

Lizards of the Northern Mongolian Deserts: Densities and Community Structure

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Abstract.— Spatial organization and population densities of three-species lizard community was studied in the Gobi Desert, Mongolia. To evaluate the effect of habitat variables on the distribution and abundance of each species we used the stepwise procedure of factor selection with ANOVA on each step. To describe the distribution of species' spatial niches in the space of environmental variables, we used stepwise discriminant function analysis (DFA). The number of species in 1-ha grid areas varied from 0 to 4. *Phrynocephalus versicolor* was the only species distributed over the 91% of grids occupied. There was a positive relationship between distribution and local species abundance. A set of two to three habitat variables determined the abundance of each species. The result of DFA signify to the well pronounced segregation, but not even distribution of species spatial niches in the space of resources.

Key words.— Lizards, Mongolia, community, ecology, density

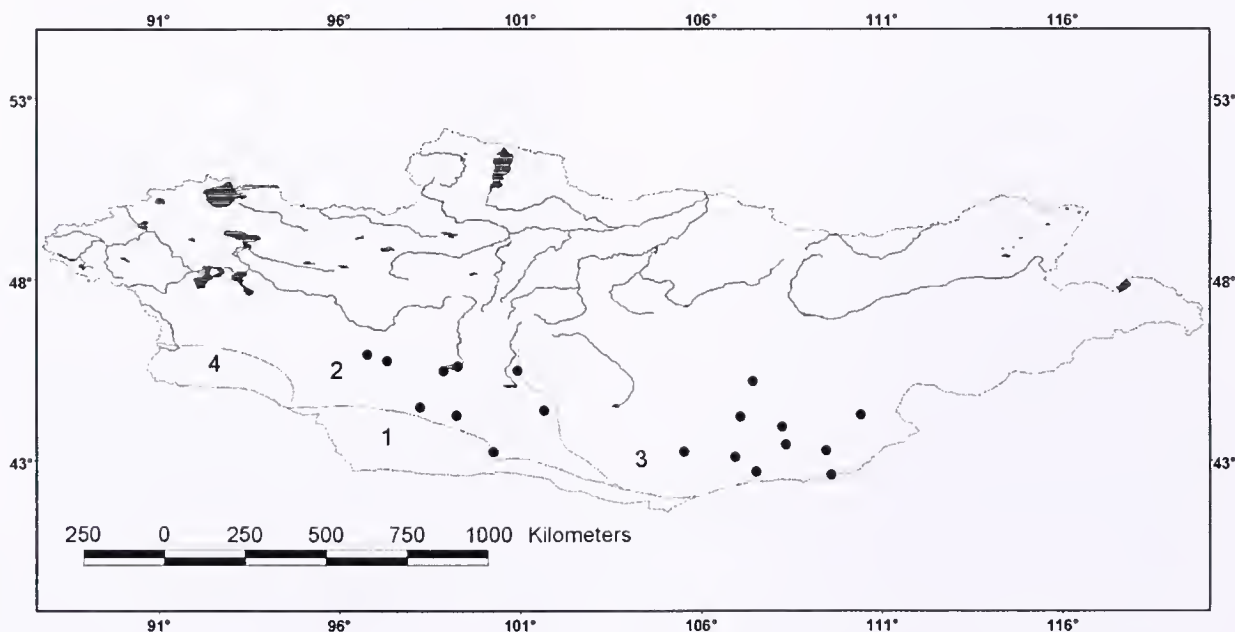


Fig 1. Map of Mongolia and location of sites where data were collected. 1 - Southern Gobi, 2-Western Gobi, 3-Eastern Gobi, 4-Barun-Churay Basin.

