



# Latitudinal gradients in niche breadth: empirical evidence from haematophagous ectoparasites

Boris R. Krasnov<sup>1,2\*</sup>, Georgy I. Shenbrot<sup>1,2</sup>, Irina S. Khokhlova<sup>3</sup>, David Mouillot<sup>4</sup> and Robert Poulin<sup>5</sup>

<sup>1</sup>Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel, <sup>2</sup>Ramon Science Center, PO Box 194, Mizpe Ramon 80600, Israel, <sup>3</sup>Desert Animal Adaptations and Husbandry, Wyler Department of Dryland Agriculture, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel, <sup>4</sup>UMR CNRS-UMII 5119 Ecosystemes Lagunaires, University of Montpellier II, CC093, FR-34095 Montpellier Cedex 5, France and <sup>5</sup>Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

## ABSTRACT

**Aim** We searched for relationships between latitude and both the geographic range size and host specificity of fleas parasitic on small mammals. This provided a test for the hypothesis that specialization is lower, and thus niche breadth is wider, in high-latitude species than in their counterparts at lower latitudes.

**Location** We used data on the host specificity and geographic range size of 120 Palaearctic flea species (Siphonaptera) parasitic on small mammals (Soricomorpha, Lagomorpha and Rodentia). Data on host specificity were taken from 33 regions, whereas data on geographic ranges covered the entire distribution of the 120 species.

**Methods** Our analyses controlled for the potentially confounding effects of phylogenetic relationships among flea species by means of the independent-contrasts method. We used regressions and structural equation modelling to determine whether the latitudinal position of the geographic range of a flea covaried with either the size of its range or its host specificity. The latter was measured as the number of host species used, as well as by an index providing the average (and variance in) taxonomic distinctness among the host species used by a flea.

**Results** Geographic range size was positively correlated with the position of the centre of the range; in other words, fleas with more northerly distributions had larger geographic ranges. Although the number of host species used by a flea did not vary with latitude, both the mean taxonomic distinctness among host species used and its variance increased significantly towards higher latitudes.

**Main conclusions** The results indicate that niche breadth in fleas, measured in terms of both its spatial (geographic range size) and biological (host specificity) components, increases at higher latitudes. These findings are compatible with the predictions of recent hypotheses about latitudinal gradients.

## Keywords

Fleas, geographic range, host specificity, latitude, niche breadth, Rapoport's rule, Siphonaptera, small mammals.

\*Correspondence: Boris Krasnov, Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel. E-mail: krasnov@bgu.ac.il

## INTRODUCTION

The most pervasive patterns in biogeography are those related to latitude. In particular, the most conspicuous of these patterns, such as latitudinal gradients in species richness and geographic range size, have been extensively studied and documented (Gaston, 2003; Willig *et al.*, 2003; Hillebrand, 2004; Ruggiero & Hawkins, 2006; Mittelbach *et al.*, 2007;

Ruggiero & Wrenkraut, 2007, for recent reviews). One of the most well-known latitudinal patterns is Rapoport's rule, which postulates an increase in the geographic range size of a species with increasing latitude (Stevens, 1989; Hawkins & Diniz-Filho, 2006).

From an ecological perspective, Rapoport's rule can represent a particular case of the more general relationship between the niche breadth of a species and the size of its geographic

range (e.g. Brown, 1984, 1995; Ruggiero & Hawkins, 2006). According to the niche-breadth explanation, specialized species can only tolerate restricted abiotic conditions, are able to use few types of resources, and/or are highly tolerant of a very limited set of competitors, predators, parasites and diseases. In contrast, generalists can tolerate a wide range of physical conditions, use a broad range of resources, and/or are able to survive in the presence of many natural enemies. As a result, the same attributes that enable a species to occur in either many or a few habitats, or to exploit either many or few types of resources, cause it to have either a broad or narrow geographic range, respectively. Indeed, a negative correlation between the degree of specialization and the size of the geographic range of a species has been documented for various taxa, both free-living and parasitic (MacArthur, 1972; Glazier, 1980; Eeley & Foley, 1999; Krasnov *et al.*, 2005; Kubota *et al.*, 2007). Furthermore, if the level of specialization is determined by population stability (MacArthur, 1955), which, in turn, is determined by environmental stability (MacArthur, 1972), negative specialization–latitude relationships can occur owing to lower stability and higher seasonality in temperate regions compared with the tropics (MacArthur, 1972; Kolasa *et al.*, 1998; Gaston & Spicer, 2001; Vázquez & Stevens, 2004; Yom-Tov & Geffen, 2005; but see, for example, Marshall & Convey, 2004). However, there is still no agreement on the generality and occurrence of particular latitudinal patterns (e.g. Chown *et al.*, 2004). For example, it has been argued that latitudinal patterns in species richness and geographic range size may be driven by global processes such as climatic changes arising from periodic changes in the orbit of the Earth (Dynesius & Jansson, 2000). If biogeographic (e.g. latitudinal) patterns are, indeed, caused by global processes, they are expected to be universal (e.g. Hillebrand, 2004; Mittelbach *et al.*, 2007). The stability-related explanations of MacArthur (1955, 1972) also suggest the universality of latitudinal patterns. In contrast, Rohde (1996, 1999) argued that, for example, Rapoport's rule is limited in relation to both taxa and latitudinal span and thus represents nothing other than a regional phenomenon.

