

# Host–habitat relations as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert

B. R. KRASNOV<sup>1\*</sup>, G. I. SHENBROT<sup>1</sup>, S. G. MEDVEDEV<sup>2</sup>, V. S. VATSCHENOK<sup>2</sup>  
and I. S. KHOKHLOVA<sup>3</sup>

<sup>1</sup>Ramon Science Center, Ben-Gurion University of the Negev, P.O. Box 194, Mizpe Ramon 80600, Israel

<sup>2</sup>Zoological Institute, Russian Academy of Science, 199034, Saint-Petersburg, Russia

<sup>3</sup>Desert Animal Adaptations and Husbandry, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel

(Received 1 May 1996; revised 5 July and 7 August 1996; accepted 7 August 1996)

## SUMMARY

We studied flea assemblages on rodents in different habitats of the Ramon erosion cirque in the Negev Desert to examine whether host–habitat relations influence flea spatial distribution. Eleven flea species parasitizing 12 rodent species were recorded. There was significant positive relationship between flea species richness and body mass of the host species; no relationships were found between relative richness of flea assemblage and either the number of habitats occupied by the host species or the size of host geographical range. The differences in pattern of flea parasitism among habitat types within host species were determined by both environmental features of a habitat and the specific pattern of habitat use by rodents. There was replacement of *Xenopsylla conformis* by *Xenopsylla ramesis* on *Meriones crassus* and *Gerbillus dasyurus* among different habitats. The results of ordination of the flea collections from each individual host demonstrated that the flea assemblages were segregated mainly along 4 axes, which explained 86% of total variance. Each of the ordination axes corresponded with a change in flea species composition. The directions of these changes were (1) among-hosts within a habitat and (2) among-habitats within a host.

Key words: ectoparasite, fleas, rodents, host–habitat relation

## INTRODUCTION

Community organization of parasites is considered to be determined mainly by their hosts (Price, 1990). A host presents a habitat for parasites, providing them with place for living, foraging and mating. Thus, hosts can be considered as biological islands (Kuris, Blaustein & Aho, 1980) and so the parasite communities should conform to principles of classical insular biogeography. For example, Guegan & Huguény (1994) demonstrated that the number of monogenean gill parasite species in the West African cyprinid fish *Labeo coubie* adheres to the principle of species–area relationship (MacArthur & Wilson, 1967), namely, larger fishes accommodate more species than smaller ones. The hypothesis that the host is a major determinant of parasite community structure has been supported by a number of studies on helminths (Bell & Burt, 1991; Buchman, 1991; Guegan *et al.* 1992).

Unlike endoparasites, however, ectoparasites are influenced not only by host characters, but also by

characters of the host environment. Therefore, a habitat of the ectoparasite should not be just a particular host, but a particular host in a particular habitat. If so, an important determinant of parasite community structure should be a complex host–habitat relationship. To investigate the effect of host–habitat relations on parasite–host relations, we studied flea assemblages of rodents in the Ramon erosion cirque (Negev Highlands, Israel).

Fleas (Siphonaptera) are permanent satellites of mammals. They are most abundant and diverse on small and medium-sized burrowing species, alternating the periods when they occur in the fur of their host with the periods when they occur in its burrow or nest. Flea species differ in the range of their hosts (monoxenous and euryxenous species) and in the preferred occurrence in the fur or in the nest of the host ('fur' species and 'nest' species (Ioff, 1941)). This diversity of flea life-histories leads us to predict that different species responded to host–habitat variation in different ways. The main objective of this study was to examine flea assemblages of different rodent species in different habitats within a relatively small area. We investigated the relative importance of host species versus host habitat in determining rodent flea assemblages and asked (a)

\* Corresponding author: Ramon Science Center P. O. Box 194, Mizpe-Ramon 80600, Israel. Tel: +972 7 6588764. Fax: +972 7 6586369. E-mail: krasnov@bgumail.bgu.ac.il.

how flea abundance and species composition on the same host species change among habitats and (b) to what extent flea abundance and species composition in a habitat are determined by host species composition in this habitat and to what extent by environmental characteristics of the habitat itself.

Previous ectoparasitological survey of small mammals of Israel have been conducted by Theodor & Costa (1967). Their study included 66 localities all over the country, including the Ramon cirque. Nevertheless, we believe that a detailed investigation of a relatively small territory allows us to add new data.

## MATERIALS AND METHODS

### *Study area*

The Ramon erosion cirque is an area of about 200 km<sup>2</sup> and is situated at the southern boundary of the Negev Highlands (30°35' N, 34°45' E). The cirque is incised into the crest of a northeast–southwest trending asymmetrical anticline and is a valley surrounded by steep walls of hard rocks (limestone and dolomite) at the top and friable rocks (sandstone) at the bottom. The altitude of the north rim of the cirque ranges between 900 and 1020 m above sea level, while the south rim is about 510 m above sea level. The level of the cirque bottom decreases gradually from the southwest (900 m above sea level) to the northeast and in the deepest part reaches 420 m above sea level.

The climate is characterized by hot, dry summers (mean daily air temperature of July is 34 °C) and relatively cold winters (mean daily temperature of January is 12.5 °C). There is a sharp decrease in annual rainfall from 100 mm on the north rim to 56 mm in the bottom of the cirque. Rainfall also decreases from southwest of the cirque bottom to its northeast (Nativ & Mazor, 1987).

### *Rodent trapping, flea collections and habitat classification*

Rodents were trapped in 1992–1995 on forty-one 1-ha plots which represented the main substrate and vegetation gradients. Seven of these plots were sampled regularly once every 2–3 months during 1992–1993 to estimate seasonal patterns of community organization. Twenty-four plots were sampled twice a year in 1993–1995. Ten other plots were sampled once. Each plot was sampled during 3–5 days using 50 Sherman live-traps placed in a grid at 5 × 5 stations with 2 traps per station with intervals of 20 m between stations. Jerboas (*Jaculus jaculus*) were caught with a net at night using a searchlight. Fat sand rats (*Psammomys obesus*) were caught with Havahart cage traps, model 1025, by placing 2 traps per burrow system. We determined the abundance and species of fleas in each rodent

only when captured the first time. The animal fur was combed thoroughly, using a tooth-brush, over a white plastic bath and fleas were carefully collected. The fur was brushed several times, until no additional fleas were recovered. After this, each rodent was sexed, weighed, marked by toe-clipping and released. Fleas were stored in 70% alcohol.

Habitat types in the Ramon cirque were classified based on the description of 13 environmental variables on 24 long-term plots. There were 3 groups of environmental variables: soil parameters (percentage of rock, gravel and clay components in the upper 10-cm layer of the soil), vegetation parameters (abundance of annual grass, forbs, geophytes and sedges (individuals/m<sup>2</sup>); percent of cover by aphyllous, microphyllous and succulent shrubs and perennial grasses) and relief parameters (altitude above sea level and angle of slope). Soil and vegetation parameters and angle of slope were measured in 25 replicates and averaged for each plot. A 0.5 kg soil sample was taken from each sample point for laboratory texture analysis. The abundance of shrubs and perennial grass clumps (by species) in each sample point was estimated by counting them in a circle, 5 m in radius. Diameter of crown of the shrubs and perennial grass clumps (up to 30 specimens of each species in the plot) was measured to determine respective crown cover. The abundance of annuals was evaluated by counting all annuals on 0.25 m<sup>2</sup> sample subplots (4 sample subplots in each sample point placed at random). Angle of slope was measured in each sample point using a clinometer. Altitudes above sea level were determined from the topographic map 1:50000. All parameters were log-transformed before analysis. Plots were classified using cluster analysis (UPGMA algorithm with Euclidean distance measure).

### *Statistical processing*

It is known that the parasite species richness is dependent on the number of individuals of the host examined (Poulin, 1995; Walther *et al.* 1995). This pattern can be assumed as a particular case of well-known species–area relationship (MacArthur & Wilson, 1967; Rosenzweig, 1995). If so, the relation between the number of parasite species found and the number of individuals of the host examined should be described by linear regression on the log–log plot (Rosenzweig, 1995). We tested this assumption for each host species using random sampling of different sizes from the whole species data pool. We have found good linear fitting for all host species ( $r^2 = 0.72–0.83$ ,  $P < 0.001$  in all cases). This permits us to use the slopes of the regressions (b) of log-number of flea species on log-number of host sample size as indices of flea species richness instead of direct estimations. Obtained indices are free of sample-size errors.

Flea distributions did not conform to the assumptions of parametric tests and could not be transformed to normality (Shapiro-Wilk's tests). Thus, non-parametric statistical analyses were used. Categorical variable (presence of fleas on an examined rodent) was compared using  $\chi^2$  contingency analysis (Zar, 1984). Other variables were analysed using Kruskal-Wallis ANOVA and Kolmogorov-Smirnov two-sample test (Zar, 1984). We applied multi-dimensional non-parametric scaling (Kruskal & Wish, 1978) to ordinate flea assemblages of individual host species, using a matrix of Spearman rank correlation coefficients (Zar, 1984) of host preference between each pair of flea species as input data. Flea assemblages from each individual host were ordinated by principal component analysis (Pielou, 1984). To avoid problems connected with differences in relative abundances of both rodent species and flea species, we calculated weighted average values of intensity of infestation of each rodent species for each flea species and used these values as a data set for principal component analysis (Morrison, Marcot & Mannan, 1992). Axes of ordination space are linear combinations of abundances of each flea species. Thus, the axes present the main directions of change in flea species composition among individual hosts. The axes are obtained independently of host species and habitat affinity.

Some rodent species were excluded from the main part of statistical analysis: *Gerbillus nanus* because of its extremely low numbers and *Mus musculus* and *Jaculus jaculus* because of their extremely low number of fleas. Single observations of a particular flea species on a particular host species were considered as incidental and, although reported, were not analysed.