Introduction

The reptile communities of Mongolian deserts are characterized by several specific features discussed elsewhere (Ananjeva and Semenov, 1986; Borkin and Semenov, 1984; Munkhbajar, 1976; Semenov and Borkin, 1986; Semenov and Shenbrot, 1988). There are few species in the fauna with low species richness

at sites, a low level of species turnover between habitats, low abundance of most species and high dominance of only one species, *Phrynocephalus versicolor*. A few common species have rather broad spatial niches, diverse behavioral and physiological characteristics (diverse range of thermobiological patterns, wide active search for food items, etc.).

The degree of interest in comparative studies of structure and function of reptile communities increased dramatically after seminal papers written by E. Pianka (Pianka, 1973, 1975). Most of the ensuing studies were devoted to the species rich and diverse communities of desert lizards in Australia, southwestern North America and southern Africa (Case, 1983; Fuentes, 1976; Henle, 1989; Inger, Colwell, 1977; Millado et al., 1975; Pianka, 1986; Scheibe, 1987; Shenbrot et al., 1992; Simbotwe, 1984). At the same time study of species poor communities in the Central Asian desert can provide a significant information not only in comparison with other continents, but also can help us to understand better which factors rule in reality structure and dynamic of lizard communities of many species. Up to now there were only two examples of such studies made in China (Chang et al., 1993; Lui et al., 1992).

The main objective of this paper was to study the specific features of spatial organization and population densities of three-species lizard community in the Gobi Desert, Mongolia. The study was conducted during a long-term research program on the biodiversity of the Mongolian desert biota, and was sponsored by the Permanent Soviet-Mongolian Biological Expedition.

Material and Methods

Mongolian desert

A map (Fig. 1) illustrates the location of desert regions of Mongolia. Three desert regions to the south of the Altai Mountains are partly separated from one another by chains of low mountains and hills. These three are Trans-Altai Gobi (South), Alashan Gobi (East) and Sungarian Gobi or Barun-Churay Basin (West) (Yunatov, 1950). Besides these deserts there are desert areas between the Altai and Hangai mountains, usually called Western cold deserts, and some arid lands in the Great Lakes and Ubsu-Nur Basins (northwest).

Three arid subzones of the Mongolian desert are defined (Sokolov and Gunin, 1986): extra-arid desert (<50 mm of rainfall per year), real desert (50---100 mm per year) and steppe-like desert (100---150 mm per year). However, the climatic border that restricts the distribution of plants (Kazantseva, 1986; Volkova et al., 1986) and animals (Podtyazhkin and Orlov, 1986; Semenov and Borkin, 1986) exists only between the southern part of Trans-Altai Gobi (< 50 mm per year) and the northern waste belt of desert lands with more predictable precipitation (100-200 mm per year). The narrow real desert subzone appears

transitive with no specific features of vegetation. Thus, only the southern (extra-arid) and northern subzones are well pronounced.

The southern desert occurs mostly in the Trans-Altai Gobi and is characterized by a few very dry, unproductive biotopes inhabited by five lizard species (two agamids, two gekkonids, and one *Eremias* species). Among this group only one species, *Phrynocephalus versicolor* is common in the northern subzone (Semenov and Borkin, 1986).

The northern deserts, which extend to the southwest, west, and south-east of Mongolia and along both slopes of the Mongolian Altai and Gobi-Altai mountains, are characterized by pronounced microrelief and rich vegetation, although the main landscape types are the same as in the southern subzone. The vegetation in rock and gravel valleys consists of perennial grass (*Stipa*), forbs, onions and succulents, and a variety of annual plant species. Shrub vegetation is often associated with foothills and sand dunes, or is spread along the dry river beds (Lavrenko, 1978). The difference in climate between western and eastern parts of the northern Mongolian desert is not pronounced (Murzaev, 1952); some differences exist in the composition of the flora (Yunatov, 1950).

Lizard species

There are four lizard species inhabiting northern Mongolian deserts: *Alsophylax pipiens*, *Phrynocephalus versicolor*, *Eremias przewalskii* and *E. multiocellata*. Among these, only the three last mentioned species are abundant and relatively widespread.

