

Steppe expansion and changes in the structure of the rodent community in north-western Caspian region (Republic of Kalmykia, RF) *

K. A. ROGOVIN**

A. N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia

Abstract In 1997–1999 I examined a 10-species rodent community in “Chernie Zemly”, a semi-desert region in the Republic of Kalmykia (Russian Federation). The region was characterized by a restoration succession of vegetation after a ten-fold decrease of live-stock. One task was to understand the habitat requirements of rodent species in order to predict species-specific responses to environmental changes. I also examined spatial patterns of community structure, niche parameters and species diversity. Stepwise Regression Analysis showed that spatial distribution of each rodent species was only partly determined by known environmental variables (from two to six variables) with significant regression coefficients. Although the equations were strongly significant, the R^2 values were low, not exceeding 18%. For most species, this result can be explained by recent steppe expansion associated with a decrease of habitat heterogeneity. The apparently low level of species’ selection of habitat conditions and resources may be the result of some inertia in species’ responses to environmental changes. Results obtained using Discriminant Function Analysis and Principal Component Analysis signifies that the community structure, as well as parameters of individual species’ niches were not stable from year to year. Spatial guild structure was well expressed during a year of high species abundance when niche overlap was higher in pairs of species with moderate and low overlap. Results of analysis of abundance, niche position and niche breadth show that species tend to respond to fluctuating conditions and resources in their own individualistic manner. At the same time, a well pronounced individualism in responses of species to the environmental dynamic may become a reason for directional change in species diversity. Results provided in a limited spatial scale with relatively uniform conditions show that rodents’ α -diversity correlates positively with habitat structural complexity and negatively with characteristics of habitat productivity. The observed steppe expansion in Kalmykia means an increase of primary productivity and a decrease in habitat heterogeneity. Over time this process may lead to a decrease of abundance and diversity of rodents of mostly desert and semi-desert origin, that still form a nucleus of the fauna [*Acta Zoologica Sinica* 53 (1): 29–43, 2007].

Key words Community ecology, Ecological niche, Guild structure, Species diversity, Rodents, Steppe expansion

里海西北部 Caspian 地区草原扩大与啮齿类群落结构的变化 *

K. A. ROGOVIN**

A. N. Severtzov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow 119071, Russia

摘要 于 1997–1999 年检测了俄罗斯联邦卡尔梅克 (Kalmyki) 共和国 Chernie Zemly 半干旱草原由 10 个物种组成的啮齿类群落。该区域的植被特点是家畜大量减少后形成的恢复植被。我们的任务之一就是了解不同啮齿动物的生境需求, 以预测不同物种对环境变化的特异性反应。我们也检测了群落空间结构、生态位参数和物种多样性。逐步回归分析表明, 各种啮齿动物的空间分布仅部分地决定于已知环境因子 (2–6 个变量)。虽然方程式具有强显著性, 但决定系数 R^2 很低, 不超过 18%。对于大多数种类, 这种结果可由最近草原扩大而来的生境异质性降低解释。物种生境选择条件和资源的明显低水平可能是由物种对环境变化的惯性反应造成的。判别函数分析和主分量分析结果表明, 群落结构以及单个物种的生态位参数在不同年间并不稳定。空间分层结构在种间中等和低重叠的高物种多样性年度表现明显。多样性、生态位组成和生态位宽度分析结果表明, 不同物种对环境条件和资源变化的反应具有不同的个性化方式。同时, 物种对环境动态的明显个性化反应成为物种多样性定向变化

Received Aug. 11, 2006; accepted Oct. 08, 2006

* From 1997 to 1999 this research was funded by the grant (No.97-04-48073) from Russian Foundation for Basic Research

** E-mail: karl2255@orc.ru

© 2007 动物学报 *Acta Zoologica Sinica*

的原因。限定空间和相对单一条件下的结果表明, 啮齿类 α 多样性与生境结构复杂性呈正相关, 而与生境生产力特征呈负相关。观察表明, 卡尔梅克国草原扩大伴随着初级生产力的升高和生境异质性的降低。随着时间的推移会导致大多数草原和半干旱区域啮齿类多样性的降低, 并形成动物区系核心 [动物学报 53 (1): 29–43, 2007]。

关键词 群落生态学 生态位 分层结构 物种多样性 啮齿动物 草原扩大

“Chernie Zemli”, a region in the southern part of the Republic of Kalmykia, Russian Federation, is located within the semi-desert belt of Eurasia ($45^{\circ} - 46^{\circ}30' E$ and $45^{\circ} - 47^{\circ} N$). There is a vast portion of virgin lands inhabiting by rodent species of desert and semi-desert origin (See review by Shenbrot et al., 1999).