## RESULTS

### Habitat structure and characteristics

We distinguished 6 main habitat types according to the results of cluster analysis (Fig. 1) as follows: (1) sand dunes with cover of *Calligonum comosum* or *Echiochilon fruticosum* under the eastern wall of the cirque; (2) dry river beds (wadis) of the eastern and central parts of the cirque with sandy-gravel soils and with cover of *Retama raetam*, *Moricandia nitens*, *Tamarix nilotica* and *Artemisia monosperma* among gravel plains (which we will refer to as east wadis); (3) flat gravel plains of the eastern part of the cirque with sparse vegetation of *Hammada salicornica*, *Anabasis articulata* and *Gymnocarpos decandrum*; (4) limestone cliffs and rocks of the eastern and central parts of the cirque with sparse cover of *Zygophyllum dumosum*, *Helianthemum kahiricum* and *Reaumuria hirtella*; (5) complex of narrow wadis and hills of the western part of the cirque covered with thin (up to

20 cm) loess cover with vegetation of *Anabasis articulata*, *Atriplex halimus* and *Artemisia herba-alba* (which we will refer to as west wadis) and (6) complex of loess hills and wide wadis with vegetation of *Anabasis articulata*, *Atriplex halimus*, *Artemisia herba-alba*, *Salsola schweinfurthii* and *Noaea mucronata* over the northern rim of the cirque. Other plots were assigned to one of above habitat types according to their physiognomy. Location of sample plots is shown of Fig. 2. This classification generally coincides with that based on rodent species composition and abundance and is described and discussed elsewhere (Krasnov *et al.* 1996).

Distinguished habitat types differ in a number of features including those that are important for flea survival and maintenance. Main habitat parameters affecting fleas are structure and microclimate of available rodent burrows that are determined by the soil type. The optimal soil for burrowing is loess that allows the construction of complex, deep and stable burrows. Sand soils are less suitable for burrowing due to relative instability of the upper layer of the substrate. Burrows in sandy-gravel soils with high rock content in wadis and plains are more stable than in sands but the property of this substrate does not allow the building of deep and complex burrows. It is not possible to dig in rocky habitats, and rodent shelters there are niches and crevices. Burrow microclimate is determined by both burrow depth and soil type. Loess soils are the best water absorbents among desert substrates. Hydrothermic properties of loess soils in spring are similar to those of meadow soils (Korovin, 1961). Sands have a little bit less water absorption ability than loess has. However, the amplitude of daily variation of the upper layer temperature in sand is higher than in loess. In addition, the humid horizon in sand is characterized by daily vertical migration (Petrov, 1973). Taking into account soil properties together with rainfall and temperature gradient in the cirque (Nativ & Mazor, 1987), we can conclude that the environment of rodent burrows is xeric in habitat types 1–4, mesic in habitat type 6 and intermediate in habitat type 5.

### Rodent species and their flea parasites

There are 12 species of rodents in the Ramon cirque: *Psammomys obesus* Cretzschmar, 1828; *Meriones crassus* Sundevall, 1842; *Gerbillus dasyurus* (Wagner, 1842); *Gerbillus henleyi* (de Winton, 1903); *Gerbillus gerbillus* (Olivier, 1801), *Gerbillus nanus* Blanford, 1875; *Sekeetamys calurus* (Thomas, 1892); *Acomys cahirinus* (Desmarest, 1819); *Acomys russatus* (Wagner, 1840); *Mus musculus* L., 1758; *Jaculus jaculus* (L., 1758) and *Eliomys melamurus* Wagner, 1840.

Eleven flea species were collected including *Xenopsylla conformis mycerini* (Rothschild, 1904);

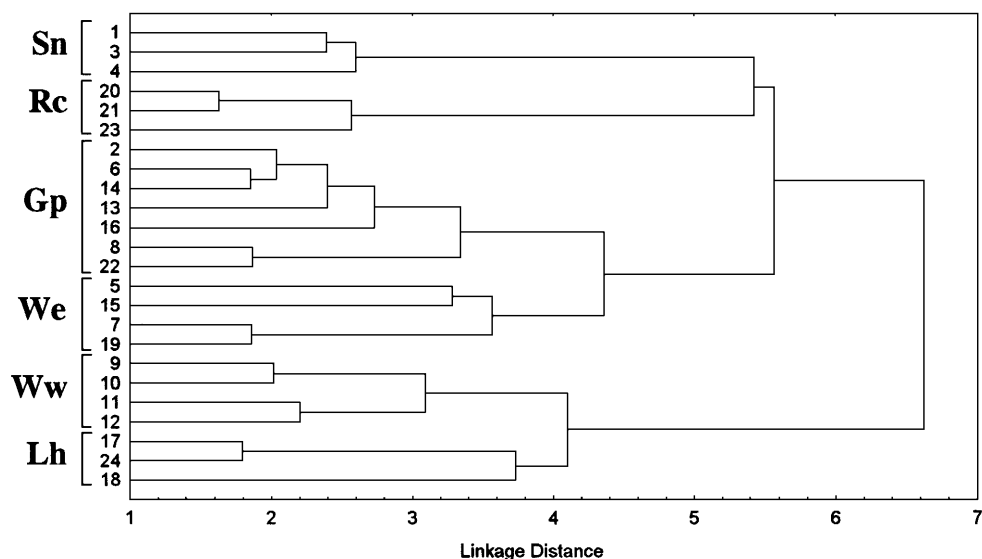


Fig. 1. Dendrogram showing results of cluster-analysis of sample plots based on their similarity in environmental characters. The figures from 1 to 24 are sample plot labels. Habitat types are: Sn – sand dunes, We – east wadis, Gp – gravel plains, Rc – rocks, Ww – west wadis, Lh – loess hills.

Table 1. Fleas collected from different rodent species in the Ramon erosion cirque (Number of individuals in parentheses.)

Rodent species	Flea species
<i>P. obesus</i> (6)	<i>X. ramesis</i> (129), <i>S. tripectinata</i> (3)
<i>M. crassus</i> (151)	<i>X. conformis</i> (1507), <i>X. dipodilli</i> (10), <i>X. ramesis</i> (187), <i>C. africana</i> (4), <i>N. theodori</i> (82), <i>S. tripectinata</i> (8)
<i>G. dasyurus</i> (423)	<i>X. conformis</i> (121), <i>X. dipodilli</i> (647), <i>X. ramesis</i> (38), <i>C. africana</i> (2), <i>N. theodori</i> (349), <i>S. tripectinata</i> (89), <i>R. masculana</i> (20), <i>P. chephrenis</i> (1)
<i>G. henleyi</i> (155)	<i>X. conformis</i> (16), <i>X. dipodilli</i> (6), <i>N. theodori</i> (12)
<i>G. gerbillus</i> (36)	<i>X. conformis</i> (11); <i>L. algira</i> (1)
<i>G. nanus</i> (1)	<i>N. theodori</i> (1),
<i>S. calurus</i> (32)	<i>X. dipodilli</i> (60), <i>N. theodori</i> (14)
<i>A. cahirinus</i> (60)	<i>X. dipodilli</i> (2), <i>X. cheopis</i> (3), <i>N. theodori</i> (10), <i>P. chephrenis</i> (212)
<i>A. russatus</i> (35)	<i>X. dipodilli</i> (2), <i>N. theodori</i> (9), <i>P. chephrenis</i> (75)
<i>M. musculus</i> (92)	–
<i>E. melamurus</i> (16)	<i>M. laverani</i> (68), <i>X. ramesis</i> (1)
<i>Ƴ. jaculus</i> (26)	<i>X. ramesis</i> (2)

*Xenopsylla dipodilli* Smit, 1960; *Xenopsylla ramesis* (Rothschild, 1904); *Xenopsylla cheopis* (Rothschild, 1903); *Coptopsylla africana* Wagner, 1932; *Nosopsyllus theodori* Smit, 1960; *Stenoponia tripectinata medialis* Jordan, 1952; *Rhadinopsylla*

*masculana* Jordan & Rothschild, 1912; *Parapulex chephrenis* Rothschild, 1903; *Myoxopsylla laverani traubi* Lewis 1966 and *Leptopsylla algira costai* Smit, 1955. In total, 1033 rodents were examined and 3702 fleas were collected (Table 1).

#### Patterns of flea distribution on individual hosts

No significant sex- and age-differences were found either in the prevalence (percentage of hosts infested) or in the intensity (number of fleas per infested host) of flea infestation within each rodent species ( $\chi^2 = 1.39\text{--}2.41$  and  $H = 0.001\text{--}0.14$ , respectively;  $n = 16\text{--}423$ ,  $P > 0.3$ ). The same was true for host density dependence of the prevalence or the intensity of infestation ( $\chi^2 = 1.25\text{--}2.05$  and  $H = 0.78\text{--}2.45$ , respectively;  $n = 16\text{--}423$ ,  $P > 0.2$ ). Body masses of infested and uninfested individuals of the same rodent species did not differ significantly (Kolmogorov-Smirnov tests, non-significant). Furthermore, we did not find significant differences in body mass of individual hosts in relation to the intensity of their infestation by fleas ( $H = 6.27\text{--}10.4$ ,  $n = 16\text{--}423$ ,  $P > 0.3$ ).