Data collection

We collected data during three field trips to the Mongolian northern deserts in June-August 1985, 1986 and 1988. Forty five 1-ha grids were established in the Northern desert subzone (see map, Fig 1). Grids were distributed so that they covered the whole range of habitats from the middle slopes of the mountains to the clay basins and sand dunes. Each habitat type was sampled equally. Two factors determined the number of grids at a desert region: diversity of habitat types and abundance of lizards. Each grid was divided into 25 smaller sample plots, 20 x 20 m. The centers of sample plots were marked with 50 cm aluminum stakes. Lizards were sampled by repeated, regular search of established grids during two to four consecutive days during periods of their maximal diurnal activity. Nearly all encountered lizards were captured by hand. Most of the surveys accounting were conducted before the appearance of hatchlings. In the rest of the cases hatchlings were not counted. Each cap-

Table 1. Density (no. ha⁻¹) of lizard species.

Lizard species	Mountain slopes	Stony foothills	Stony and gravel planes	Sandy-loam plains	Clay hollows	Loess hills in saline depressions	Sand hills
<i>P. versicolor</i>	1.7±0.9 0 - 3	52.8±8.9 24 - 91	54.4±8.7 32 - 83	36.6±8.2 10 - 106	5.5±4.5 1 - 10	41.2±6.3 22 - 64	0.8±0.4 0 - 3
<i>E. przewalskii</i>	0	0	0	2.6±1.3 0 - 18	0	16.3±6.3 0 - 44	0.9±0.5 0 - 4
<i>E. multiocellata</i>	0	2.1±1.3 0 - 12	0.4±0.4 0 - 2	0.5±0.4 0 - 5	0	2.0±1.8 0 - 11	0

tured lizard was marked by toe-clipping (the most distal phalange only) and/or by a number painted with permanent color marker on its back, and released. Densities of lizard species were estimated by the total number of animals caught on a grid. The reliability of density estimates was verified by recapture of marked individuals and by the observation of marked lizards on grids. Two days were sufficient to catch > 80% of lizards.

A 0.5 kg soil sample was taken from the center of each plot for laboratory texture analysis. The number of shrubs (by species) in each plot was counted in a circle, 5 m in radius. To determine vegetation cover and volume by height layers within each plot, the height and diameter of crown of the shrubs (up to 30 shrubs of each species in the grid) were measured. The abundance of annuals was evaluated by clipping all annuals on 0.25 m² sample plots (4 sample plots placed at random in each of 25 plots in 1-ha grid area). Twenty three parameters were used in the subsequent analysis (Table 2). Data on 1125 descriptions of sample plots and 1710 records of 3 lizard species were used in the analysis. In total, we recorded 1528 individuals of the agamid lizard *P. versicolor*, 142 of the lacertid lizard *Eremias przewalskii* and 40 *E. multiocellata*.

Statistical data processing

To evaluate the effect of habitat variables on the distribution and abundance of each species we used the stepwise procedure of factor selection (Shenbrot, 1988) with ANOVA of each step. Before analysis, the original values of species' densities and habitat variables were transformed to an interval scale with five intervals for habitat variables and three intervals for species' abundance variables. The influence of each variable was estimated separately by ANOVA and the variables with nonsignificant effect were omitted. In the next step, each of variables that was not omitted earlier was added separately to the most powerful variable to select the most powerful pair of variables. This procedure was repeated until all possible variables were included in the analysis or until the addition of the new variable does not increase the proportion of explained dispersion.

To describe the distribution of species' spatial niches in the space of environmental variables (ecological space) and to reduce the dimensionality of this space, we used stepwise discriminant analysis. Discriminant axes were calculated based on the data set consisting of the values of habitat variables for each point of lizard's registrations and with lizard species as a grouping variable.

