

# Geographic variation in the role of gerbils and jirds (Gerbillinae) in rodent communities across the Great Palaeartic Desert Belt

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## Introduction

The Great Palaeartic Desert Belt is the largest desert area in the world, extending from the Atlantic coast of northwest Africa in the west to northeastern China in the east. Environmental conditions (including climate, landscape and vegetation types) of different parts of this belt differ significantly both due to their distinct geographic positions and as a result of unique geological histories (PETROV, 1973). Consequently, significant faunal changes take place along the belt (for rodent biogeography of the Palaeartic desert belt, see SHENBROT *et al.*, 1999). The Gerbillinae is the only rodent taxon represented across the whole belt, although its species richness and species composition varies geographically. In many deserts of the Old World, gerbils and jirds are important components of ecosystems and in some cases they can be agricultural pests and reservoirs of

dangerous diseases such as plague and cutaneous leishmaniasis (PAVLINOV *et al.*, 1990).

The aim of this paper is to review and quantify patterns of geographic variation in the relative importance of Gerbillinae across the Great Palaeartic Desert Belt using both biogeographic and ecological approaches.

## I Material and methods

### *Biogeography*

We restricted our analysis to the species that we consider to belong to desert faunas and we analyzed the distribution of these species within the borders of the Palaeartic desert zone only. We considered a species as a desert species if its geographical range is either entirely or mostly located in the desert and if it occupies zonal desert habitats rather than intrazonal ones (mountains, river valleys and lake shores). The taxonomic composition for different rodent groups followed PAVLINOV *et al.*, (1990) for Gerbillinae, SHENBROT *et al.*, (1995) for Dipodoidea and WILSON and REEDER (1993) for other rodents. In total, we analyzed the distribution of 109 rodent species in Palaeartic deserts. For each of these species we compiled a geographic range map based on data published in the following regional monographs: North Africa - RANCK (1968), OSBORN and HELMY (1980), LE BERRE (1990), and KOWALSKI and RZEBIK-KOWALSKA (1991); Southwest Asia - LAY (1967), HASSINGER (1973), ROBERTS (1977), HARRISON and BATES (1991), CORBET and HILL (1992), SHALMON (1993), and QUMSIYEH (1996); Central Asia (former USSR) - BOBRINSKY *et al.* (1965), SLUDSKY *et al.* (1969, 1977, 1978), YANUSHEVICH *et al.* (1972), and GROMOV and ERBAJEVA (1995); Mongolia and China - BANNIKOV (1954), SOKOLOV and ORLOV (1980), and MA *et al.* (1987). Finally, we divided each map of a species distribution by a 2° by 2° grid, and compiled a list of rodent species for each grid cell.

## Ecology

Analysis of community composition requires a preliminary ecological classification of all the species in the community. Such a classification is meaningful if it is based on those characters and features that facilitate resource partitioning among coexisting species. Thus, ecological classification has to be based on the type of resources that are used (diet composition) and on the conditions of resource acquisition in space (habitat distribution) and time (activity patterns).

Our ecological data were obtained over the last twenty years in the course of studying desert rodent communities. Data were collected in 1980-1982 and 1989-1990 in the Kyzylkum Desert (Uzbekistan), in 1984-1988 in the Gobi Desert (Mongolia), in 1989 in the Thar desert (India) and in 1992-1999 in the Negev Desert (Israel). Rodents were trapped on 1-ha plots that were chosen to represent main substrate and vegetation gradients. The number of sampled plots was 24 in the Southern Kyzylkum (39°33'-39°41'N, 64°35'-64°43'E), 22 in South-Western Kyzylkum (39°37'-40°38'N, 62°31'-64°00'E), 26 in Northern Gobi (44°46'-47°31'N, 92°23'-100°59'E), 18 in Western Gobi (42°50'-44°23'N, 96°36'-100°15'E), 26 in Eastern Gobi (42°34'-44°52'N, 104°19'-111°07'E), 15 in Thar (26°-28°N, 73°-75°E), 24 in central Negev (30°22'-30°52'N, 34°27'-35°03'E) and 24 in northern Negev (30°52'-31°17'N, 34°17'-34°49'E). Each plot was sampled for three consecutive days using 50 Sherman live-traps or Museum Special snap-traps placed in a grid of 5 x 5 stations with two traps per station and an interval of 20 m between stations. Jerboas were caught with a net at night using a searchlight. Large jirds (*Psammomys*, *Rhombomys* and some *Meriones*) and ground squirrels (*Spermophilus* and *Spermophilopsis*) which usually avoid traps were counted in the morning using binoculars. Each trapped animal was sexed, weighed and either marked by toe-clipping and released or collected to analyze reproductive condition and stomach content and for subsequent museum deposition.