#### Patterns of flea distribution on different host species

We recorded both host-specialist and host-generalist fleas. Five flea species occurred only on 1 or 2 host species each (*M. laverani*, *P. chephrenis*, *R. masculana*, *C. africana*, *S. tripectinata*), 2 flea species parasitized 4 host species (*X. conformis*, *X. ramesis*) and 2 flea species were found on 6 or 7 host species (*X. dipodilli*, *N. theodori*). Three groups of flea species could be distinguished in relation to taxonomic affinity of their hosts: fleas of gerbillid species

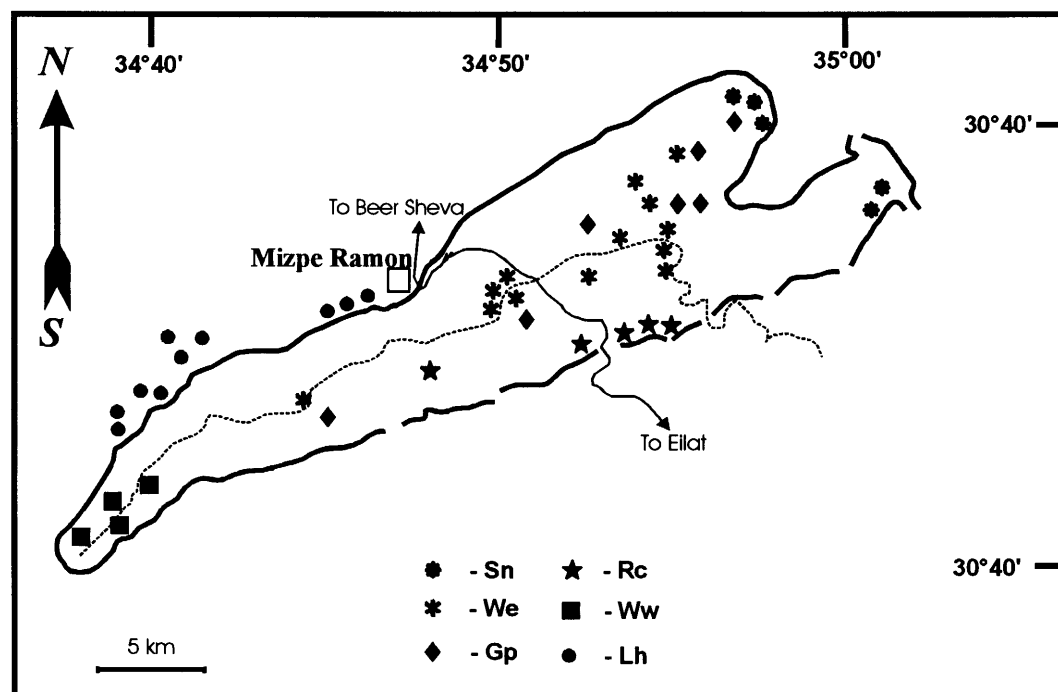


Fig. 2. Map of the Ramon cirque with locations of sampling plots marked. For designation of habitat types see Fig. 1.

Table 2. Estimations of relative richness of flea assemblages of different host species using regression analyses

(Slope of the regression ( $b$ ) of log-number of flea species found on log-number of individuals of the host examined is an index of flea species richness.)

Host species	Regression slope ( $b \pm \text{s.e.}$ )
<i>P. obesus</i>	$0.71 \pm 0.12$
<i>M. crassus</i>	$0.42 \pm 0.04$
<i>G. dasyurus</i>	$0.46 \pm 0.04$
<i>G. henleyi</i>	$0.25 \pm 0.02$
<i>G. gerbillus</i>	$0.30 \pm 0.06$
<i>S. calurus</i>	$0.43 \pm 0.08$
<i>A. cahirinus</i>	$0.31 \pm 0.06$
<i>A. russatus</i>	$0.44 \pm 0.08$
<i>E. melanurus</i>	$0.39 \pm 0.08$
<i>J. jaculus</i>	$0.30 \pm 0.10$

(*X. conformis*, *X. ramesis*, *X. dipodilli*, *N. theodori*, *R. masculana*, *C. africana*, *S. tripectinata*), a flea of murid species (*P. chephrenis*) and a flea of glirid species (*M. laverani*) (Fig. 3).

Host species differed in the number of parasitizing flea species from 1 (*G. gerbillus*) to 7 (*G. dasyurus*). Calculations of indices of flea species richness demonstrated that there was 1 host species (*P. obesus*) with extremely high flea species-richness ( $b = 0.71$ ), whereas other species form a continuum with flea species-richness indices from moderate ( $b = 0.39$ – $0.44$ ) to low ( $b < 0.32$ ) (Table 2). The last group, beside species listed in Table 2, includes also *M. musculus*. No-dependence between index of the relative richness of flea assemblage and either the

number of habitats occupied by the host species or the size of host geographical range was found (regression analyses,  $r^2 = 0.002$ ,  $F = 0.002$ , D.F. = 8,  $P = 0.9$  and  $r^2 = 0.01$ ,  $F = 0.12$ , D.F. = 8,  $P = 0.7$ , respectively). There was significant positive dependence of the index on body mass of the host species ( $r^2 = 0.72$ ,  $F = 20.5$ , D.F. = 8,  $P = 0.002$ ).

Host species differed significantly in both prevalence ( $\chi^2 = 217.2$ ,  $n = 10$ ,  $P < 0.0001$ ) and intensity of infestation ( $\chi^2 = 103.5$ ,  $n = 10$ ,  $P < 0.0001$ ). Prevalence and intensity of infestation were the highest in *P. obesus* and *M. crassus* (Table 3). Prevalence of infestation was the lowest in *Mus musculus*, *J. jaculus* and *G. henleyi*, whereas the intensity of infestation was the lowest in *G. henleyi*, *G. gerbillus* and *J. jaculus* (Table 3).

#### Seasonal patterns of flea distribution

Four of 8 common flea species occurred in all seasons. These were all *Xenopsylla* species (except *X. cheopis* that has been recorded only in a single case) and *P. chephrenis*. *N. theodori*, *S. tripectinata*, *C. africana* and *R. masculana* occurred in the fur of their hosts in the cold season only (November–March). No data on seasonal preference of *M. laverani* are available because its host, *E. melanurus*, was captured in winter only.

No significant between-season variation was found either in the prevalence or in intensity of overall infestation in any host species ( $\chi^2 = 1.12$ – $4.82$  and  $H = 3.47$ – $6.12$ , respectively;  $P > 0.3$ ). Occurrence of winter fleas was different for different rodent species (Table 1). There were no winter fleas on *G. gerbillus*.

Table 3. Prevalence (% individuals with fleas) and intensity (number of fleas per individual) of infestation of different rodent species in the Ramon cirque

Rodent species	Prevalence (%)	Intensity	
		Mean	Interquartile range
<i>P. obesus</i>	100.0	22.17	7.0–30.0
<i>M. crassus</i>	94.7	12.52	5.0–18.0
<i>G. dasyurus</i>	65.0	4.57	1.0–4.0
<i>G. henleyi</i>	11.6	1.89	1.0–2.0
<i>G. gerbillus</i>	22.2	1.37	–
<i>S. calurus</i>	62.5	3.70	1.0–5.0
<i>A. cahirinus</i>	85.0	4.47	2.0–5.0
<i>A. russatus</i>	60.0	3.90	2.0–5.5
<i>M. musculus</i>	0.0	–	–
<i>E. melanurus</i>	56.2	7.00	2.0–9.0
<i>J. jaculus</i>	7.6	1.00	–

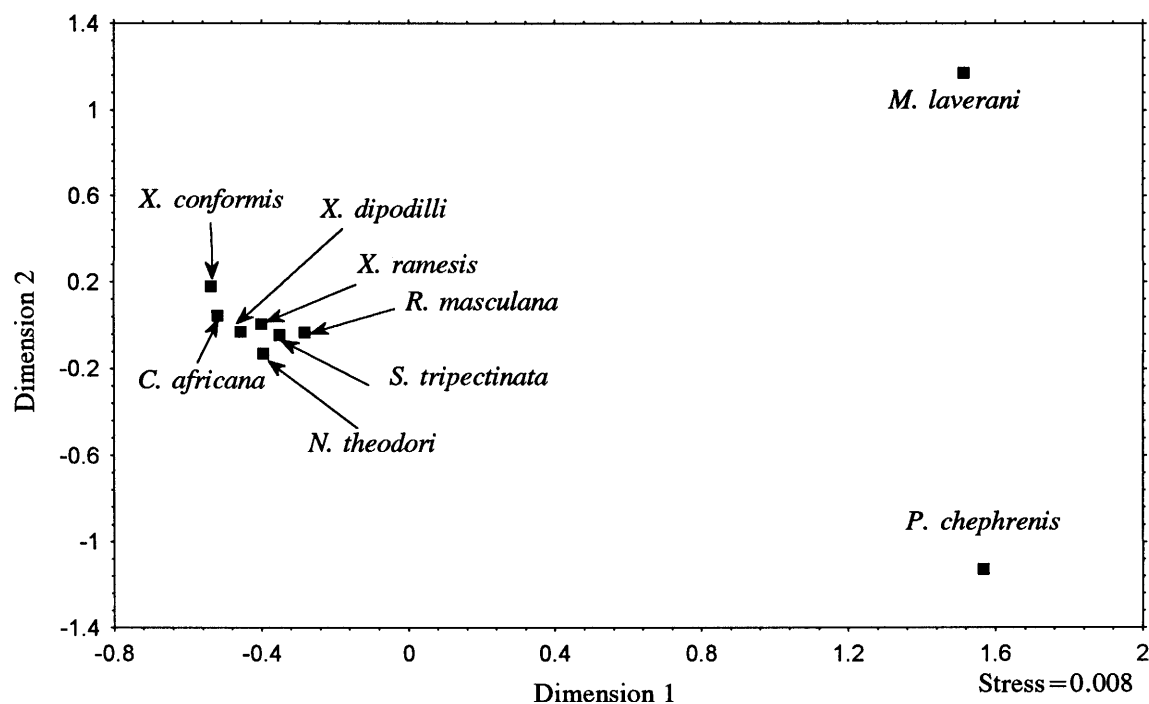


Fig. 3. Distribution of flea species in the ordination space obtained using multidimensional scaling. Non-parametric multidimensional scaling was based on the matrix of similarities (Spearman rank correlation coefficients) in host preferences between each pair of flea species.