Results

Densities and distribution through habitat types

The results of lizard density and diversity estimations on the 1-ha grids indicate the low local species diversity in Mongolian deserts (Table 1). The number of species in our grid areas varied from zero to three. Among 45 grids there were two grids with no lizards, 21 grids with only one species, 18 grids with two species and four grids with three species. *Phrynocephalus versicolor* was the only species distributed over the most number of grids (91% of grids occupied). *Eremias przewalskii* was found on 33%, *E. multiocellata* on 24% and *A. papiens* on 4% of grids. Regarding distribution through the main habitat types (Table 1), *P. versicolor* was also the most widely distributed spe-

cies but with the pronounced habitat preference. The second was *E. multiocellata*, and the third was *E. przewalskii*. The last species had the most restricted habitat preference, namely sandy-loess hills in saline depressions with shrub vegetation of *Nitraria* sp.

The abundance of *P. versicolor* was positively correlated with its broad distribution. The density of this species varied from 1 to 106 individuals per 1-ha (Table 1). The second most abundant *E. przewalskii* (44 individuals per 1-ha maximum), and the third was *E. multiocellata* (11 individuals per 1-ha maximum). All three species coexisted at rather high densities in saline depressions with sandy-loess hills covered with *Nitraria* sp. shrubs. There were no pronounced negative correlation between the densities of two dominant species on grids situated within this habitat type (*P. versicolor*-*E. przewalskii*: $R^2=0.04$, $n=20$, ns).

Table 2. Designation and description for the 23 habitat variables included in the analysis.

Mnemonic	Variable	Unit
RCK	Content of rocks in the soil	%%
GRW	Content of gravel in the soil	%%
CLY	Content of clay in the soil	%%
SCS	Sand cover area	%%
SCH	Sand cover height	cm
WDS	Dry river bed area	%%
WDD	Dry river bed depth	cm
NRB	Number of rodent burrows	no/sq.m.
FRB	Abundance of annual forbs	no/sq.m.
AGR	Abundance of annual grasses	no/sq.m.
ANN	Overall abundance of annual grasses and forbs	no/sq.m.
ALL	Perennial <i>Allium</i> cover	%%
PGR	Perennial grass cover	%%
MIC	Cover of microphyllous shrubs	%%
HAL	Cover of halophytous shrubs	%%
SUC	Cover of small succulent shrubs	%%
HLX	Cover of <i>Haloxylon</i>	%%
NIT	Cover of <i>Nitraria</i>	%%
SHC	Overall shrub cover	%%
SV1	Perennial plant crown volume at the level 0-25 cm	%%
SV2	Perennial plant crown volume at the level 25-50 cm	%%
SV3	Perennial plant crown volume at the level 0.5-1 m	%%
SV4	Perennial plant crown volume at the level 1-2 m	%%

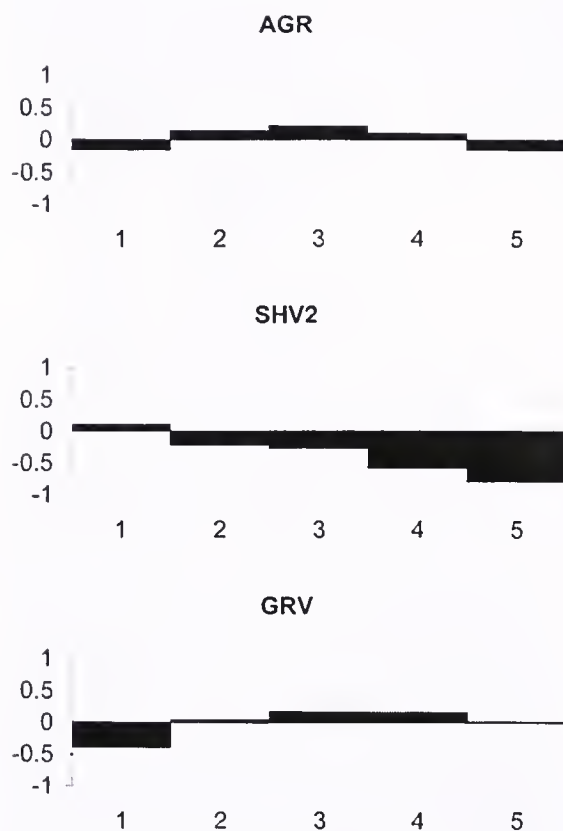


Fig 2. Habitat use profiles of *P. versicolor*. For each habitat variable rank, mean use by species is plotted as a difference between capture frequency on plots of this rank and capture frequency of all plots. The size of histograms therefore denote the selectivity (positive or negative) of habitat use. For mnemonics see Table 2