One of the greatest challenges in macroecological/biogeographical studies is therefore to understand why latitudinal patterns hold for some taxa but not for others. Recently, Vázquez & Stevens (2004) carried out a meta-analysis evaluating the assumptions and predictions of the niche-breadth–latitude hypothesis. They found that neither the assumptions nor the predictions of the hypothesis, in its classical form, were well supported by available evidence. Instead, they proposed an alternative explanation for the relationship between latitude and niche breadth based on entirely different mechanisms. According to these authors, the positive relationship between niche breadth and latitude (equivalent to a negative relationship between the level of specialization and latitude) will occur only if there is (1) a latitudinal gradient in species richness, and (2) an effect of richness on niche breadth. The latter effect can occur if the species of interest are involved in an asymmetrically specialized interaction network in which specialists tend to interact with generalists (Vázquez & Aizen, 2003, 2004). An

important characteristic of asymmetrically specialized interaction networks is that asymmetric specialization among species increases with an increase in the number of species in the network (Vázquez & Aizen, 2004). In particular, this tendency is manifested by an increase in the number of extreme specialists with an increase in community size (Vázquez & Stevens, 2004); in other words, higher species richness may lead to more extreme specialization. Therefore, a decrease in niche breadth (equivalent to an increase in specialization) at low latitudes is a predictable by-product of an increase in species richness. In other words, if species richness affects the niche breadth, this should result in a link between niche breadth and latitude.

This hypothesis can thus explain among-taxa variation in the occurrence of the latitudinal gradient of niche breadth. However, the Vázquez–Stevens hypothesis remains to be validated. The simplest way to do this is to search for latitudinal gradients in niche breadth within a taxon. Then, if this trend is found, it needs to be checked whether the taxon of interest meets the assumptions of the hypothesis. Various taxa of parasites represent convenient models for such a validation. First, the niche breadth of a parasite is represented by both environmental and biological components. The former consists of the range of environmental conditions that a parasite can tolerate, and it can be evaluated, albeit indirectly, by means of the size of its geographic range. The latter, on the other hand, is the range of host species that a parasite is able to exploit, which can be evaluated by its level of host specificity. Second, many, although not all, parasite taxa demonstrate latitudinal gradients in species richness (e.g. Poulin & Rohde, 1997; Calvete *et al.*, 2004; but see Poulin, 1995, 2001). Third, parasite–host interaction networks are highly asymmetric, with specialist parasites tending to interact with hosts with high parasite richness, and hosts with low parasite richness tending to interact mainly with generalist parasites (Vázquez *et al.*, 2005).

Here we tested the relationship between latitude and the level of specialization among species of fleas (Siphonaptera) parasitic on Palaearctic small mammals, using published data on the geographic distribution and host occurrences from 33 distinct geographic regions. We evaluated both spatial and biological components of flea niche breadth by estimating geographic range size and the level of host specificity, respectively, for each flea species. We hypothesized that estimates of flea niche breadth should increase with increasing latitude.

## MATERIALS AND METHODS

We used published data on the host specificity of 120 Palaearctic flea species parasitic on small mammals (Soricomorpha, Lagomorpha and Rodentia) in 33 regions of the Palaearctic. The sources provided data on the number of individuals of a particular flea species found on a given number of sampled individuals of a particular host species during comprehensive surveys within a region (see Appendix S1

in Supplementary Material). In all surveys, most species were captured using snap-traps; shrews were also captured using pitfall traps, sciurids and lagomorphs were hunted, and moles were captured using mole-traps. Single findings of a flea species on a host species were considered accidental and were not included in the analysis. We included in the analysis only flea species occurring in at least two regions from the data set, and in at least four mammalian host species across the entire data set. This resulted in the exclusion of only the most strictly host-specific flea species and does not bias the results, as the vast majority of species can use more than one host species.