*N. theodori* were recorded occasionally on *G. henleyi*, *S. calurus* and both *Acomys* species, whereas *S. tripectinata* was found twice on *P. obesus*. However, the intensity of infestation by all-season fleas did not differ significantly between seasons in these hosts ( $\chi^2 = 2.12-4.31$ ,  $P > 0.3$ ). The same was true for the prevalence of infestation ( $\chi^2 = 3.01-3.92$ ,  $P > 0.2$ ). Intensity of infestation by winter fleas was relatively high in *M. crassus* and *G. dasyurus*. In addition, this parameter for *X. dipodilli* decreased significantly from summer to winter in these two host species ( $0.12 \pm 0.02$  fleas per host versus  $0.04 \pm 0.02$  and  $3.54 \pm 0.45$  versus  $1.23 \pm 0.21$ , respectively;  $P < 0.0001$  for both).

#### Flea distribution in different habitats

Habitat distribution of rodent species in the Ramon cirque was described in detail elsewhere (Krasnov *et al.* 1996). Here, we present only general information on habitat preferences of different species (Table 4). Six of 9 host species that we analysed occurred in more than 1 habitat. No significant among-habitat variation in flea abundance and species composition was found in *P. obesus* and *A. russatus*.

*G. henleyi*, in sand dunes in all seasons, had only 1 flea species (*X. conformis*), whereas in other habitats it had also *X. dipodilli* (east wadis in winter and gravel plains in summer) and *N. theodori* (east wadis

Table 4. Average rodent density (individuals per 1 ha) in main habitat types of the Ramon cirque

(Habitat types are 1 – sand dunes, 2 – east wadis, 3 – gravel plains, 4 – rocks, 5 – west wadis, 6 – loess hills.)

Species	Habitat types					
	1	2	3	4	5	6
<i>P. obesus</i>	0.00	0.00	0.00	0.00	0.12	10.39
<i>M. crassus</i>	4.81	1.12	0.05	0.00	0.42	1.86
<i>G. dasyurus</i>	0.00	4.58	0.20	0.75	3.58	9.33
<i>G. henleyi</i>	0.73	1.56	1.70	0.00	0.04	0.00
<i>G. gerbillus</i>	4.47	0.00	0.00	0.00	0.00	0.00
<i>G. nanus</i>	0.00	0.01	0.00	0.00	0.00	0.00
<i>S. calurus</i>	0.00	0.00	0.00	1.43	0.00	0.00
<i>A. cahirinus</i>	0.00	0.02	0.00	1.27	0.08	0.18
<i>A. russatus</i>	0.00	0.12	0.00	0.63	0.00	0.00
<i>M. musculus</i>	0.00	0.02	0.00	0.00	0.04	0.50
<i>J. jaculus</i>	0.33	0.27	0.75	0.00	0.75	0.00
<i>E. melanurus</i>	0.00	0.00	0.00	0.00	0.09	0.44

in winter). The relatively low infestation of *G. henleyi* did not permit statistical comparison of its flea assemblages among habitats.

*A. cahirinus*, in all its habitats, was infested mainly by *P. chephrenis*. This host was rarely infested by *X. dipodilli* and *N. theodori* in rocky sites (in summer and winter, respectively). We have single records of *X. cheopis* and *S. tripectinata* in loess hills on *A. cahirinus* (both in winter).

Both prevalence and intensity of overall infestation by fleas in *G. dasyurus* differed significantly among habitats in summer ( $\chi^2 = 17.8$ , and  $H = 10.6$ , respectively, D.F. = 4,  $P < 0.001$ ), but did not differ in winter ( $\chi^2 = 4.6$ , D.F. = 4,  $P = 0.32$  and  $H = 5.3$ , D.F. = 4,  $P = 0.25$ , respectively). In summer, the highest fraction of infested individuals was recorded in gravel plains (81.2%) and the lowest in east wadis (46.5%), whereas the intensity of infestation was the highest in rocky habitats ( $5.17 \pm 1.12$ ) and the lowest in gravel plains ( $1.42 \pm 0.32$ ). Prevalence as well as intensity of infestation of *G. dasyurus* by most flea

species differed statistically among habitats in both seasons (Table 5, Fig. 4). In summer, *G. dasyurus* was parasitized mainly by *X. dipodilli*, while sub-dominant flea species were *X. conformis* in east wadis and gravel plains and *X. ramesis* in west wadis and loess hills. In winter, abundance of *X. dipodilli* decreased significantly ( $H = 47.8$ , D.F. = 223,  $P < 0.0001$ ) and *N. theodori* predominated in all habitats but rocks. *G. dasyurus* inhabiting west wadis and loess hills were infested also by *X. ramesis*, *C. africana*, *S. tripectinata* and *R. masculana*.

Almost all individuals of *M. crassus* in all habitats were infested by fleas all year round (Table 6), while the intensity of overall infestation differed significantly among habitats in winter only ( $H = 43.2$ , D.F. = 4,  $P < 0.0001$ ; Fig. 5), being the lowest in loess hills ( $5.22 \pm 0.81$ ). In addition, the intensity of infestation by individual flea species differed significantly among-habitats both in winter and in summer ( $H = 12.6-24.2$  and  $H = 10.5-79.5$ , respectively, D.F. = 4,  $P < 0.01$  for both). *X. conformis* was dominant on *M. crassus* in sand dunes, east wadis and gravel plains, whereas in west wadis it occurred alongside with *X. ramesis*. In loess hills *X. conformis* was replaced by *X. ramesis* completely (Fig. 5). *X. dipodilli* was recorded occasionally on this host in all habitats but loess hills (this species was absent also in west wadis in winter). The most diverse flea assemblage occurred in west wadis where we recorded 3 species in summer (*X. conformis*, *X. dipodilli* and *X. ramesis*) and 5 species in winter (*X. conformis*, *X. ramesis*, *C. africana*, *N. theodori* and *S. tripectinata*).

The results of the ordination of the flea collections from each individual host demonstrated that the flea assemblages were segregated mainly along 4 axes, which explained 86% of total variance (Table 7). The contribution of the first axis exceeded that of the second axis by 1.5 times and that of both the third and the fourth axes by 3 times. The contributions of the third and the fourth axes were almost the same. Each of the ordination axes corresponded with a

Table 5. Prevalence of infestation of *G. dasyurus* (%) by different flea species in different habitats

((Number of examined individuals in parentheses.). Xc – *X. conformis*, Xd – *X. dipodilli*, Xr – *X. ramesis*, Ca – *C. africana*, Nt – *N. theodori*, St – *S. tripectinata*, Rm – *R. masculana*, Pc – *P. chephrenis*; seasons are s – summer, w – winter. N.S. Non-significant; \* $P < 0.01$ . Data by seasons are presented only for all-seasonal species.)

Season	Flea species											
	Xc		Xd		Xr		Ca	Nt	St	Rm	Pc	
	s	w	s	w	w	s	w	w	w	w	s	w
East wadis (192)	21.8	19.8	30.7	25.0	0.0	1.0	1.0	57.3	1.0	0.0	0.0	0.0
Gravel plains (25)	10.5	0.0	63.2	0.0	0.0	0.0	0.0	17.6	0.0	0.0	0.0	0.0
Rocks (58)	2.5	10.7	77.5	64.3	0.0	3.6	0.0	39.3	3.6	3.6	2.5	0.0
West wadis (46)	4.3	8.7	65.2	26.4	4.3	0.0	4.3	69.6	34.8	4.34	0.0	0.0
Loess hills (91)	0.0	2.0	48.8	12.0	29.3	16.0	0.0	50.0	30.0	16.0	0.0	0.0
$\chi^2$ among habitats	19.8*	10.7*	31.5*	27.2*	17.6*	17.8	–	6.8 <sup>N.S.</sup>	38.7*	18.2*	–	–

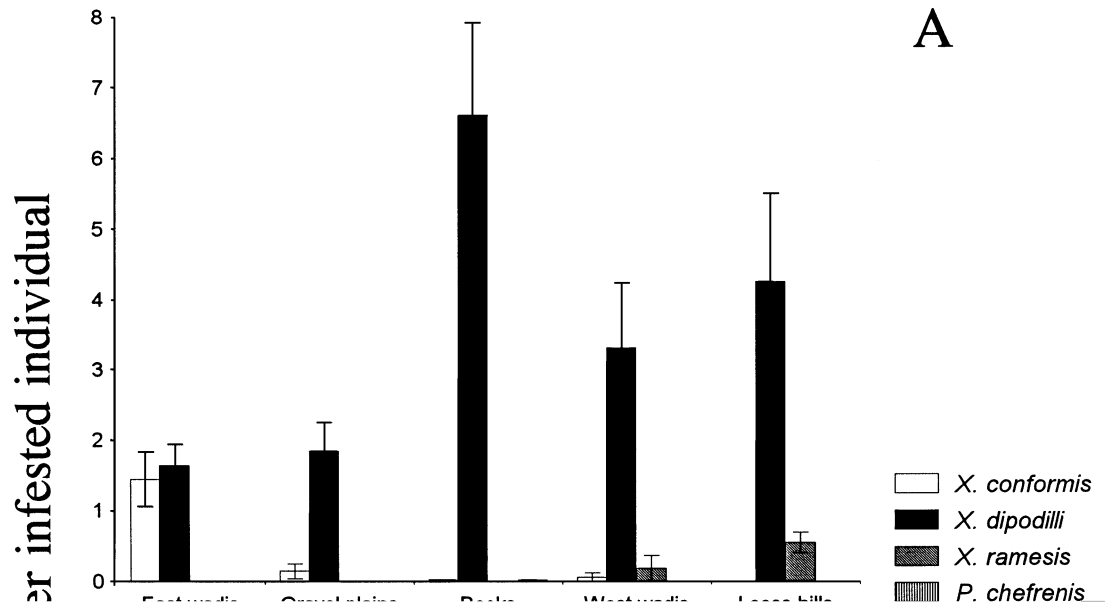


Fig. 4. Intensity of infestation of *Gerbillus dasyurus* by different flea species in different habitats. (A) Summer, (B) winter. Vertical lines are  $\pm$ S.E.

change in flea species composition. The first axis represented the change from *X. dipodilli*, *N. theodori*, *S. tripectinata* and *R. masculana* on gerbils (positive zone of the first axis) to *P. chephrenis* on *Acomys*. This change is illustrated by segregation of *G. dasyurus*, *S. calurus* and partly *G. henleyi* from *Acomys* species along the first axis (Fig. 6). The second axis responded mainly to fleas of *M. crassus* (*X. conformis* and *C. africana*). So, *M. crassus* was distanced from all other host species to the positive zone of the second axis (Fig. 6). The third and the fourth axes were correlated with the relative abundances of *X. ramesis* and *M. laverani*, respectively, and thus, they determined positions of *P. obesus* and *E. melamurus*, respectively.