Spatial niches

There was a statistically significant influence of habitat variables on the distribution and abundance of all three studied lizard species (Table 3). For each of these species we extracted a set of two to three habitat variables, determining 6.6-28.7% of observed variance in abundance. Densities of two species (*P. versicolor*, *E. przewalskii*) were moderately affected by habitat variables, whereas density of *E. multiocellata* was weakly affected.

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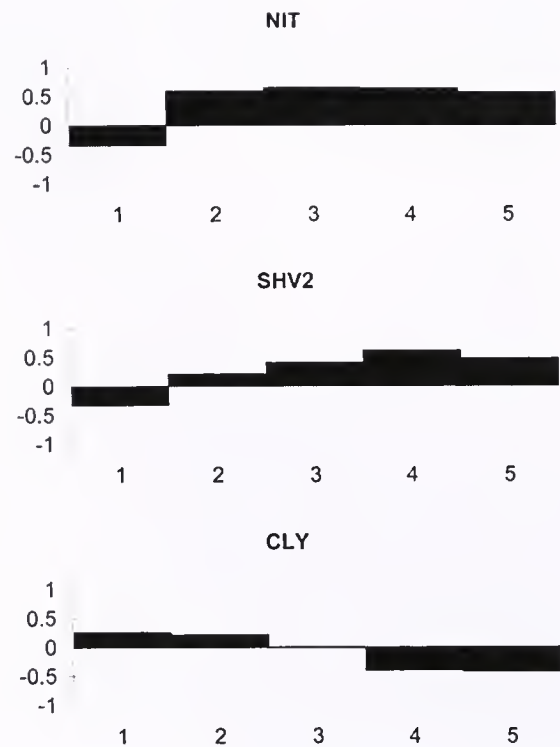


Fig.3. Habitat use profiles of *E. przewalskii*. For explanation see Fig.2.

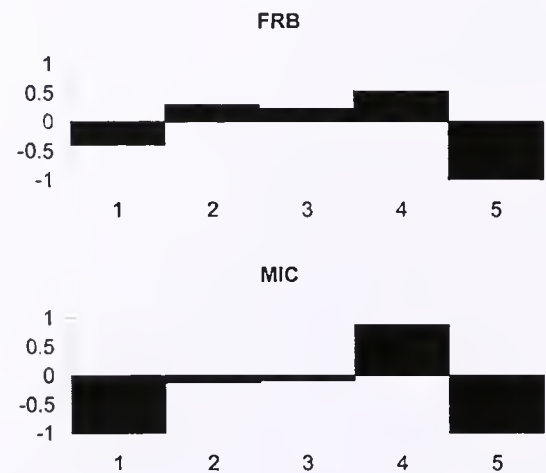


Fig.4. Habitat use profiles of *E. multiocellata*. For explanation see Fig.2.

Patterns of habitat usage based on selected variable sets for each species are presented on Figures 2-4. *Phrynocephalus versicolor* clearly avoided microsites with low gravel content, very low and very high annual grass abundance, moderate and high shrub crown volume in the level 0.25-0.5 m and preferred microsites with moderate gravel content, moderate annual grass abundance and very low shrub

Table 3. Summary of ANOVA analyses of influence of habitat variables on individual species' abundance. Values are proportions of total dispersion determined by given variable. Total proportion of variance determined by a set of variables may be greater than sum of influences of individual variables as a result of high-order interactions.