For each species of flea, two measures of host specificity were used, namely (1) the number of mammalian species on which the flea species was found, and (2) the specificity index,  $S_{TD}$ , and its variance,  $VarS_{TD}$  (Poulin & Mouillot, 2003). The index  $S_{TD}$  is based on the taxonomic or phylogenetic affinities of the various host species and measures the average taxonomic distinctness of all host species used by a parasite species. Thus, this measure places the emphasis on the phylogenetic diversity of the host spectrum of a flea, providing a different (from number of host species) perspective on host specificity, one that truly focuses on the specialization of the flea for its host habitat. When 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 (see Poulin & Mouillot, 2003, for details). For any given pair of host species, the number of steps corresponds to half the path length connecting the two species in the taxonomic tree, with equal step lengths of one 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. Using the taxonomic classification of Wilson & Reeder (2005), all mammal species included here were fitted into a taxonomic structure with five hierarchical levels above species, i.e. genus, subfamily, family, order, and class (Mammalia). The maximum value that the index  $S_{TD}$  can take (when all host species belong to different orders) is thus 5, and its lowest value (when all host species are congeners) is 1. The variance in  $S_{TD}$ ,  $VarS_{TD}$ , provides information on any asymmetries in the taxonomic distribution of host species (Poulin & Mouillot, 2003). To calculate  $S_{TD}$  and  $VarS_{TD}$ , D.M. and R.P. developed a computer program using BORLAND C++ BUILDER 6.0 (available at <http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2>).

For each flea species, both measures of host specificity were averaged across regions where the species was recorded. The number of host species on which the flea species was found was positively correlated with the number of hosts examined ( $r^2 = 0.13$ ,  $F_{1,118} = 17.1$ ,  $P < 0.001$ ). To remove the confounding effect of sampling effort, original values of the number of hosts were substituted with their residual deviations

from the regression against the number of hosts examined. The number of host species used by a flea species was significantly positively correlated (albeit weakly) with both  $S_{TD}$  and  $VarS_{TD}$  ( $r^2 = 0.29$ ,  $F_{1,118} = 48.1$  and  $r^2 = 0.16$ ,  $F_{1,118} = 22.6$ , respectively;  $P < 0.001$  for both), indicating that these measures were influenced by the number of host species in the host spectrum of a flea. Therefore, in the subsequent analyses,  $S_{TD}$  and  $VarS_{TD}$  were corrected for host species richness in an assemblage using residual deviations from the respective regressions. We used Moran's index to test for spatial autocorrelation among variables in the resulting data set, calculating it using the spatial statistics tools of ARCVIEW 9.1. The value of this index for the number of host species used by a flea species and its  $S_{TD}$  were 0.01 ( $z$ -score = 0.34) and 0.05 ( $z$ -score = -0.86), thus demonstrating that these variables were not spatially autocorrelated. However,  $VarS_{TD}$  was significantly spatially autocorrelated (Moran's index = 0.15,  $z$ -score = 3.11). To remove the effect of spatial autocorrelation we applied cluster and outlier analyses (Anselin Local Moran's index; Anselin, 1995). In these analyses, we sequentially removed species with the highest  $z$ -score values from the data set and recalculated Moran's index until spatial autocorrelation became non-significant (Moran's index = 0.04,  $z$ -score = 0.83). The resulting data set included 106 flea species. We ran the analyses twice (once with the entire data set and once with 106 instead of 120 species). Both runs of the analyses provided the same results. Consequently, in this paper we report only the results of analyses performed on the entire data set.

The latitudinal position of the centre of the geographic range and its entire size were determined for each flea species from distribution maps using the ARCVIEW 9.2 software. Use of the midpoint approach in biogeographical studies has been justified elsewhere (e.g. Johnson, 1998; Rohde, 1999; but see Ruggiero & Werenkraut, 2007, for caveats).

The maps were based on published maps (e.g. Traub *et al.*, 1983) and various literature sources and museum records (see Krasnov *et al.*, 2005; Shenbrot *et al.*, 2007). In other words, the range size of each flea was based on all records of its presence, including many more than the surveys used here, with the number of records per flea species ranging from 14 record points (*Paradoxopsyllus dashidorzhii*) to a maximum of 772 record points (*Ctenophthalmus agyrtes*). To estimate the size of the geographic range of a species, we combined the minimal convex polygon (MCP; Fortin *et al.*, 2005) method and the GARP algorithm (Stockwell & Peters, 1999). The latter is a genetic algorithm that creates ecological niche models for each species. We constructed a MCP around the outermost record points and added around it a 25-km buffer. We then used the modelling approach based on the GARP algorithms (DESKTOPGARP 1.1.3 software, University of Kansas Biodiversity Research Centre). For each species, we calculated a set of 60–120 models using range and logistic regression methods and combinations thereof. We included only areas that were located inside the original buffer polygon in the estimated geographic range, because estimation of the potential distri-

bution of a species beyond the known distributional limits has low reliability (Anderson, 2003; Anderson *et al.*, 2003). We overlapped all models thus obtained, and included areas for which 90% of models predicted a species' presence in the estimated geographic range. Geographic ranges of only four of 120 flea species extended beyond the Palaearctic (into the Nearctic). For these species, their entire geographic range was taken into account.