The transitional state between steppe and desert makes lands in this region acutely sensitive to anthropogenic pressure. During the 1970s – 1980s overgrazing in Kalmykia led to a digression of 83% of natural pastures and to the critical desertification of the territory (Zonn, 1995). Desertification in the '90s did not continue only because of the economic crisis that affected Russia at the beginning of the decade. A 10-fold decrease in livestock per capita and increased humidity because of the Caspian Sea transgression caused the process of desertification to stop, and the steppe vegetation to expand quickly. These fast changes in vegetation presumably influenced animal populations and communities of many species. With respect to rodents, this process may mean a decline in populations and diversity of species adapted to desert and semi-desert environments and an increased participation of steppe-adapted forms.

The purpose of this study was to examine the rodent community of southern Kalmykia (“Chernie Zemli”) in order to understand the responses of rodent species to environmental variables. I sought to predict species-specific responses to environmental changes in a relatively long-term perspective. My second objective was to determine temporal changes in the spatial organization of the rodent community by using of uniform methods of data collection and analysis. I examined spatial community structure, niche parameters and species diversity during three spring seasons characterized by a recovery and succession of vegetation towards steppe-like plant communities.

I used a traditional comparative approach in community ecology to construct models designed to test specific hypotheses (Schoener, 1986; Wiens, 1989; Brown 1995; Shenbrot et al., 1999). I defined an “ecological niche” as a multidimensional projection of the distribution of a species along axes of ecological space representing environmental gradients (Schoener, 1989), and analyzed quantitative responses of species of the community to a combination of environmental factors (Shenbrot and Krasnov, 2004). Based on this definition, I dealt mainly with the spatial component and indirectly

with trophic components of realized Hutchinsonian niches. I defined a “community” as an association of species coexisting in a region. Topological relationships of niches of coexisting species in the multidimensional space of environmental variables (ecological space) represent the spatial structure of the community. A group of species, comparable in their responses to the habitat variables and similarly distributed along environmental gradients I defined as a “spatial guild” (Shenbrot et al., 1999).

1 Material and methods

1.1 Study area

I conducted research from 1997 to 1999 near V. Achinery ($45^{\circ}25' E$, $45^{\circ}30' N$) in the “Chernie Zemli” region, in the southern part of Kalmykia, between the cities Elista and Astrakhan in the north, the Caspian Sea in the east, the Kuma River in the south, and the Manych River in the west. The climate is dry and continental, with precipitation varying from 210 to 340 mm per year and with the sum of temperatures $> 10^{\circ}$ varying from 3 400 – 3 600°. The area consists of five different habitats: (1) sandy and sandy-loess plains with sagebush (*Artemisia lerchiana* and *A. austriaca*) and grass (*Poa bulbosa*, *Bromus japonicus*, *Stipa capillata*, *Agropiron fragile*) vegetation; (2) low stabilized sand hills and sand ridges covered by small shrubs (*Artemisia lerchiana*, *Kochia prostrata*, *Tanacetum achilleifolium*), grass vegetation (*Agropiron fragile*, *Stipa capillata*, *S. lessingiana*, *Koeleria sabuletorum*, *Poa bulbosa*) and herbs (*Alyssum turkestanicum*, *Anisantha tectorum*, *Artemisia csoparia*, *Ceratocarpus arenarius*, *Veronica verna*, *V. triphyllus*, etc.); (3) non-stabilized and semi-stabilized sand dunes vegetated with tall perennial grass *Elymus giganteus* and annuals (*Xanthium strumarium*, *Agriophyllum* sp., *Climacoptera crassa*); (4) clay loam plains with sage-bush (*Artemisia* sp.) and grass (*Stipa capillata*, *S. pennata*, *S. sareptana*, *Agropiron fragile*, *Puccinellia distans*) vegetation; (5) chains of clay depressions formed by ancient stream beds and covered with sparse vegetation of succulents (*Halocnemum strobilaceum*, *Anabasis* sp., *Salsola* sp. and grass *Puccinellia distans*).