Species	V a r i a b l e s							Total
	GRV	CLY	AGR	FRB	MIC	NIT	SHV2	
<i>P. versicolor</i>	0.0226		0.0387				0.0458	0.1900
<i>E. przewalskii</i>		0.0593				0.1592	0.0102	0.2872
<i>E. multiocellata</i>				0.0180	0.0232			0.0662

crown volume in the level 0.25-0.5 m (Fig. 2). *Eremias przewalskii* avoided microsites with high and very high clay content, very low *Nitraria* cover, very low shrub crown volume in the level 0.25-0.5 m, and preferred microsites with low clay content, moderate to high *Nitraria* cover, moderate to high shrub crown volume in the level 0.25-0.5 m (Fig. 3). *Eremias multiocellata* avoided microsites with very high and very low forb abundance and microphyllous shrub cover, and preferred microsites with moderate forb abundance and rather high microphyllous shrub cover (Fig. 4).

Structure of ecological space occupied

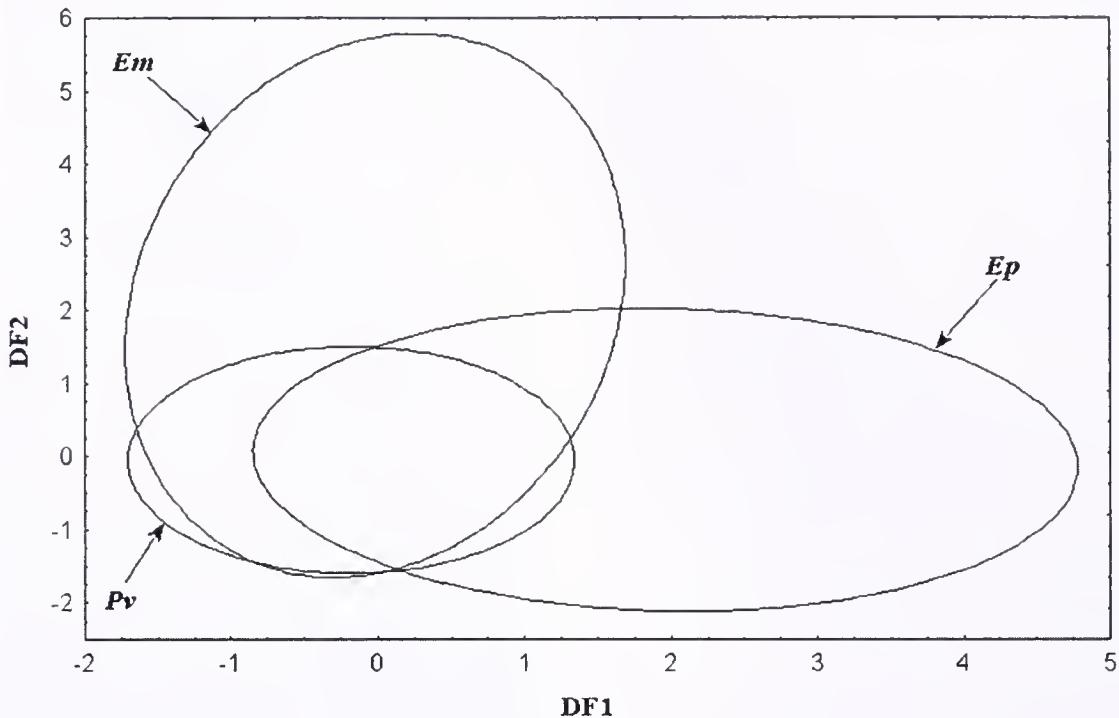
The results of reducing habitat space dimensionality using discriminant analysis showed that division of this space by lizard species occurred along the first two axes. Both axes accounted in sum for 100 % of variance and reflected some complex environmental gradients (Table 4). The first axis represented a general gradient of decreasing rock and gravel content in the soil as well as an increase in the sand cover area, sand mound height, number of rodent burrows and general shrub (especially *Nitraria*) cover. This axis characterized the between-habitat component of environmental variation rather than within-habitat variation, and described in general spatial segregation of lizard species according to their preference of physiognomically distinctive habitats. The second axis reflected an increase of dry river bed area, *Allium* abundance and microphyllous shrub cover, and characterized both between- and within-habitat components of species segregation. The first axis described habitat division between *E. przewalskii* and two other species, whereas the second axis reflected habitat segregation between *E. multiocellata* and two other species (Fig. 5). All three lizard species had spatially remote niche centers and less than 30% niche overlap (Fig. 5).