To meet the assumptions of parametric tests, all variables were log-transformed prior to analyses. These transformations produced distributions that did not deviate significantly from normality (Kolmogorov–Smirnov tests, non-significant). Untransformed data on the size and position of geographic ranges are, however, presented in the figures. To test for the relationships between the position of the geographic range (independent variable) and (1) host specificity measures and (2) size of the geographic range (dependent variables), we performed regressions of each dependent variable against the independent variable using both conventional statistics and the method of independent contrasts (Felsenstein, 1985). This method has rarely been used in studies of latitudinal gradients of niche breadth and geographic range (e.g. Rohde, 1993; but see Johnson, 1998). The rationale for using this method is that a geographic pattern may be a combination of phylogenetic and adaptive effects. The latter are species-level responses that operate independently of phylogeny. We used independent contrasts to test for the occurrence of the adaptive component in latitudinal gradients of flea niche breadth. Furthermore, use of the independent-contrasts method may diminish the possibility that the centres of the geographic ranges of widespread species fall predictably into the middle of the latitudinal range of the study area (Lyons & Willig, 1997) and, thus, mask real relationships between, for example, size of the geographic range and latitude (see Johnson, 1998, for an explanation).

Phylogenetic trees of flea species were derived from morphological characters and taxonomy (see Krasnov & Shenbrot, 2002; Krasnov *et al.*, 2005, for details, and Krasnov & Shenbrot, 2002, and Krasnov *et al.*, 2004a, for examples) separately for individual families. These phylogenies were then combined using the phylogenetic relationships among flea families suggested by Medvedev (1995). The topology of the resulting phylogenetic tree in Newick tree format is available in Appendix S2. There were only four polytomies in the tree, involving 16 species (all Ceratophyllidae). These polytomies were considered as soft (we assumed a lack of knowledge about the common ancestor) and were resolved randomly. The initial branch length was set to 1.0. To compute independent contrasts, we used the PDAP:PDTREE module (Garland *et al.*, 1993; Midford *et al.*, 2006) implemented in the Mesquite Modular System for Evolutionary Analysis (Maddison & Maddison, 2006). Pairs of sister branches that diverged long ago are likely to yield greater contrasts than pairs of sister branches that diverged recently. To avoid this, we standardized each contrast by dividing it by its standard deviation (Garland *et al.*, 1992). To verify that contrasts were properly standardi-

zed, we plotted the absolute values of standardized contrasts against their standard deviation (Garland *et al.*, 1992). No significant linear or non-linear trend was found in these plots, suggesting that the contrasts were adequately standardized. We then regressed standardized contrasts in log-transformed measures of host specificity or size of the geographic range against standardized contrasts in log-transformed latitudinal position of the geographic range using major-axis regressions forced through the origin (Pagel, 1992; Garland *et al.*, 1993).

The null distribution of range sizes is triangular when using the midpoint method because it is impossible for a widely distributed species to have the centre of its geographic range at the edge of the Palaearctic (see Lyons & Willig, 1997) whereas a species with a small range can be anywhere. Therefore, the significance of each regression model was tested using a randomization approach (Manly, 1997) using the RT 2.1 software (Western EcoSystems Technology, Inc.; Cheyenne, WY). All regression probabilities were based on 10,000 permutations.

To test whether data points for  $Var_{STD}$  are significantly concentrated in a triangular area of the bivariate space when plotted against the position of the centre of the geographic range (see Results), we used the boundary test implemented in the EcoSIM 7 software (Gotelli & Entsminger, 2004). This test uses a null-model approach and calculates (1) the number of points that fall beyond the boundary, and (2) the sum of squares of those points for observed and simulated data. If some corners of the space are unusually empty, the observed number of points and/or the sum of squares in the observed data set will be significantly lower than in the simulated data sets.

In addition, to evaluate the relationships between variables, we employed path analysis using structural equation modelling (SEM). Path analysis represents a method for the partitioning of correlations among variables. The initial step of path analysis is the construction of a path diagram demonstrating causal relationships among all variables in a system. Causal models in SEM are proposed based on prior biological knowledge. Consequently, we constructed a path diagram suggesting not only the effects of the position of the centre of the geographic range on its size and on estimates of host specificity, but also possible effects of host specificity on the size of the geographic range (see Shenbrot *et al.*, 2007). The goodness of fit of the models to the data was evaluated using the likelihood chi-square value. Models with non-significant likelihood ratio chi-square values are considered adequate descriptions of the data (Bollen, 1989).

