of solar radiation and wind speed on metabolic heat-production by two mammals with contrasting coat color. Journal of Experimental Biology 198:1499–1507.

Ward, S. A. 1992. Assessing functional explanations of host-specificity. American Naturalist 139:883–891.

Wilson, D. E., and D. M. Reeder, eds. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution, Washington, D.C.

Wright, D. H. 1991. Correlation between incidence and abundance are expected by chance. Journal of Biogeography 18:463–466.

Yudin, B. S., V. G. Krivosheev, and V. G. Belyaev. 1976. Small mammals of the northern Far East. Nauka, Siberian Branch, Novosibirsk. [In Russian.]

Zagniborodova, E. N. 1960. Fauna and ecology of fleas on the western Turkmenistan. Pages 320–334 *in* Problems of natural nidi and epizootology of plague in Turkmenistan. Turkmenian Anti-Plague Station and All-Union Scientific Anti-Plague Institute, Microbe, Ashkhabad. [In Russian.]

Associate Editor: Dale H. Clayton