Flea collections plotted according to their habitat occurrences in the space of the same axes demonstrated that 5 directions of shift in flea species composition could be distinguished (Fig. 7). These directions of shift were (1) from rocky habitats to east wadis and sand dunes along the first axis (gradient of rodent burrow availability); (2) the shift in flea composition within east wadis along the first axis (among-host species from *G. dasyurus* to *M. crassus*); (3) the shift in flea composition within rocky habitats along the first axis (among-host species from gerbillids to murids); (4) from sand dunes and east wadis to west wadis and loess hills along the second axis (gradient of soil humidity and temperature) and (5) the shift in flea species composition within loess



Table 6. Prevalence of infestation of *Meriones crassus* (%) by different flea species in different habitats

((Number of examined individuals in parentheses.) Xc – *X. conformis*, Xd – *X. dipodilli*, Xr – *X. ramesis*, Ca – *C. africana*, Nt – *N. theodori* and St – *S. tripectinata* ; seasons are s – summer, w – winter. n.s. Non-significant, \*  $P < 0.01$ . Data by seasons are presented only for all-seasonal species.)

Season	Flea species								
	Xc		Xd		Xr		Ca	Nt	St
	s	w	s	w	w	s	w	w	w
Sand dunes (24)	87.5	93.3	0.0	6.7	0.0	0.0	6.7	20.0	0.0
East wadis (74)	100.0	85.0	2.8	2.5	0.0	0.0	0.0	65.0	0.0
Gravel plains (24)	100.0	76.9	0.0	7.7	0.0	0.0	0.0	0.0	0.0
West wadis (7)	66.6	25.0	66.6	0.0	66.6	100	75	100	100
Loess hills (21)	33.3	0.0	0.0	0.0	100	100	0.0	16.6	5.5
$\chi^2$ among habitats	2.3 <sup>n.s.</sup>	6.5 <sup>n.s.</sup>	25.9*	4.8 <sup>n.s.</sup>	45.2*	78.0*	43.4*	31.7*	72*

habitats along the third axis (among-host species from gerbils to *Acomys* and dormouse).

## DISCUSSION

### *Ecological aspects of host–flea relations*

We have found that the larger the rodent species the richer the fauna of fleas it can maintain. A similar pattern was reported for gill parasites of fish *Labeo coubie* (Guegan & Hugueny, 1994) and explained mainly by species-area effect. In contrast, in desert rodents this effect can be easily explained by evident direct relation between their size and depth and complexity of burrow systems. Complex and deep burrow systems of large rodents provide specific microclimate conditions that are relatively independent on aboveground environment and are favourable for many flea species (Kucheruk, 1983). Surprisingly, we did not find any relationship between flea species richness and breadth of host species distribution both in habitat and geographical aspects. Local richness of specific parasites, such as fleas, is determined primarily by both environmental conditions and co-evolutionary history of a host and its parasites (Rall, 1960). Thus, broad comparisons of flea species richness across different rodent taxa can not reveal local habitat patterns because the latter are camouflaged by more general factors. Nevertheless, the comparison of two congeneric host species of the same size (*G. dasyurus* and *G. gerbillus*) shows that habitat generalist (*G. dasyurus*) comprises more flea species than habitat specialist (*G. gerbillus*) does. It is well known that parasite species diversity is associated with host geographical range (e.g. Pavlinov *et al.* 1990; Shenbrot *et al.* 1995). The explanation of the absence of a relationship between host geographical range and its flea species richness in our study can be that this pattern is revealed considering the whole geographical range of a host rather than its local population.

Six of 10 analysed rodent species occupy more than 1 habitat type. Four of these 6 species did not demonstrate any among-habitat variation in their flea assemblages. The absence of this variation can reflect either strong dependence of a particular flea species on a particular host species or just statistical inadequacy of our data. It seems that the second explanation is more likely. *G. henleyi* that is abundant in our samples from different habitat types has very low ectoparasite burden, so extremely large samples are needed for validation of any trend. Three species (*P. obesus*, *A. cahirinus* and *A. russatus*) are recorded in several habitat types, but are numerous really in 1 of them, so our sample sizes were adequate for only primary habitat types for each species. Both the above causes are equally true for 2 species that we did not analyse (*M. musculus* and *J. jaculus*).

Two species (*G. dasyurus* and *M. crassus*) are representative for the analysis of among-habitat variation in patterns of flea parasitism, and this variation was revealed in both. The differences in pattern of flea parasitism among habitat types within host species can be determined by both environmental features of a habitat and specific pattern of habitat use by rodents. For example, all individuals of *G. dasyurus* in gravel plains are transients (Khokhlova *et al.* 1994). They can collect fleas during short-term visits to other rodents' burrows, but can not maintain fleas for a long time due to absence of their own burrows. This can explain the highest prevalence together with the lowest intensity of infestation of *G. dasyurus* in this habitat type. The nests of *G. dasyurus* in rocky habitats are constructed in deep crevices and niches. They sustain intake during a long period and are not subjected to either flooding or destruction by predators. The result is high infestation of this rodent in rocks. The opposite is true for east wadis where burrows are regularly flooded.

The results of this study support the hypothesis of host–habitat relations and provide evidence that

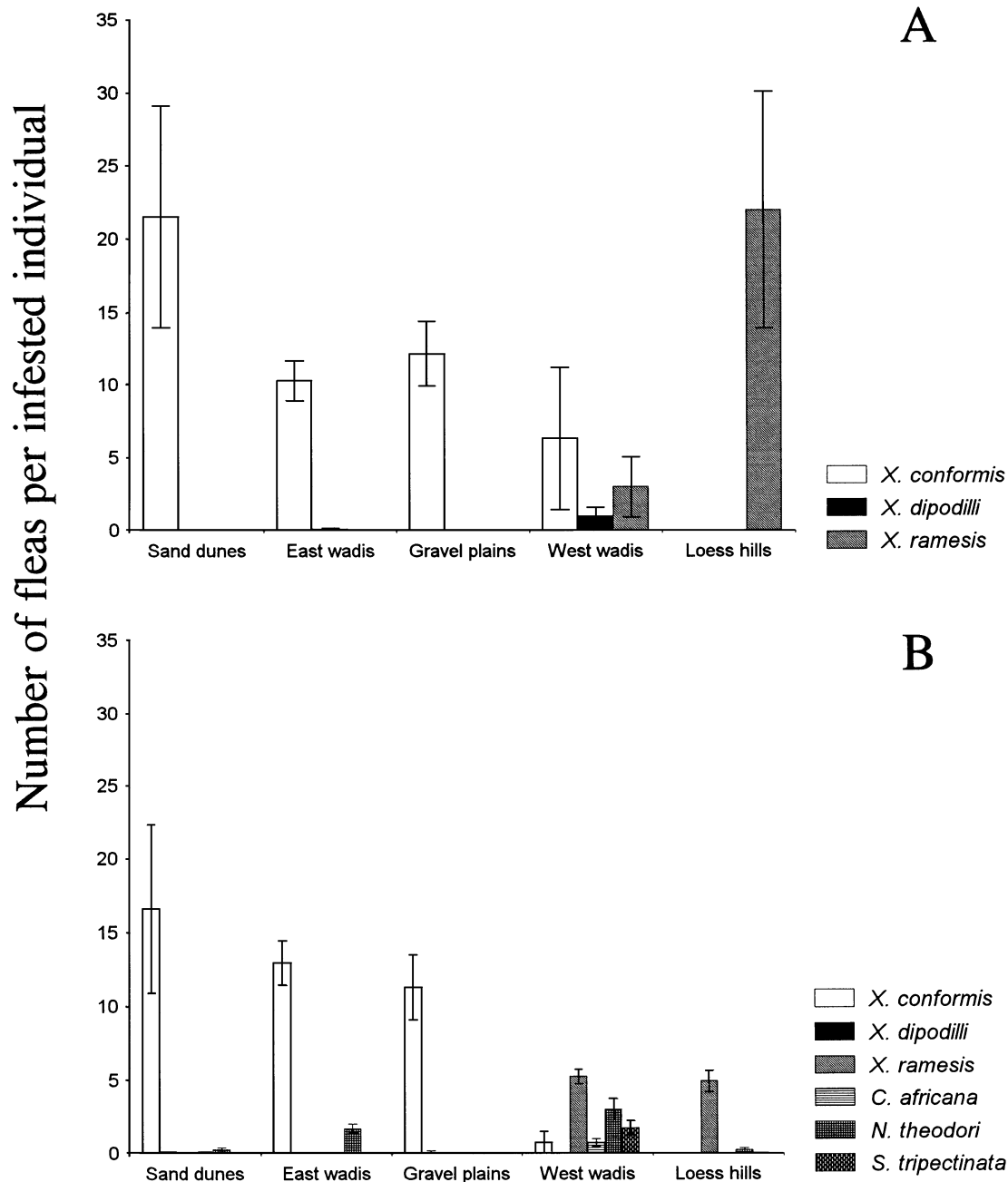


Fig. 5. Intensity of infestation of *Meriones crassus* by different flea species in different habitats. (A) Summer, (B) winter. Vertical lines are  $\pm$ s.e.

species compositions of fleas on a host species is determined not only by host-specificity of flea species, but also by host-habitat relations. There were both host-dependent fleas and host-habitat-dependent fleas. Furthermore, even the first group suggests that the relatively strong host specificity is also environmentally restricted. For example, *P. chephrenis*, which parasitized *Acomys* rodents in all habitats in our study, can be considered as a highly host-dependent species. Nevertheless, this flea does not occur on *A. cahirinus* throughout its entire distribution within Israel; it occurs only in the southern region and in the Jordan Valley north to Lake Tiberias, where climatic conditions are similar

to those of southern Israel (Theodor & Costa, 1967). It should be mentioned that *A. cahirinus* and *A. russatus* do not build deep burrows but live in rock crevices and between stones. The latter results in the strong dependence of a flea on an individual host, on one hand, and its relatively high susceptibility to climatic conditions, on the other hand.