To analyze relationships between rodent distribution and abundance and parameters of the environment, we described a set of environmental variables around each trap station. To make analyses of the spatial structure of rodent communities from different deserts as comparable as possible, our approach was standardized by measuring almost the same set of environmental variables in each study area.

The total number of measured or derived variables varied from 18 to 24 in the different deserts. Three of these variables described the mechanical composition of the soil, six the abundance and composition of annual plants and geophytes, and the remainder characterized the structure of the perennial vegetation. The last mentioned group of environmental variables comprised cover by perennial grasses, aphyllous, microphyllous and succulent shrubs and the volume of shrub crowns in 4 or 5 vertical layers.

We classified our sample plots into habitat types using both similarities in environmental parameters and in rodent species composition. Details of analysis were published earlier (KRASNOV *et al.*, 1996; SHENBROT *et al.*, 1999). Species were considered as habitat specialists if they occurred in only one or two similar (e.g. stabilized and semi-stabilized sand dunes) habitats and as habitat generalists in other cases.

Diet was identified using stomach content analysis. Stomach content was examined under a stereoscopic dissection microscope, and food remains were divided into four categories, namely seeds, green parts of vegetation, underground parts of vegetation (bulbs and roots) and animal remains. The amount of each food category in each stomach was estimated visually as a percentage of the total volume with 5%-accuracy. We classified species by their diets as granivorous or folivorous if the primary food types (seeds or green parts of vegetation, respectively) comprised not less than 80% of diet by volume. Otherwise, a species was classified as omnivorous (if all food types were represented in its diet more or less equally) or mixivorous (if the diet was the mixture of two or three food types).

## Results and discussion

### *Biogeography*

The results of zoogeographical analysis demonstrate that the Gerbillinae are represented in all Palaearctic deserts. The greatest number of coexisting gerbil and jird species (11-13 species) is observed

in the relative narrow strip along the Mediterranean coast of North Africa (fig. 1). High Gerbillinae species richness (9-10 species) is recorded in the northern and central parts of the Sahara Desert, and moderate species richness (7-8 species) is typical for most other parts of the Sahara, central parts of Arabian Peninsula and Iranian deserts. Species richness decreases slightly towards the southern borders of the North African and Arabian deserts and much more sharply in a northeastern direction within Asian deserts.

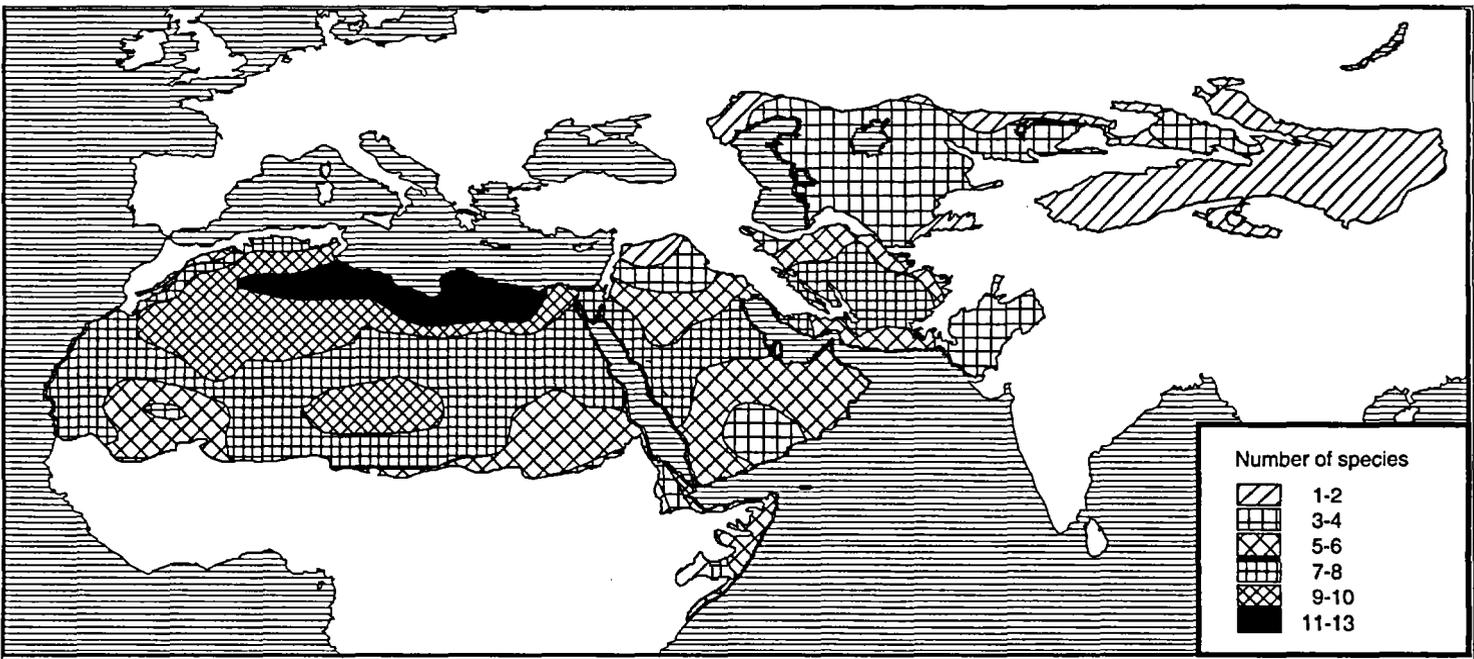
Gerbil and jird species richness varies within Palaearctic deserts from 1 to 13 species, whereas general rodent species richness in this region varies from 5 to 22 species (SHENBROT *et al.*, 1999). Due to this, patterns of geographic variation of the proportion of Gerbillinae in Palaearctic desert rodent faunas generally match the patterns of Gerbillinae species richness (fig. 2). Gerbillines comprise the largest fraction of the entire rodent fauna (50-70%) in most parts of the Sahara and in eastern Arabia. This fraction decreases to the south, to the north-west and to the north-east, comprising 30-50% of all rodents in the peripheral parts of the Sahara and in the deserts of the Horn of Africa, Arabia, Iran and Sind, 10-30% in Turanian deserts and less than 10% in the Gobi desert. These patterns can be explained mainly by the history of Gerbillinae: their origin and early stages of radiation took place in Africa, whereas their Asian history is much shorter (PAVLINOV *et al.*, 1990).