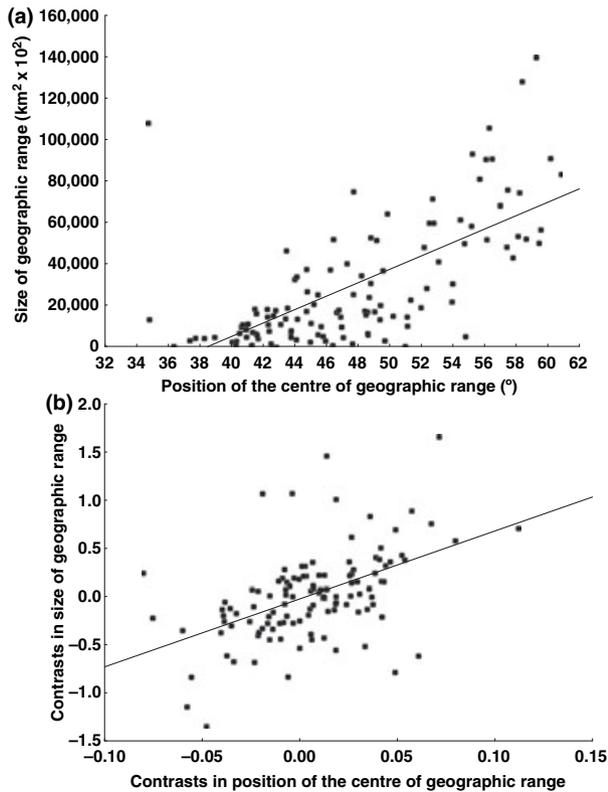
## RESULTS

The size of the geographic range of 120 flea species ranged from 6470 km<sup>2</sup> (*Ctenophthalmus inornatus*) to 13,959,042 km<sup>2</sup> (*Corrodopsylla birulai*). The southernmost position of the centre of the geographic range occurred for *Xenopsylla conformis*, whereas the northernmost position occurred for *Oropsylla alaskensis* (34.7° and 60.7°, respectively). Extreme

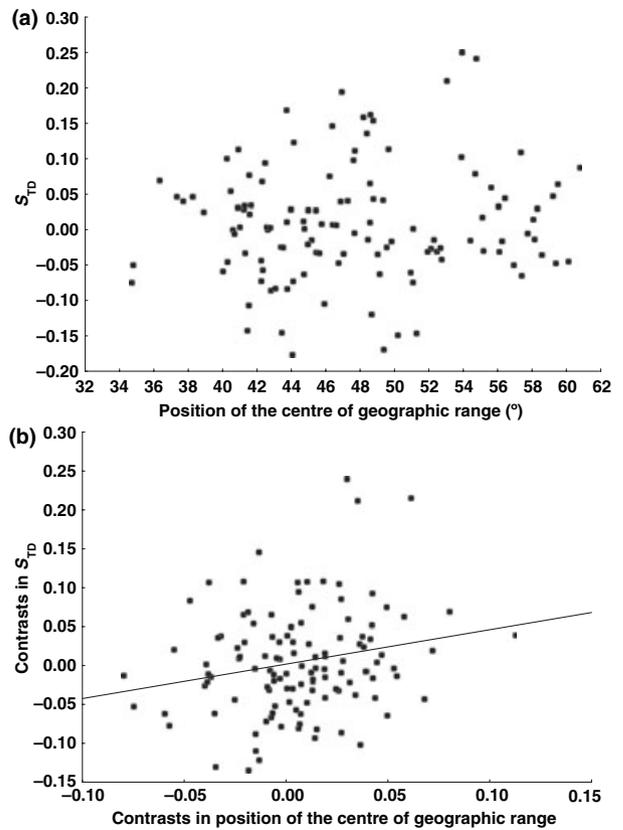
values of average (across regions) host specificity in terms of the number of hosts were seen in *Oropsylla silantiewi* and *Ctenophthalmus agyrtes* (1.8 and 14.0, respectively). The centres of the geographic ranges of the 120 flea species are shown on a map in Appendix S3. The extreme values of the taxonomic distinctness of the host spectrum were found in *Mesopsylla hebes* and *Palaeopsylla kohauti* (0.6 and 4.7, respectively). The least taxonomically asymmetric host spectrum found was for *Amphipsylla kuznetzovi*, whereas *Rhadinopsylla pseudodahurica* exploited the most asymmetric assemblage of host species (0 and 2.8, respectively).

Geographic range size was positively correlated with the position of the centre of the range ( $r^2 = 0.34$ ,  $F_{1,118} = 60.7$ ,  $P < 0.01$ ). In other words, species with more northerly distributions were characterized by larger geographic ranges (Fig. 1a). This relationship also held when the confounding effect of flea phylogeny was controlled for ( $r = 0.49$ ,  $P < 0.001$ ; Fig. 1b).

The number of species in the host spectrum of a flea did not correlate with the position of the centre of the geographic range. This was true both using conventional regression ( $r^2 = 0.003$ ,  $F_{1,118} = 0.3$ ,  $P = 0.59$ ) and with independent contrasts ( $r = -0.079$ ,  $P = 0.44$ ). The index of host specificity,  $S_{TD}$ , also did not correlate with the position of the centre of the geographic range ( $r^2 = 0.01$ ,  $F_{1,118} = 1.1$ ,  $P = 0.3$ ; Fig. 2a).