*X. conformis* and *X. ramesis* on *M. crassus* exemplify host-habitat-dependent fleas. *X. conformis* parasitized *M. crassus* in the habitats with sandy-gravel soils whereas it was replaced by *X. ramesis* in the habitats with loess soils. Both species occur on the soils of intermediate character, although their abundances were relatively low. It seems that the

Table 7. Summary of principal component analysis of the positions of flea collections from each individual host in the ordination space

(\* Indicates coefficient of correlation > 0.7.)

Information		Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue		3.4905	1.9214	1.2236	1.1124
Percentage of variance explained		36.36	23.39	13.18	13.16
Linear correlation (r) between each ordination axis and abundance of each species in the observation vector	<i>X. conformis</i>	0.06	0.98*	0.03	0.03
	<i>X. dipodilli</i>	-0.81*	-0.15	0.01	-0.01
	<i>X. ramesis</i>	0.22	-0.12	-0.90*	0.15
	<i>C. africana</i>	-0.17	0.95*	0.03	0.04
	<i>N. theodori</i>	-0.88*	0.22	0.18	0.18
	<i>S. tripectinata</i>	-0.89*	0.17	0.03	0.03
	<i>R. masculana</i>	-0.91*	0.02	0.01	0.01
	<i>P. chephrenis</i>	0.71*	-0.30	0.75*	0.59
	<i>M. laverani</i>	0.23	-0.16	0.18	-0.88*

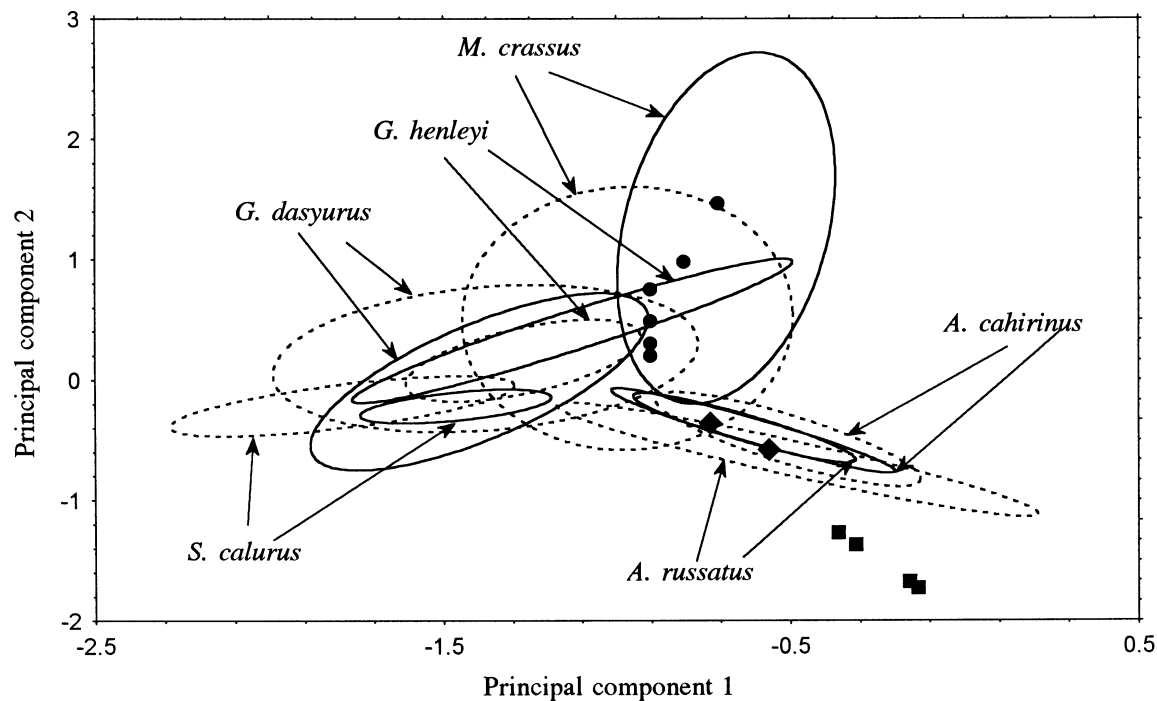


Fig. 6. 75% confidence ellipses for flea assemblages from each examined animal in the space of two first principal component axes according to the host species. (—) Summer; (---) winter. Data for *Psammomys obesus* (■), *Gerbillus gerbillus* (●) and *Eliomys melanurus* (◆) are presented for both seasons.

distribution of these fleas conforms to the distinct-preference model of community organization (Pimm & Rosenzweig, 1981). The pattern of among-habitat distribution of these two fleas on *G. dasyurus* was the same, except that, in contrast to *M. crassus*, *X. conformis* and *X. ramesis* were subdominants whereas *X. dipodilli* was dominant.

In addition, there were also fleas in which host- or host-habitat dependence were weakly expressed. For example, *N. theodori* occurred on 7 host species in all habitat types.

Therefore, flea species composition in a habitat is determined not only by host species composition,

but also by some environmental parameters of the habitat itself. These parameters determine the conditions of the burrow or the nest of the host (temperature, humidity, material) and, thus, affect the flea assemblage. The composition of flea community of the study area is determined by 2 directions of change in flea species composition, namely among-hosts within a habitat and among-habitats within a host. The first direction of change can be illustrated by the different flea composition between gerbils (*G. dasyurus* and *S. calurus*) and murids (*A. cahirinus* and *A. russatus*) within rocky habitats and between *M. crassus* and *G. dasyurus*

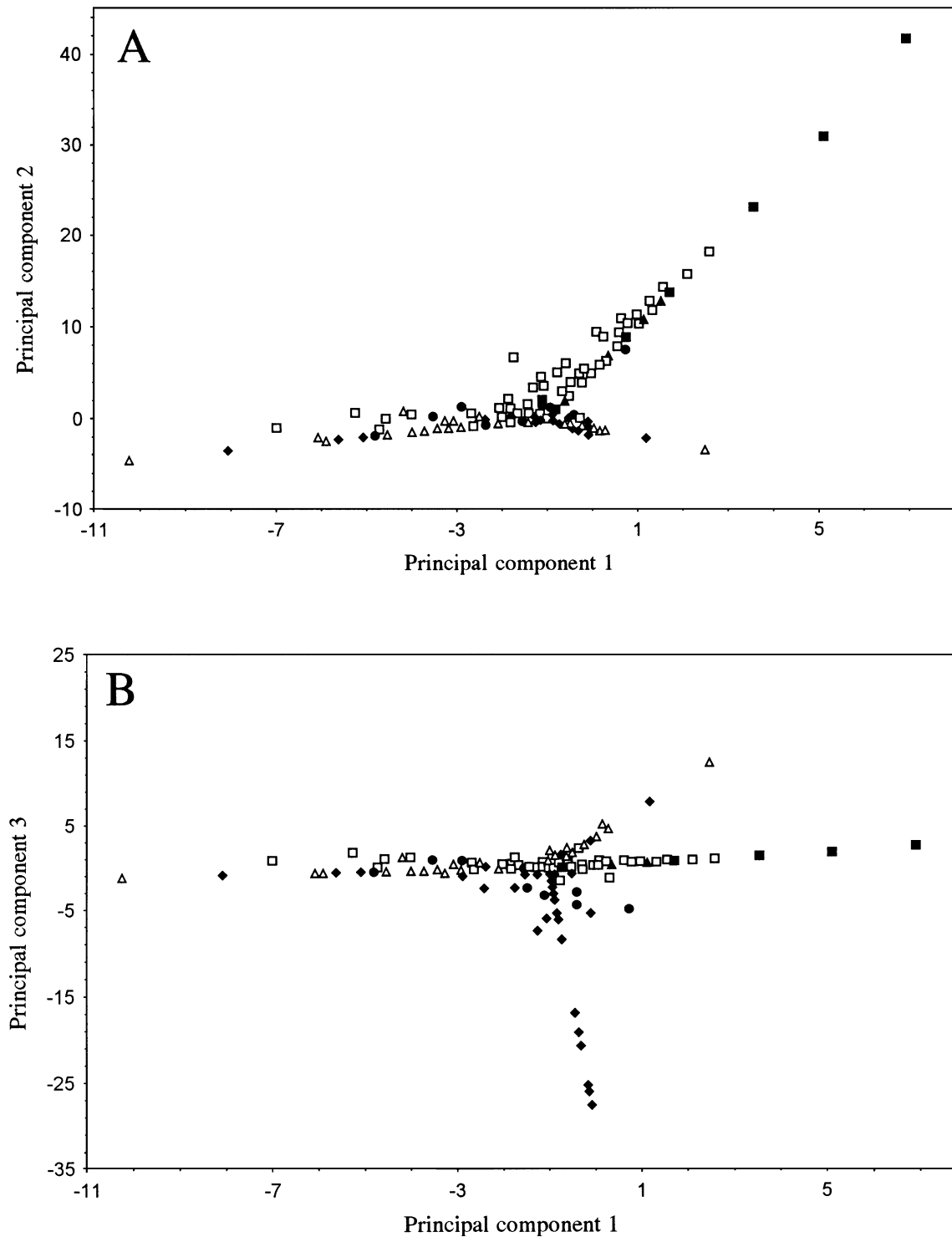


Fig. 7. Scatterplots for flea assemblages from each examined animal in the space of the first and the second (A) and the first and the third (B) principal component axes according to habitat type. Habitat types are sand dunes (■), east wadis (□), gravel plains (▲), rocks (△), west wadis (●) and loess hills (◆).

within east wadis. The second direction of change is demonstrated by different fleas on *M. crassus* and *G. dasyurus* in east wadis, west wadis and loess hills.