## *Community structure*

### **Quantitative community parameters**

The results of estimations of quantitative parameters for some Palaearctic desert rodent communities based on our data are presented in table I. In the Negev and Thar communities, gerbils and jirds dominate both in relative abundance (the Gerbillinae fraction represents 86-96% of all rodent individuals) and in relative biomass (89-98% of all rodent biomass). Nevertheless, the fraction of Gerbillinae in these faunas is not especially high (62-64% in the Negev and 40% in the Thar Desert). Thus, the important role of Gerbillinae in the Negev and Thar communities in terms of relative abundance and biomass is determined by the fact that most gerbil and jird species

Figure 1  
Species richness  
of Gerbillinae in  
Palaearctic deserts.



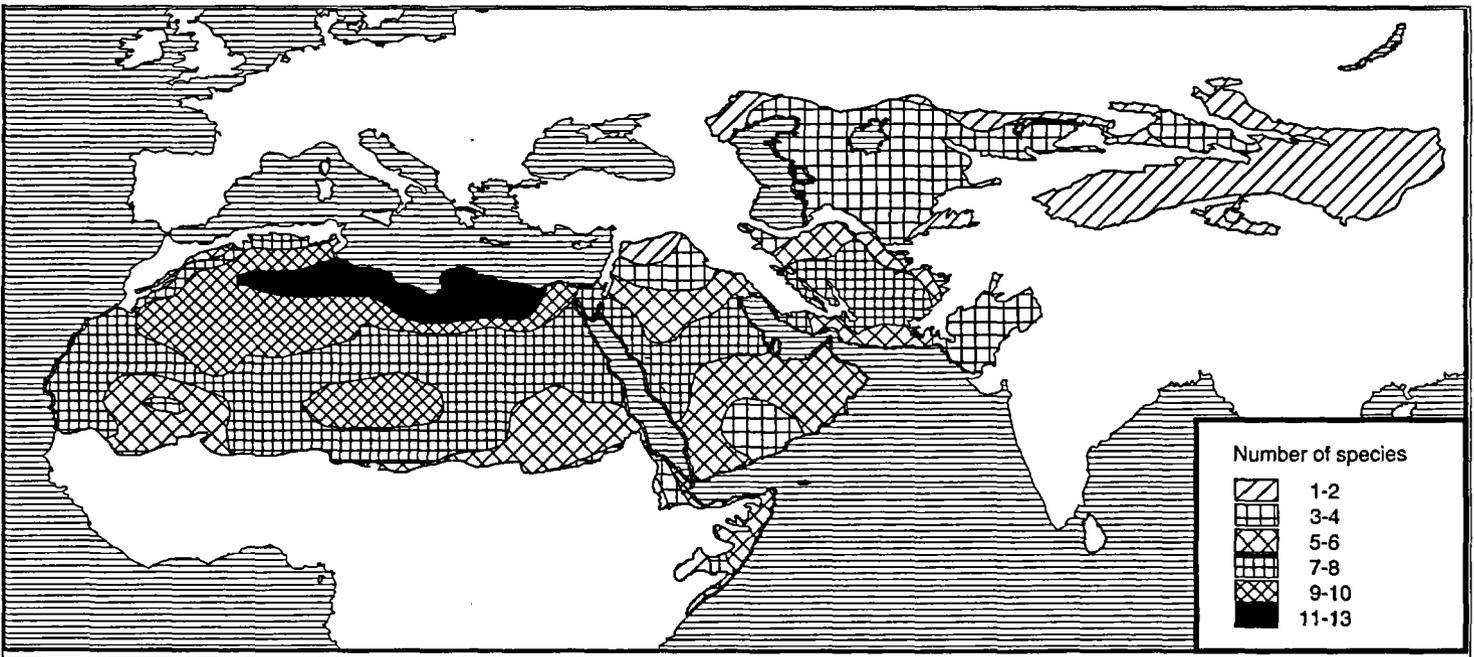


Figure 2  
 Fraction of Gerbillinae  
 species in taxonomic  
 composition of  
 Palearctic desert  
 rodent faunas.

are numerous and also that jirds have relatively large body mass. Unfortunately, there are no comparable data on Saharan desert rodent communities (with density and biomass estimations of all rodents including jerboas and ctenodactylids and taking into account the whole spectrum of habitats at a place). Provisional analysis of data on the specimens composition in local samples and in owl pellets published in regional monographs (e.g. KOWALSKI and RZEBIK-KOWALSKA, 1991) showed that relative Gerbillinae abundance in the Sahara varies in most cases within limits of 80-90%. Considering the above data and faunal composition, it is possible to hypothesize that the pattern that was revealed for the Negev and Thar deserts would be typical for the entire Saharo-Sindian desert region.

The role of Gerbillinae in Palaearctic desert rodent communities decreases in a northeastern direction. Gerbillinae continue to be the dominant rodent group in Turan deserts (Kyzylkum) both in terms of relative abundance and biomass (58-72% and 55-73%, respectively) despite comprising relatively little (21-23%) of the community taxonomic composition. Further to the east, in the Gobi Desert, Gerbillinae become a minor fraction of rodent communities in terms of all estimated parameters. This is especially true for the eastern Gobi (table 1).

### Qualitative community composition

The diet of Gerbillinae in Thar, Kyzylkum and Gobi deserts is presented in table II. Based on these data, we can classify *Gerbillus gleadowi* and *G. nanus indus* as granivores, *Meriones hurrianae*, *M. erythrorurus*, *M. meridianus*, and *Tatera indica* as mixivores, and *Rhombomys opimus* as a folivore. Unfortunately, we have no comparable data on the diet of Gerbillinae in the Negev desert. However, available information (BAR *et al.*, 1984; DEGEN *et al.*, 1986, 1988; KHOKHLOVA *et al.*, 1995), as well as our observations on gerbil feeding in captivity suggest that *Gerbillus gerbillus* and *G. henleyi* are granivores, *Gerbillus andersonii*, *G. pyramidum*, *G. dasyurus*, *Meriones crassus*, and *M. sacramenti* are mixivores, *Sekeetamys calurus* is an omnivore, and *Psammomys obesus* is a folivore. Thus, there are two types of feeding mode among Gerbillinae in each of the rodent communities of Kyzylkum, Gobi and Thar deserts. In the communities of the Negev desert gerbillines are more diverse with respect to

Region	Species richness		Rodent density (ind/ha)	Relative Gerbillinae abundance (in %)	Rodent biomass (kg/ha)	Relative Gerbillinae biomass (in %)
	All rodents	Gerbillinae				
N. Negev	13	8	13.3	89.9	1.54	88.5
C. Negev	11	7	11.7	85.9	1.31	95.8
Thar	10	4	55.5	95.8	5.88	98.3
S. Kyzylkum	13	3	16.9	72.2	1.39	73.0
S.W. Kyzylkum	14	3	15.4	58.4	1.24	54.6
N. Gobi	17	3	13.3	33.5	1.20	38.9
W. Gobi	14	2	13.5	16.0	1.06	23.2
E. Gobi	14	2	18.9	9.0	1.56	13.3

Table 1  
Quantitative parameters of some rodent communities  
of Palaeartic deserts

diet (three types of feeding mode in the northern Negev and four types of feeding mode in the central Negev).