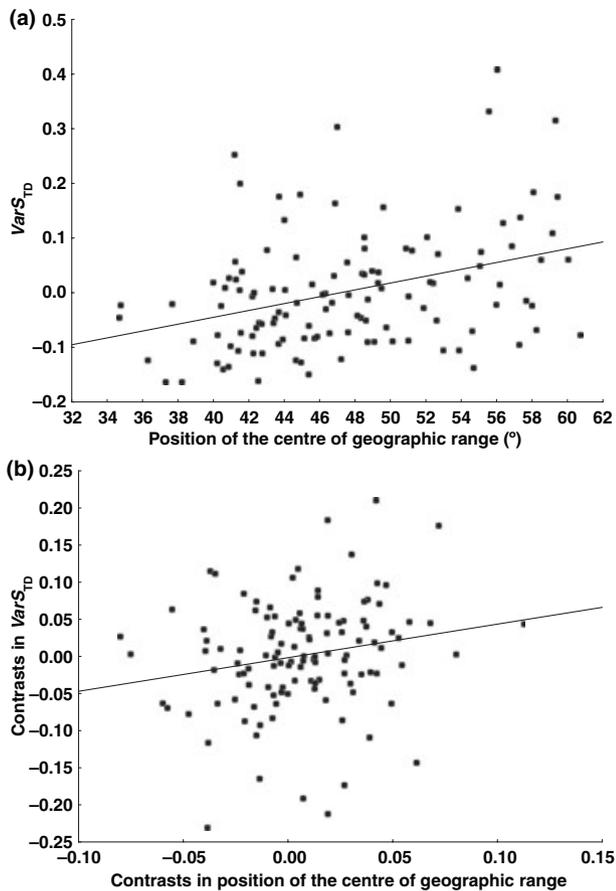
**Figure 1** Relationship between the position and size of the geographic range across 120 Palaearctic flea species using (a) conventional statistics and (b) the method of phylogenetically independent contrasts.



**Figure 2** Relationship between the position of the geographic range and the index of host specificity,  $S_{TD}$ , across 120 Palaearctic flea species using (a) conventional statistics and (b) the method of phylogenetically independent contrasts. The index  $S_{TD}$  was corrected for the number of host species in a flea's host spectrum.

However, when the confounding effect of phylogeny was controlled for, a significant positive correlation between these two parameters was revealed ( $r = 0.22$ ,  $P < 0.01$ ; Fig. 2b). Finally, variance in the taxonomic distinctness of the host spectrum increased significantly with an increase in the distance of the centre of a flea's geographic range from the equator ( $r^2 = 0.12$ ,  $F_{1,118} = 16.9$ ,  $P < 0.001$  for conventional regression, and  $r = 0.19$ ,  $P < 0.03$  for independent contrasts; Fig. 3). The distribution of data points in Fig. 3a is roughly triangular. The boundary number of points and the boundary sum of squares tests confirmed the statistical significance of a predominant scatter of data points in the lower right corner of the space ( $P < 0.05$  for both). This suggests that northern flea species may have either a highly or weakly taxonomically asymmetric host spectrum, whereas mammals from different taxonomic lineages are evenly represented in the host spectra of southern species.

Application of SEM to our data produced essentially the same results. Path models adequately described the observed data, although the fit of the model to the data was not especially high (chi-square = 5.58, d.f. = 3,  $P = 0.13$  for non-transformed data, and chi-square = 6.02, d.f. = 3,  $P = 0.11$  for phylogenetically corrected data). There were significant positive

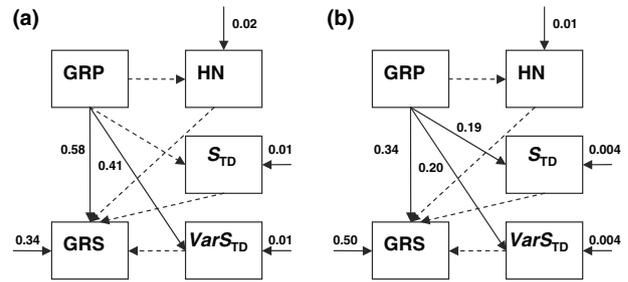


**Figure 3** Relationship between the position of the geographic range and the variance of the index of host specificity,  $VarS_{TD}$ , across 120 Palaearctic flea species using (a) conventional statistics and (b) the method of phylogenetically independent contrasts. The index  $VarS_{TD}$  was corrected for the number of host species in a flea's host spectrum.

effects of latitude on the size of the geographic range and on  $VarS_{TD}$  (for both original data and independent contrasts) as well as on  $S_{TD}$  (for independent contrasts only) (Fig. 4).