The highest flea species richness on *M. crassus* and *G. dasyurus* in west wadis supports the hypothesis that the environment is an important determinant of flea assemblage composition. Soil- and vegetation-structure characteristics of west wadis are inter-

mediate between those of east wadis and loess hills (Krasnov & Shenbrot, 1996). Thus, these conditions are suitable for both flea species groups; those preferring xeric east wadis (*X. conformis*) and those preferring mesic loess hills (*X. ramesis*, *R. masculana*, *S. tripectinata*). Details of ecological physiology and environmental demands of studied flea species are unknown. Nevertheless, we can speculate that west

wadis should be considered as suboptimal for both flea species groups, because their relative abundances in west wadis are lower than those in their respective optimal habitats.

#### Seasonal dynamics

Seasonal dynamics of a particular flea species depends on the features of the reproductive biology of the flea. Fleas are traditionally subdivided to 'summer' and 'winter' species according to their phenology (e.g. Wagner, 1939; Ioff, 1941; Ioff & Scalon, 1965; Nazarova, 1981). Summer fleas usually spend winter in the host's nest in reproductive diapause (Vatschenok, 1988) and, thus, their abundance on the hosts decreases. This subdivision is agreeable with a seasonal environment. In a subtropical desert like the Negev, the winter fleas can be distinguished (*C. africana*, *N. theodori*, *R. masculana*, *S. tripectinata*), whereas most other fleas occur all year round (*X. conformis*, *X. ramesis*, *P. chephrenis*). The absence of strong seasonality in these species can be explained by the relatively warm winters in the study region. The beginning and the termination of reproduction of fleas has been shown to be affected by the ambient temperature (Ioff, 1941). For example, the percentage of reproducing females in populations of *X. conformis* in different areas of Caucasus in February and November was strongly correlated with mean monthly temperatures (Kadatskaya & Tschirova, 1983). It seems, that winter temperature in Negev is not sufficiently low to affect the reproduction of those species that are considered to be 'summer' in strongly seasonal environments.

#### Geographical aspects of host–flea relations

Results of this study provided additional information for the survey of Siphonaptera in Israel (Theodor & Costa, 1967). For example, most fleas collected hitherto from *P. obesus* in Israel were *X. conformis*, whereas in the Ramon cirque the dominant flea of this host was *X. ramesis*, which has been considered as a parasite of *Meriones tristrami* and *Meriones libycus* in dry steppes (Lewis, 1982; Lewis & Lewis, 1990). The southern border of *X. ramesis* was designated about 60 km north of the Ramon cirque (Theodor & Costa, 1967). Nevertheless, this flea was recorded on *P. obesus* in Egypt (Lewis, 1967a). We have found *X. ramesis* on *G. dasyurus* also, although earlier collections of fleas from this rodent in Israel did not include this species.

*C. africana* has previously been found in Israel once only and was known hitherto only from Tunisia (Theodor & Costa, 1967). The checklist of fleas of Egypt does not include this species (Lewis, 1967a). Launay & Beaucournu (1987) argued that the occurrence of *C. africana* in Israel is questionable,

because only a single female was found. In our study, 4 males and 2 females of *C. africana* were found on *G. dasyurus* and *M. crassus*, indicating that the geographical range of this flea is broader than was previously thought.

*R. masculana* was known to date in Israel from a single collection from *G. dasyurus* (Theodor & Costa, 1967), whereas in Egypt it was found on *P. obesus* and *M. libycus* (Hoogstraal & Traub, 1965, Lewis, 1967a). We recorded *R. masculana* from 10 individuals of *G. dasyurus*, which is congruent with Lewis & Lewis' (1990) statement that it is a common parasite of this gerbil. The relative rarity of *R. masculana* in collections from rodents can be explained by the preference of this flea for the nest and not the fur of its host (Lewis, 1967a).

The principal hosts for *S. tripectinata* in Israel were considered to be *M. tristrami* occurring on heavy soils (subspecies *S. t. spinellosa*) and the psammophilous species of genus *Gerbillus* (subspecies *S. t. acmaea*) (Theodor & Costa, 1967). The subspecies *S. t. medialis*, which we found here, has been described from jirds of genus *Meriones* inhabiting sandy soils (Theodor & Costa, 1967). These data led Theodor & Costa (1967) to hypothesize that *S. t. medialis* should be considered as an ecological modification of *S. t. spinellosa* when its *Meriones* hosts live on sands. Our findings of *S. t. medialis* mainly on *G. dasyurus* and *M. crassus* in the habitats with stony-loess soils far apart from sand dunes did not support ecological evidence of the hypothesis of the taxonomic identity of *S. t. spinellosa* and *S. t. medialis*.

The recording of *L. algira costai*, albeit a single individual from a single individual of the host, is noteworthy. This was the first record of this flea (1) south of Jerusalem, (2) from *G. gerbillus* and (3) from a sandy habitat. *L. algira costai* has been described from Israel and recorded earlier on *Crocidura suaveolens*, commensal *Mus musculus* (Theodor & Costa, 1967), *Rattus rattus*, *M. tristrami* and *Meriones shawi* (Lewis & Lewis, 1990). Some problems of synonymy need to be noted here. *Crocidura suaveolens* was referred to as *Crocidura russula* by Theodor & Costa (1967). The last taxonomic revision of genus *Crocidura* in Israel showed that *C. russula* was absent from the East Mediterranean and that all specimens originally referred to this species were *C. suaveolens* (Catzeflis *et al.* 1985). *M. shawi* is a typical species of the Mediterranean coast of North Africa that had never been reported in Israel. Its range does not extend east of the Nile valley (Pavlinov *et al.* 1990). Specimens from Jordan, originally referred to as *M. shawi* were re-identified later as *M. libycus* (Harrison & Bates, 1991).

*G. gerbillus* inhabiting dunes of the Ramon cirque were not infested with fleas specific for psammophilous gerbils of Israel (*Synosternus cleopatrae*, *S.*

*t. acmaea*, *Nosopsyllus sinaiensis* (Theodor & Costa, 1967)). This can be explained by the relatively young age of the dunes in the Ramon, their aeolian origin and the isolation from main sand habitats of southern Israel (Plakht, personal communication).

No dipodid-specific flea species (genera *Mesopsylla*, *Desertopsylla*, *Ophtalmopsylla*, *Hopkinsipsylla* (Goncharov, 1985) were found on *J. jaculus*. Theodor & Costa (1967) have recorded *Ophtalmopsylla volgensis palestinica* on *J. jaculus* once only; other fleas were *Xenopsylla nubica*, *X. conformis* and *Synosternus cleopatrae*, which are specific for gerbillid rodents. It should be noted that all individuals of *J. jaculus* studied by the above-mentioned authors were collected in sands of the coastal plain and dunes of the Negev Desert. *O. volgensis* has also been collected from *J. jaculus* in northern Arabia (Lewis, 1964, 1982), Jordan and Syria (Lewis & Lewis, 1990). Seven flea species were recorded for *J. jaculus* in Egypt; none of them was specific for dipodids (Lewis, 1967a), whereas other Egyptian jerboas (*Jaculus orientalis* and *Allactaga tetradactyla*) were commonly parasitized by the host-specific fleas *Mesopsylla tuschkan propinacta* and *Hopkinsipsylla occulta occulta*. In the checklist of the fleas of the Middle East, 9 species parasitizing *J. jaculus* were reported and only 1 of them was the host-specific *O. volgensis*, whereas rodents of the genus *Allactaga* were reported to be parasitized by specific *O. volgensis* and *Mesopsylla apscheronica* only (Lewis & Lewis, 1990). It seems that *J. jaculus* does not have its own specific flea species, but it obtains fleas sporadically by contact with other rodents (including co-existing jerboas) and their burrows.

The Ramon erosion cirque is considered as part of the Ramon-Zohar line, a proposed biogeographical border between Irano-Turanian and Saharo-Arabian phytogeographic provinces (Zohary, 1964; Ward & Olswig-Whittaker, 1993). Attempts to match this line with animal distribution did not provide evidence for zoogeographic subdivision at this high level (Shenbrot, Krasnov & Khokhlova, 1994). Nevertheless, the flea fauna of rodents of this area provides circumstantial support for the consideration that the Ramon is a junction of different biogeographic units. In spite of the relatively small area studied, fleas of different geographic origin were recorded as follows. Central and North Asian species were represented by *X. conformis* and *N. theodori*. The latter is close to the Asian *Nosopsyllus iranensis* and sometimes is considered as a subspecies of the latter (Lewis, 1967b; Theodor & Costa, 1967; Lewis & Lewis, 1989, 1990). North African elements were *X. ramesis*, *C. africana* and *R. masculana*. Ethiopian species were represented by *P. chephrenis* (monoxenous parasite of murine rodents of the genus *Acomys*) and *X. dipodilli* (closely related to Ethiopian *Xenopsylla nubica*), while the Mediterranean and West European element is presented by *M. laverani*.