There are two main groups of desert rodents in terms of habitat selection, namely habitat generalists and habitat specialists. In turn, habitat specialists can be subdivided into three subgroups, namely psammophiles (specialist sand dwellers), petrophiles (specialist rock dwellers) and sclerophiles (specialist occupants of open plains with hard clay substrate). Some habitat generalists with extensive geographic ranges narrow their habitat distribution towards the periphery of their range where they demonstrate habitat specialisation (for a review, see SHENBROT *et al.*, 1999). Table 3 provides a summary of our data on habitat selection of Gerbillinae in the studied Palaeartic desert rodent communities (see SHENBROT, 1992; ROGOVIN *et al.*, 1994; SHENBROT *et al.*, 1994; ROGOVIN and SHENBROT, 1995; SHENBROT and ROGOVIN, 1995; KRASNOV *et al.*, 1996; KRASNOV and SHENBROT, 1998; SHENBROT *et al.*, 1999 for details). No sclerophilous species and only one petrophilous species (*Sekeetamys calurus*, Negev Desert) were found among gerbils and jirds. Most Gerbillinae species are habitat generalists. The fraction of psammophiles varies from three species in the northern Negev to one species in the central Negev and Thar deserts. There are no psammophilous jirds in Kyzylkum Desert. *Rhombomys opimus*, which is

Species	Region	Sample size	Food type				Source
			Insects	Seeds	Bulbs	Green	
<i>T. indica</i>	Thar	122	10.83	18.75	47.08	23.33	2
<i>G. gleadowi</i>	Thar	9	0	93.75	0	6.25	1
<i>G. n. indus</i>	Thar	6	0	93.00	0	7	1
<i>M. hurrianae</i>	Thar	172	5.83	34.17	36.25	23.75	2
<i>M. erythrourus</i>	Kyzylkum	64	6.64	48.67	2.81	41.87	1
<i>M. meridianus</i>	Kyzylkum	71	4.51	60.992	0.70	33.80	1
<i>M. meridianus</i>	Gobi	63	7.70	67.22	3.17	21.90	1
<i>R. opimus</i>	Kyzylkum	24	1.67	3.33	13.54	81.46	1
<i>R. opimus</i>	Gobi	15	2.15	4.76	11.32	81.77	1

Table 2

Diet composition (percentages by fresh volume) of Gerbillinae in some Palaearctic deserts. Sources of information:

1 – our data, 2 – PRAKASH, 1993.

a strict sand dweller in the Gobi desert but occupies diverse habitats in the Kyzylkum Desert, represents a typical case of habitat generalist with peripheral decrease in habitat breadth. Thus, there are three types of habitat selection among Gerbillinae in the central Negev, two types in the northern Negev and Thar and only one type in the Kyzylkum and Gobi deserts.

One jird species with diurnal activity always exists in each desert rodent community, whereas all other species are nocturnal. Such diurnal species are *Psammomys obesus* in the Negev Desert, *Rhombomys opimus* in the Kyzylkum and Thar deserts and *Meriones hurrianae* in the Thar Desert. It is important to note that these diurnal jird species construct more complex and extensive burrow systems than nocturnal species. In desert rodents diurnal activity usually correlates with sociality. So, existence of such complex burrow systems can be explained by its additional function to provide enough room for family groups together with other common functions (place for nest and food storage, safe access to aboveground food resources, refuges from predators, etc.) (SHENBROT *et al.*, 1999). These burrows provide a specific environment and refuge for a number of invertebrate and small vertebrate species and can be considered as sites of “environmental engineering”.