## DISCUSSION

The results of this study demonstrate: (1) that fleas follow Rapoport's rule, i.e. the sizes of their geographic ranges increase from low to high latitudes; and (2) that the level of host specificity in fleas decreases towards higher latitudes. In other words, the positive niche breadth–latitude relationship holds for fleas in terms of both the spatial (i.e. geographic range size) and biological (i.e. taxonomic diversity of host spectrum) components of the niche. Moreover, the positive relationship between size and position of the geographic range persists despite sharp departures from the general trend demonstrated by some species. For example, *X. conformis* has a broad geographic range (10,787,560 km<sup>2</sup>), but it is distributed mainly in the southern parts of the Palaearctic (deserts and semi-deserts of the Saharo-Gobian desert belt, including North Africa). In contrast, the geographic ranges of *Ctenophthalmus hypanis*, which occurs in



**Figure 4** Path diagram for the proposed structural equation model testing relationships between (a) logarithms and (b) independent contrasts of the position of the geographic range (GRP), size of the geographic range (GRS), number of host species exploited (HN), taxonomic distinctness of the host spectrum ( $S_{TD}$ ), and its variance ( $VarS_{TD}$ ) in 120 flea species parasitic on Palaearctic small mammals. HN was corrected for sampling effort;  $S_{TD}$  and  $VarS_{TD}$  were corrected for the number of host species in a flea's host spectrum. Long arrows are causal effects of one variable on another; short arrows indicate unexplained variability of endogenous (dependent) variables. Numbers next to arrows are standardized path coefficients. Solid arrows – significant relationships ( $P < 0.05$ ); dashed arrows – non-significant relationships.

the Caucasus, and *Nosopsyllus monstrosus*, which occurs in arid south-central Turkmenistan, are relatively small (7325 km<sup>2</sup> and 36552 km<sup>2</sup>, respectively).

Rapoport's effect has received much attention and has been explained by a vast number of mechanisms (see Gaston *et al.*, 1998; Gaston, 2003; Hawkins & Diniz-Filho, 2006; Ruggiero & Wrenkraut, 2007). The validity of many of these explanations has been strongly criticized (e.g. see Vázquez & Stevens, 2004, for the climatic variability hypothesis; and Gaston & Blackburn, 1996, and Blackburn & Gaston, 1996, for the land area hypothesis). Thus, purely ecological and mechanistic explanations for Rapoport's effect remain controversial. Indeed, neither of the above hypotheses, at least in their classical form, can be easily used to explain the results of our study. Nevertheless, the observed pattern may be produced by the interplay between several mechanisms. For example, explanations of Rapoport's effect often invoke niche breadth (e.g. the differential extinction hypothesis, Brown, 1995; and the global climate change hypothesis, Dynesius & Jansson, 2000). In other words, this effect may be the product of positive relationships between (1) niche breadth and geographic range size, and (2) latitude and niche breadth.

In an earlier study, we demonstrated a negative relationship between host specificity (a reciprocal measure of niche breadth) and geographic range size among fleas parasitic on small mammals from seven large geographical regions (Krasnov *et al.*, 2005). The results of the present study demonstrate that a relationship between niche breadth and latitude also exists. Fleas with more northerly ranges appeared generally less host-specific than fleas with more southerly ranges. This pattern can be explained in the framework of the hypothesis proposed by Vázquez & Stevens (2004).

In general, fleas meet both assumptions of the Vázquez–Stevens hypothesis. First, in biogeographical realms in which an effect of latitude on flea species richness has been found, it is a negative relationship (Krasnov *et al.*, 2007), although this pattern emerged from an analysis performed at the level of host communities rather than at that of host species (see Krasnov *et al.*, 2004b). Furthermore, in many mountainous regions flea species richness decreases with increasing altitude (e.g. Manhart, 1972; Bartkowska, 1973; Haitlinger, 1989; but see Haitlinger, 1975), which can be considered as an equivalent for a latitudinal gradient of species richness. Second, patterns of interaction among fleas and their mammalian hosts in 21 of the 33 regions considered here have been shown to be asymmetric (Vázquez *et al.*, 2005) (the flea–mammal interaction networks in the remaining 12 regions have not been evaluated). Most flea species tend to be specialists interacting with ‘generalist’ hosts (i.e. hosts that harbour rich flea assemblages), or are generalists themselves. Similarly, most host species either are exploited by a few generalist fleas or are ‘generalists’ themselves. Third, the niche breadth of a flea species evaluated by its degree of host specificity may vary geographically, although it stays within species-specific boundaries (Krasnov *et al.*, 2004c). In any event, the results of this study fit well with the explanation for a latitudinal gradient of niche breadth in the framework of Vázquez & Stevens’s (2004) hypothesis.