There were also species with a broad geographical range, namely *X. cheopis* and *S. tripectinata*. The latter has recently been found south of Sahara (Senzota, 1992).

We thank V. Matin (Saint-Petersburg) and N. Darskaya (Moscow) for their help in flea identification. Professor A. Degen and Dr D. Ward (Ben-Gurion University of the Negev) read the earlier version of the manuscript and made helpful comments. This study was supported by the Ministry for Science and Art of Israel and Ministry for New Immigrant Absorption of Israel (B.R.K. and G.I.S.). This is publication 47 of Ramon Science Center and 98 of Desert Animal Adaptations and Husbandry.

#### REFERENCES

- BELL, G. & BURT, A. (1991). The comparative biology of parasite species diversity: intestinal helminths of freshwater fishes. *Journal of Animal Ecology* **60**, 1046–1063.
- BUCHMAN, K. (1991). Relationship between host size of *Anguilla anguilla* and the infection level of the monogeneans *Pseudodactylogyrus* spp. *Journal of Fish Biology* **35**, 599–601.
- CATZEFLIS, F., MADDALENA, T., HELLWING, S. & VOGEL, P. (1985). Unexpected findings on the taxonomic status of East Mediterranean *Crocidura russula* auct. (Mammalia, Insectivora). *Zeitschrift für Säugetierkunde* **50**, 185–201.
- GUEGAN, J. F. & HUGUENY, B. (1994). A nested parasite species subset pattern in tropical fish: host as major determinant of parasite infracommunity structure. *Oecologia* **100**, 184–189.
- GUEGAN, J. F., LAMBERT, A., LEVEQUE, C. & EUZET, L. (1992). Can host body size explain the parasite species richness in tropical freshwater fishes? *Oecologia* **90**, 197–204.
- GONCHAROV, A. I. (1985). On fleas parasitizing jerboas. In *Distribution and Ecology of Jerboas of the USSR Fauna* (ed. Sokolov, V.), pp. 189–194. USSR Academy of Science Publications, Moscow. (In Russian.)
- HARRISON, D. & BATES, P. (1991). *The Mammals of Arabia*. Harrison Zoological Museum Publication, Sevenoaks.
- HOOGSTRAAL, H. & TRAUB, R. (1965). The fleas (Siphonaptera) of Egypt. Host-parasite relationships of cricetid rodents (Family Cricetidae, Subfamily Gerbillinae). *Journal of the Egyptian Public Health Association* **40**, 141–175.
- IOFF, I. G. (1941). *Ecology of Fleas in Relevance to their Medical Importance*. Piatigorsk Publishers, Piatigorsk. (In Russian.)
- IOFF, I. G. & SCALON, O. I. (1965). *A Handbook for Identification of Fleas of Middle Asia and Kazakhstan*. Meditzina Publishers, Moscow. (In Russian.)
- KADATSKAYA, K. P. & TSCHIROVA, L. F. (1983). Seasonal changes in reproduction in fleas *Xenopsylla conformis* in Azerbaijan. In *Prophylactic of Diseases of Natural Foci* (ed. Suchkov, J. G. & Taran, I. F.), pp. 238–240. Anti-plague Institute of Caucasus Publications, Sravropol. (In Russian.)
- KHOKHLOVA, I., KRASNOV, B., SHENBROT, G. & DEGEN, A. (1994). Factors determining the pattern of seasonal

- body mass change in several rodents from the Ramon erosion cirque (Negev Highlands, Israel). *Zoologicheskii Zhurnal* **73**, 106–114. (In Russian.)
- KOROVIN, E. P. (1961). *Vegetation of Middle Asia and Southern Kazakhstan*. Uzbekistan Academic Science Press, Tashkent. (In Russian.)
- KRASNOV, B. & SHENBROT, G. (1996). Spatial structure of community of darkling beetles (Coleoptera: Tenebrionidae) in the Negev Highlands, Israel. *Ecography* **19**, 139–152.
- KRASNOV, B., SHENBROT, G., KHOKHLOVA, I. & IVANITSKAYA, E. (1996). Spatial patterns of rodent communities in the Ramon erosion cirque, Negev Highlands (Israel). *Journal of Arid Environments* **32**, 319–327.
- KRUSKAL, J. B. & WISH, M. (1978). *Multidimensional Scaling*. Sage Publications, Beverly Hills.
- KUCHERUK, V. V. (1993). Mammal burrows – structure, usage and typology. *Fauna and Ecology of Rodents* **15**, 5–54. (In Russian.)
- KURIS, A. M., BLAUNSTEIN, A. R. & AHO, J. J. (1980). Hosts as islands. *The American Naturalist* **116**, 570–586.
- LAUNAY, H. & BEAUCOURNU, J.-C. (1987). Coptosyllidae Africaines: repartition, morphologie, statut taxonomique et relations phyletiques avec les autres representants de la famille. *Annales de Parasitologie Humaine et Comparée* **62**, 159–173.
- LEWIS, R. E. (1964). A collection of fleas (Siphonaptera) from northern Saudi Arabia. *Journal of Parasitology* **50**, 313–318.
- LEWIS, R. E. (1967a). The fleas (Siphonaptera) of Egypt. An illustrated and annotated key. *Journal of Parasitology* **53**, 863–885.
- LEWIS, R. E. (1967b). Contributions to a taxonomic revision of the genus *Nosopsyllus* Jordan 1933 (Siphonaptera: Ceratophyllidae). I. African species. *Journal of Medical Entomology* **4**, 123–142.
- LEWIS, R. E. (1982). Insects of Saudi Arabia. Siphonaptera. A review of the Siphonaptera of the Arabian peninsula. *Fauna of Saudi Arabia* **4**, 450–462.
- LEWIS, R. E. & LEWIS, J. H. (1989). A catalogue of invalid or questionable genus-group and species-group names in the Siphonaptera (Insecta). *Theses Zoologicae* **11**, 1–263.
- LEWIS, R. E. & LEWIS, J. H. (1990). An annotated checklist of the fleas (Siphonaptera) of the Middle East. *Fauna of Saudi Arabia* **11**, 251–277.
- M.CARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- MORRISON, M. L., MARCOT, B. G. & MANNAN, R. W. (1992). *Wildlife-Habitat Relationships: Concepts and Applications*. The University of Wisconsin Press, Madison.
- NATIV, R. & MAZOR, E. (1987). Rain events in an arid environment – their distribution and ionic and isotopic composition patterns: Makhtesh Ramon basin, Israel. *Journal of Hydrology* **89**, 205–237.
- NAZAROVA, I. V. (1981). *Fleas of Volga-Kama Region*. Nauka Publishers, Moscow. (In Russian.)
- PAVLINOV, I., DUBROVSKY, Y., ROSSOLIMO, O. & POTAPOVA, E. (1990). *Gerbils of the World*. Nauka Publishers, Moscow. (In Russian.)
- PETROV, M. P. (1973). *Deserts of the World*. Nauka Press, Leningrad. (In Russian.)
- PIELOU, E. C. (1984). *The Interpretation of Ecological Data*. John Wiley & Sons, New York.
- PIMM, S. L. & ROSENZWEIG, M. L. (1981). Competitors and habitat use. *Oikos* **37**, 1–6.
- POULIN, R. (1995). Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs* **65**, 283–302.
- PRICE, P. W. (1990). Host populations as resource defining parasite community organization. In *Parasite Communities: Patterns and Processes* (ed. Esch, G., Bush, A. & Aho, J.), pp. 21–40. London: Chapman & Hall.
- RALL, Y. M. (1960). *Rodents and Natural Nidi of Plague*. Medical Publishing House, Moscow. (In Russian.)
- ROSENZWEIG, M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- SENZOTA, R. B. M. (1992). Rodent ectoparasites in the Serengeti National Park, Tanzania. *Tropical Ecology* **33**, 29–33.
- SHENBROT, G., KRASNOV, B. & KHOKHLOVA, I. (1994). Patterns of animal distribution at the boundary of two biogeographical zones as possible indicator of Global Climate Changes: an example with beetles, lizards and rodents at the Ramon-Zohar line (Central Negev). In *Annual Meeting of the Ecological Society of Israel* (ed. Maman, Y.), pp. 77–78, Ecological Society of Israel, Tel-Aviv.
- SHENBROT, G. I., SOKOLOV, V. E., HEPTNER, V. G. & KOVALSKAYA, Y. M. (1995). *Mammals of Russia and Adjacent Regions. Dipodoid Rodents*. Nauka Press, Moscow. (In Russian.)
- THEODOR, O. & COSTA, M. (1967). *A Survey of the Parasites of Wild Mammals and Birds in Israel. (I) Ectoparasites*. Jerusalem: Israel Academy of Science and Humanities, Jerusalem.
- VATSCHENOK, V. S. (1988). *Fleas – Vectors of Pathogens Causing Diseases in Humans and Animals*. Nauka Publishers, Leningrad. (In Russian.)
- WAGNER, J. (1939). *Aphaniptera. Klassen und Ordnungen des Tierreichs*. Leipzig.
- WALTHER, B. A., COTGREAVE, P., PRICE, R. D., GREGORY, R. D. & CLAYTON, D. H. (1995). Sampling effort and parasite species richness. *Parasitology Today* **11**, 306–310.
- WARD, D. & OLSWIG-WHITTAKER, L. (1993). Plant species diversity at the junction of two desert biogeographic zones. *Biodiversity Letters* **1**, 172–185.
- ZAR, J. H. (1984). *Biostatistical Analysis*, 2nd Edn. Prentice-Hall, London.
- ZOHARY, M. (1964). *Plant Life of Palestine*. Ronald Press, New York.