Discussion

Our data confirm the general opinion of low reptile species richness in Mongolian deserts. There were only four 1-ha grids where three lizard species coexisted. If we take into account rare encounters with snake species, the maximum reptile species number is five. Another opinion about wide spatial niches of Gobiian lizards (Semenov and Borkin, 1986) partly contradicts our results. At the one hand *P. versicolor* is the an abundant species that can be found everywhere in the Gobi desert, including sandy, clay and rocky habitats. This feature of its distribution distinguishes this species greatly from its western congeners that share habitat types in Middle Asia (Shenbrot et al., 1991). At the other hand, *P. versicolor* did have well pronounced spatial preferences as it is seen from Table 1. The two species of *Eremias* lizards had distinctly non-preferable habitats. *Eremias przewalskii* was mainly restricted to one habitat type, and *E. multiocellata* to two habitat types.

Results of analysis of microhabitat preferences demonstrate the existence of significantly distinct environmental variables determining spatial distribution of each lizard species. The variables elucidated can be regarded as axes of species spatial niche. Spatial niches for *P. versicolor* and *E. przewalskii* appeared to be determined by three axes of environmental variation and for *E. multiocellata* by two axes. The distribution of species along each axes can be interpreted in accordance with the biological characteristics of each species. The absence of *P. versicolor* at microsites with dense vegetation is explained by typical *Phrynocephalus* locomotion on straightened legs and by the group-specific visual orientation when foraging (in contrast to *Eremias*, which look for food items using olfaction). *Phrynocephalus versicolor* preferred microsites with moderate gravel content, moderate annual grass abundance and very low shrub crown volume, which characterizes the species as an inhabitant of stony and gravel desert valleys (Fig. 2). *Eremias przewalskii* selected microhabitats in accor-

Fig.5. Seventy-five percent confidence ellipses for the species observations on two discriminant axes (DF1 and DF2). Em-*Eremias multiocellata*, Ep- *Eremias przewalskii*, Pv - *Phrynocephalus vesicolor*.



dance with food abundance and a species-specific tactic of antipredator behavior. It preferred microsites with moderate to high *Nitraria* cover and moderate to high shrub crown volume at 0.25-0.5 m (Fig. 3). In summer *E. przewalskii* feed predominantly on berries and young green twigs of *Nitraria*, and also find protection under the dense cover of the crowns of low spiny shrubs. In contrast to *E. przewalskii*, *E. multiocellata* avoided microsites with very high annual plant abundance and shrub cover, but also preferred microsites with moderate and rather high values of these variables (Fig. 4). This difference can be interpreted in accordance with thermobiological and size characteristics of two *Eremias* species. The larger species, *E. przewalskii* is not so quick as the smaller *E. multiocellata*. The first one digs well in soft soil, and thermoregulates climbing on or escaping under the shrub periodically, being active throughout the day. Small *E. multiocellata* that occupy habitats with relatively low vegetation cover (with small sparsely-distributed shrubs) must cross open sites in search for food items and escape predator's attacks by quickly rushing into small shrubs or burrows. This species reduces heat by escaping into burrow during the day-time.