Another, not necessarily alternative, explanation for the observed pattern may be that the link between latitude and host specificity is merely a product of the negative relationship between geographic range size and host specificity (Krasnov *et al.*, 2005). For example, having a broad geographic range allows a flea to ‘sample’ many host taxa, leading to high values of  $S_{TD}$ . However, this explanation is weakened by the fact that, although a relationship between geographic range size and the number of hosts exploited was found by Krasnov *et al.* (2005), no relationship between latitude and the size of the host spectrum was found in the present study, and path models implemented here failed to find any relationship between the size of the geographic range and any host-specificity measure. Similarly, although no relationship between the size of the geographic range and the index  $VarS_{TD}$  was found by Krasnov *et al.* (2005), a clear link between  $VarS_{TD}$  and latitude is revealed here.

An important finding of this study is that the latitudinal gradient in flea specialization is manifested in the taxonomic diversity rather than in the size of a flea’s host spectrum. This means that fleas with southern distributions may exploit the same number of hosts as fleas with northern distributions, but hosts of ‘southern’ fleas are, in general, more closely related. The reason for this is unlikely to be associated with differences in host community composition between ‘northern’ and ‘southern’ fleas, because the relatedness among hosts used by a flea has been shown to be higher than that among hosts from the entire host pool of a locality (Krasnov *et al.*, 2004c). The reason why we found a latitudinal gradient of  $S_{TD}$  rather than of host number may be that  $S_{TD}$  specifically captures

evolutionary facets of host specificity (Poulin & Mouillot, 2003) and is thus a more appropriate measure of niche breadth in studies of macroecological patterns.

Asymmetries in the taxonomic structure of the host species used by a flea as measured by  $VarS_{TD}$  correlated positively with the latitude of the centre of the geographic range. This means that the level of taxonomic heterogeneity among a group of host species was higher in fleas from temperate regions than in fleas from desert regions, and that with an increase in latitude the host taxonomic tree becomes not only more diverse but also more complex. However, the triangular shape of the scatter of points in Fig. 3a suggests that the main reason for this pattern is that, although ‘northern’ fleas can have both taxonomically symmetric and taxonomically asymmetric host spectra, no main host branch can be distinguished in the host spectrum of a ‘southern’ flea. This trend certainly requires further investigation. Furthermore, the link between the latitude of the centre of the geographic range of a flea and  $VarS_{TD}$  held when independent contrasts were used. This means that this geographic pattern is a combination of phylogenetic/historical effects and adaptive effects that operate independently of phylogeny.

Rapoport’s effect has been shown for many species that harbour parasites (see Ruggiero & Werenkraut, 2007). The strong link between parasites and their hosts is often thought to be mainly physiological, but this link should also manifest itself on larger scales, including biogeographical scales. In other words, ectoparasite biogeography should *a priori* mirror host biogeography, and, consequently, if hosts demonstrate latitudinal increases in niche breadth, their parasites should demonstrate this pattern too. Indeed, many taxa of mammalian hosts of fleas have been shown to demonstrate an increase of niche breadth with increasing distance from the equator (e.g. Letcher & Harvey, 1994; Hernández Fernández & Vrba, 2005). Consequently, the findings of our study may also represent a manifestation of biogeographical patterns characteristic of hosts but seen in the biogeographical patterns of their parasites.

Finally, the latitudinal gradient in flea host specificity measured with the index  $S_{TD}$  was detected only when the confounding effect of phylogeny was controlled for. The contrasting results between the two types of analysis suggest that phylogenetic effects may mask true relationships. In other words, there can be an adaptive component in a geographic pattern (i.e. resulting from species-level responses) that may occur independent of phylogeny. It is, therefore, quite possible that the lack of phylogenetic correction was the reason behind the negative results of some earlier studies of latitudinal gradients (e.g. Rohde, 1993).

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

**Appendix S1** Data on small mammals and fleas (number of species/number of individuals) contained in the 33 surveys.

**Appendix S2** Description of the phylogenetic tree of fleas in Newick tree format.

**Appendix S3** Centres of geographic ranges of the 120 flea species used in the analyses. The map is an Asia North Albers equal-area conic projection.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01800.x>

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## BIOSKETCHES

**Boris Krasnov, Georgy Shenbrot and Irina Khokhlova** are senior researchers at Ben-Gurion University of the Negev and Ramon Science Centre. Boris Krasnov's research focuses on the evolutionary ecology of host–parasite relationships, and the population ecology and ecophysiology of hematophagous ectoparasites. The main research interests of Georgy Shenbrot are community ecology and the systematics of desert rodents. Irina Khokhlova conducts research into the ecophysiology of animals and the effect of ectoparasites on a host's physiological parameters.

**David Mouillot** belongs to a research unit at the University of Montpellier II investigating the ecology and evolution of fishes in marine and lagoon ecosystems.

**Robert Poulin** is a professor at the University of Otago. His research interests include all ecological and evolutionary aspects of host–parasite interactions.

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