Region	Type of habitat selection			
	Habitat generalists	Psammophyles	Petrophytes	Sclerophyles
Negev	<i>Gerbillus dasyurus</i> <i>Gerbillus henleyi</i> <i>Meriones crassus</i> <i>Meriones tristrami</i> <i>Psammomys obesus</i> 1 Myoxidae sp. 1 Dipodidae sp. 1 Muridae sp.	<i>Gerbillus andersoni</i> <i>Gerbillus gerbillus</i> <i>Gerbillus pyramidum</i> <i>Meriones sacramenti</i>	<i>Sekeetamys calurus</i> 2 Muridae sp.	1 Dipodidae sp.
Thar	<i>Tatera Indica</i> <i>Gerbillus nanus</i> <i>Meriones hurrianae</i> 1 Sciuridae sp. 3 Muridae sp.	<i>Gerbillus gleadowi</i>	2 Muridae sp.	
Kyzylkum	<i>Meriones erythrorus</i> <i>Meriones meridianus</i> <i>Rhombomys opimus</i> 2 Sciuridae sp. 2 Dipodidae sp. 1 Arvicolidae sp. 1 Cricetidae sp. 1 Muridae sp.	3 Dipodidae sp.		3 Dipodidae sp.
Gobi	<i>Meriones meridianus</i> 1 Sciuridae sp. 4 Dipodidae sp. 2 Arvicolidae sp. 4 Cricetidae sp.	<i>Rhombomys opimus</i> 2 Dipodidae sp.	1 Arvicolidae sp. 1 Cricetidae sp.	2 Dipodidae sp.

Table 3  
Types of habitat selection  
in some Palaearctic desert rodent communities.

Combining the above three classifications, we calculated the final ecological classification of the Gerbillinae. Local communities of gerbils and jirds consist of five ecological groups in the central Negev, four groups in the northern Negev and Thar Desert, and two groups in the Kyzylkum and Gobi deserts (table 4).

Region	Habitat generalists				Psammophytes			Petrophytes
	Nocturnal		Diurnal		Nocturnal		Diurnal	Nocturnal
	Granivores	Mixivores	Mixivores	Folivores	Granivores	Mixivores	Folivores	Omnivores
N. Negev	<i>G. henleyi</i> <i>M. tristrami</i>	<i>G. dasyurus</i> <i>M. crassus</i>		<i>P. obesus</i>		<i>G. andersoni</i> <i>G. pyramidum</i> <i>M. sacramenti</i>		
C. Negev	<i>G. henleyi</i>	<i>G. dasyurus</i> <i>M. crassus</i>		<i>P. obesus</i>	<i>G. gerbillus</i>			<i>S. calurus</i>
Thar	<i>G. nanus</i>	<i>T. indica</i>	<i>M. hurrianae</i>		<i>G. gleadowi</i>			
Kyzylkum		<i>M. meridianus</i>		<i>R. opimus</i>				
Gobi		<i>M. meridianus</i>					<i>R. opimus</i>	

Table 4

Composition of ecological groups of Gerbillinae in some Palearctic local rodent communities.

Considering taxonomic composition of rodent faunas, it is possible to hypothesize that the presence of four-five ecological groups in communities of Gerbillinae should be typical for the whole Saharo-Sindian part of the Palaearctic desert belt, whereas two ecological groups of jirds should be common in communities of the Turano-Gobian deserts. The simplification of Gerbillinae community structure in Turano-Gobian deserts is the result of the absence of granivorous and omnivorous species. It has been suggested that in most rodent phylogenetic lineages (including Gerbillinae), such forms are evolutionarily most primitive (VORONTSOV, 1967). Thus, their absence in the Turano-Gobian deserts may be explained by the late penetration of Gerbillinae into this region (PAVLINOV *et al.*, 1990) when ecological niches of small granivores and omnivores were already occupied by endemic species (jerboas and hamsters).

In addition, species composing an ecological group differ substantially in their size. For example, the group of nocturnal mixivorous habitat generalists of the Negev Desert consists of two species, *Gerbillus dasyurus* and *Meriones crassus*, with a threefold difference in body mass (22 and 72 g, respectively). The group of nocturnal mixivorous psammophiles of the northern Negev is composed of *Gerbillus andersoni*, *G. pyramidum* and *Meriones sacramenti*, with a 1.5-3-fold difference in body mass (24, 38 and 120 g, respectively). The group of nocturnal mixivorous habitat generalists of the Kyzylkum

Desert consists of two species, *Meriones meridianus* and *M. erythrorus*, with about two-fold difference in body mass (42 and 77 g, respectively). Such differences are typical for desert rodent communities and can be explained as a mechanism facilitating coexistence of ecologically-similar species (BROWN, 1995).