Another result of the above comparison is the positive relationship between distribution and local abundance among the species considered. Distribution

here means not the size of the species range area, but the number of sites where each species was found. *Phrynocephalus vesicolor* was encountered on 41 grid areas and had the highest population density (mean: 37.3, median: 26 ind/ha, maximum: 106 ind/ha). With the edge-effect correction (Semenov, 1991) maximum density was 70.02 ind/ha (175.5 g/ha biomass). *Eremias przewalskii* was found on 15 grid areas and was the second abundant species (mean: 9.5, median: 4 ind/ha, maximum: 44 ind/ha). *Eremias multiocellata* was found on 11 grid areas and its maximum density was 12 ind/ha (mean: 3.6, median: 2 ind/ha). *Alsophilax pipiens* was met on two grids with density 3 ind/ha.

Brown (1995) explains this rather common relationship by the "Hutchinsonian niche model" (see also for one species, Brown 1984), suggesting that "the species that is slightly more tolerant of some abiotic conditions or biotic interaction or is slightly better able to use some resource should not only be able to occur in more places but also to attain higher abundance in some of those places." In the approach we use here niche breadth reflects microhabitat requirements of each species, namely the range of microconditions where each lizard species occurred. Diversity of these microhabitats is not necessarily correlated with the diversity of macrohabitats as well as with the

Table 4. Summary of discriminant analysis of the habitats of lizard species. DF1 and DF2 are the first two components (all are significant, $P < 0.001$). Mnemonics for habitat variables are from Table 1.

	DF1	DF2
Eigenvalue	0.351	0.102
Chi-square	676.1	165.5
Cumulative % of variance	62.58	37.42
Factor loading		
RCK	-0.350	0.295
GRV	-0.291	0.124
SCS	0.544	-0.221
WDD	-0.091	0.241
NRB	0.442	0.253
SHH	0.627	0.190
ALL	-0.141	0.252
MIC	-0.021	0.410
NIT	0.642	0.193
SHC	0.650	0.148
SV1	0.712	0.067
SV2	0.693	-0.069

size of the landmass studied. *Phrynocephalus versicolor* that was distributed everywhere in the Gobi, and in many different macrohabitats used a rather limited range of microconditions (Fig. 2). In this respect its spatial niche was not broader than the niche of *E. multiozellata*, and was even narrower in comparison with *E. przewalskii*. (Fig. 5). *Eremias przewalskii* which inhabits a rather limited range of macrohabitats is characterized by relatively broad requirements for microconditions along the first discriminant axis which represents the main direction of spatial segregation of lizard species.

The structure of ecological space occupied by three lizard species has a complex character, explaining both macrohabitat and microhabitat segregation of spatial niches. Primarily, each discriminant axis characterizes the range of variation of microconditions in the study area. This can characterize macrohabitats only if variation in a set of variables included into analysis reflects the macrohabitat variation. In our case DF1 and DF2 possess such a feature: DF1 characterizes better the between-habitat component of spatial niche segregation and DF2 characterizes more

the within-habitat component. Three species of lizards share microconditions in two-dimensional ecological space, so that the niche centers appeared to be almost equally distant from the geometrical center of the model (Fig. 5). The two species of *Eremias* lizards share ecological space to a greater extent than each *Eremias* with *P. versicolor*. Niche overlap between species was less than 15%.

It seems difficult to speculate about processes that led to such spatial relationships. Interspecific competition could contribute to spatial segregation of *Eremias* lizards in past, and could determine the low level of niche overlap. The competitive relationship between *E. przewalskii* and *P. versicolor* is unclear. In a pair of neighboring grid areas at one location within one habitat type when one species is in high density, the other one is usually at low density and vice-versa. However, there were no correlation between population densities of these two dominant species when all grid areas within one habitat type were put together. This result is easily explainable because different localities must have different upper limits of species densities according to the local environmental capacities. However, the climatic conditions of Gobi Desert are so unfavored for reptiles (extremely low winter temperatures, great interannual, between- and within-seasonal contrasts in precipitation and temperatures) that it appears unrealistic to assume the space of resources is saturated by individuals, and that populations are at equilibrium.

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