### *Among-variable statistical interactions*

There was a very strong positive correlation between relative abundance and relative biomass of gerbils and jirds ( $r = +0.96$ ,  $P < 0.001$ ). The relationships between relative abundance and relative biomass of Gerbillinae and their fraction in rodent communities are also positive but not linear (fig. 3). These relationships are best fitted by regression equations  $Rab = 1.233 + 0.477 * Ln (Fr)$  and  $Rbm = 1.243 + 0.478 * Ln (Fr)$ , where  $Rab$  is relative abundance,  $Rbm$  is relative biomass and  $Fr$  is fraction of Gerbillinae in a rodent community. Both regression equations are statistically significant ( $R^2 = 0.796$  and  $0.791$ , respectively;  $P < 0.005$  in both cases). Such a pattern means that the ecological significance of Gerbillinae increases faster than their taxonomic importance. Gerbils and jirds become the dominant components of rodent communities (in terms of abundance and biomass) as soon as they comprise approximately one quarter of all rodent species only. This result can be considered as evidence of the evolutionary success of the taxon. The observed patterns can be discussed also in terms of the species abundance – body size concept. It has been shown that the relationship between body size and population abundance is negative, but the proportion of variance in abundance explained by body size is always low and plots of the relationship tend to be polygonal (BLACKBURN *et al.*, 1993; BROWN, 1995). If so, a linear relationship between relative abundance and relative biomass may be observed only if Gerbillinae represent the modal size class of a rodent community, or if they are equally distributed among all size classes. The former is found in the Turano-Gobian communities, whereas the latter is observed for those in the Thar and Negev communities. Non-linearity of the relationships between relative abundance and relative biomass of Gerbillinae and their fraction in rodent communities may be explained by differences between Turano-Gobian and Saharo-Sindian rodent communities in species distribution within abundance

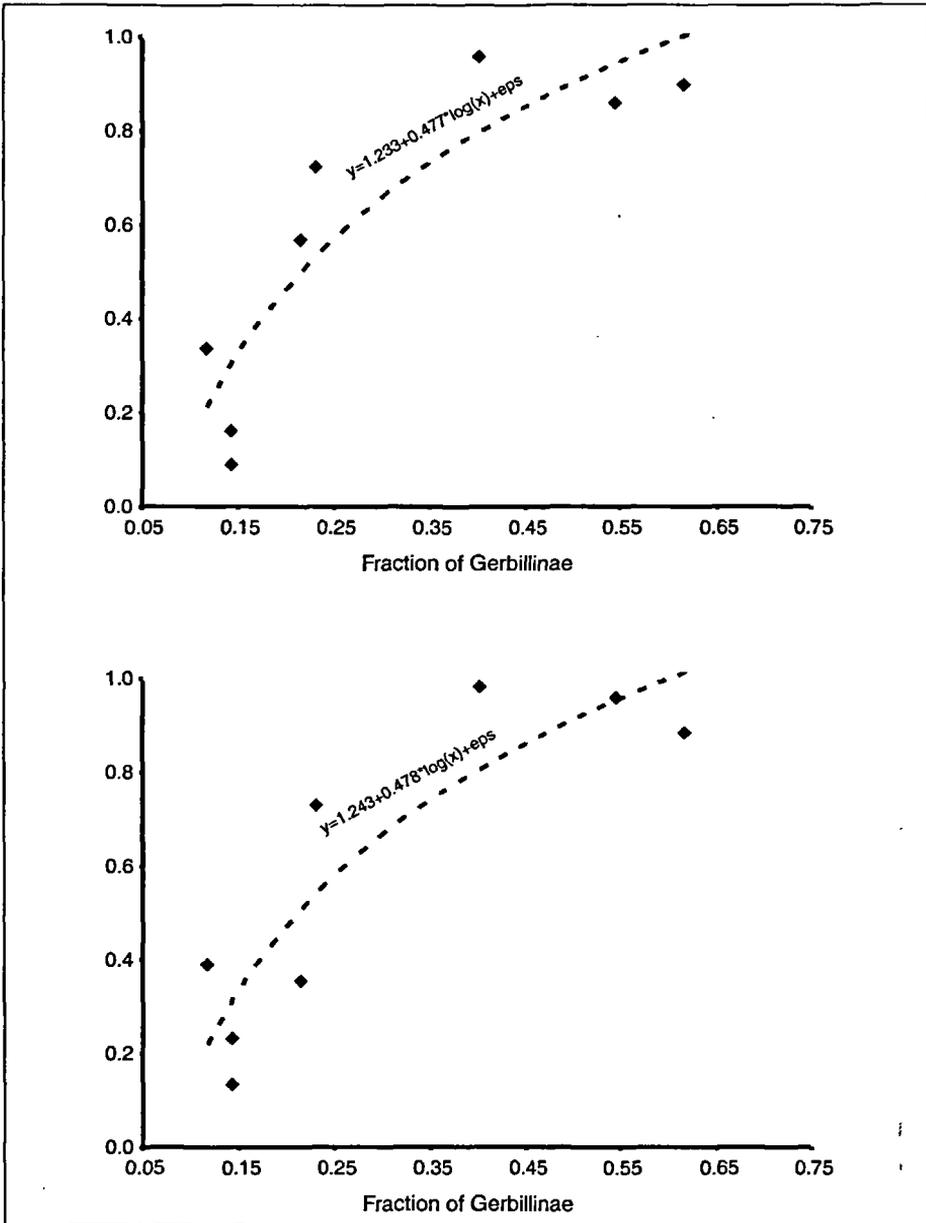


Figure 3  
 Relationships between relative abundance (top), relative biomass (low) and the proportion of Gerbillinae in taxonomic composition of Palaearctic desert rodent communities.

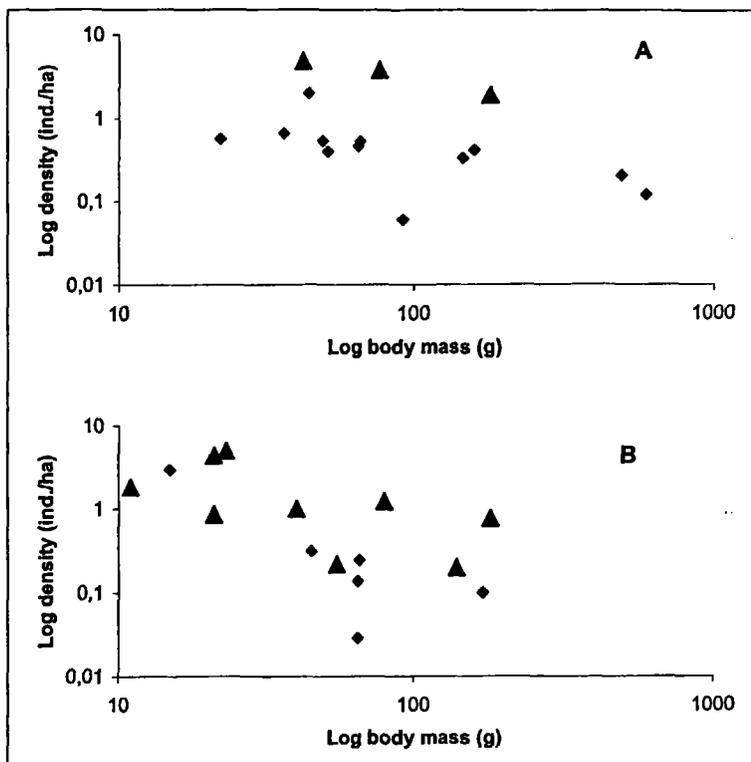


Figure 4

Relationships between body mass and abundance in rodent communities of the Negev Desert (A) and the Kyzylkum Desert (B). Gerbillinae species are denoted by the large triangles, non-gerbillinae species by small diamonds.

– body size polygons. Few jird species of the Turano-Gobian communities occupy the upper part of these polygons (fig. 4A). It means that Gerbillinae are represented here by species of the modal size class but with high densities. In such a case, a small increase in the Gerbillinae fraction in a community will lead to a rapid growth of their relative abundance and biomass. Conversely, numerous gerbil and jird species of the Thar and Negev communities occupy abundance – body size polygons evenly (fig. 4B), demonstrating their diversity of body size classes and density levels. The well-known positive relationship between species abundance and geographic range size among groups of closely related species (BROWN, 1995; GASTON

*et al.*, 1997), suggests that any increase in the Gerbillinae fraction of a community will most likely occur as a result of the addition of relatively rare species with narrow geographic ranges. In such a case, even a significant increase in the Gerbillinae fraction of a community will provide only a slow growth of their relative abundance and relative biomass.

There is a strong positive correlation ( $r = +0.88$ ,  $P < 0.005$ ) between the number of Gerbillinae species and the number of their ecological groups. This pattern reflects an increasing level of ecological diversification with growth in the number of coexisting species. It should be noted that this pattern is demonstrated for Asian communities only, in the absence of appropriate data on Saharan communities. Nevertheless, one may expect that a similar pattern will be revealed within Saharan rodent communities. However, the relative morphological uniformity of Gerbillinae should put an upper limit to the number of their potential ecological groups. A working hypothesis for future ecological studies of the Saharan desert rodent communities might be that the relation between the number of Gerbillinae species and the number of their ecological groups should be positive but non-linear. The number of ecological groups should attain an upper limit at some moderate species richness. Additional increases of species richness from moderate to high values should produce an ecological diversification within each ecological group by subdividing it into different size classes.

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