Specific habitats occur around artesian springs and wells with saline loam soils and in areas around abandoned folds for sheep. These areas are characterized by patchy vegetation. The areas around springs and wells associated with gaps of hard clay surface are covered by a mosaic of vegetation of *Atriplex* sp., *Salsola* sp., grass

(*Eremopyrum triticeum*, *Puccinellia distans*) and suppressed sagebrush *Artemisia lerhiana*. The areas of abandoned sheep-folds represent different stages of recovery and succession of vegetation, depending on the date of the end of use and on the intensity of the late anthropogenic pressure (Neronov et al., 1997).

My study sites included all the above types of habitats, that were distributed in a radius of 15 km northward of the village Achinery. Livestock decreased in the Achinery district from 50 000 head of sheep and cattle at the beginning of 1990s to 4 500 head in 1999 and this caused rapid vegetation changes in all types of habitats. The most intensive succession of vegetation towards steppe-like landscape takes place in sandy soils. This process generally means a fast increase in abundance and distribution of perennial tussock grass, *Stipa capillata*, *S. lessingiana*, *Agropiron fragile* in an upper layer and of *Poa bulbosa* in a lower layer of vegetation, and a decline of perennial shrub vegetation and a decrease in the abundance and diversity of small ephemeral grass and herbs common for desertiform and semi-desert landscapes. Steppe expansion leads to the stabilization of moving sands thanks to several species of pioneer psammophilous plants, and to a reduction in the size of gaps without vegetation both in areas with sand ridges and in sandy plains (Neronov, 1997a, b). Less pronounced changes in vegetation appear in loam and clay areas.

1.2 Species of rodents

Ten species of rodents formed the community. Sciuridae: *Spermophilus pygmaeus* (Pallas, 1778) (mean body mass 214 g); Dipodidae: Allactaginae: *Allactaga major* (Kerr, 1792) (180 g), *A. elater* (Lichtenstein, 1825) (45 g), *Pygeretmus pumilio* (Kerr, 1792) (52 g); Dipodinae: *Stilodipus telum* (Lichtenstein, 1823) (67 g); Muridae: Arvicolinae: *Microtus socialis* (Pallas, 1773) (24 g), *Ellobius talpinus* (Pallas, 1770) (40 g), Gerbillinae: *Meriones meridianus* (Pallas, 1773) (46 g), *Meriones tamariscinus* (Pallas, 1773) (127 g), Murinae: *Mus musculus* (L., 1758) (17 g). The ranges of seven species are distributed within desert and semi-desert belt. Among them, *A. elater*, *P. pumilio*, *M. meridianus* appear to be relicts of Turan desert fauna (Heptner, 1945; Shenbrot et al., 1995). The ranges of two other species, *A. major* and *E. talpinus*, are also distributed in the steppe, however, taking into account species ecology, they were placed recently among desert/semi-desert dwellers (Shenbrot et al., 1999). *Mus musculus* has a very broad range. In desert and semi-desert regions it inhabits typical zonal habitats (Kutcheruk, 1994).

Of the above ten species, three (*S. pygmaeus*, *A. major*, *M. musculus*) are omnivorous, one (*M. socialis*) is folivorous, and one (*E. talpinus*) is an underground forager. All other species have a mixed diet of seeds and green parts of vegetation. Seeds dominate in

the diet of *M. meridianus*, green vegetation in that of *M. tamariscinus*, and *P. pumilio*. An equal proportion of both types of food is common for *A. elater*, and *S. telum*.

Besides these species, three other species were rare in the region and I did not consider them real community members. These are Dipodidae: Sicistinae: *Sicista subtilis* (Pallas, 1773), Cricetinae: *Cricetulus migratorius* (Pallas 1773), Arvicolinae: *Microtus rossiaemeridionalis* (Ognev, 1924). I did not find *Dipus sagitta* (Pallas, 1773) (Dipodidae), although it was registered there earlier (Popov et al., 1995). *S. subtilis* is a representative of steppe fauna (Tupikova, 1995). *D. sagitta* is a typical desert species (Shenbrot et al., 1995). The range of *M. rossiaemeridionalis* includes in semi-desert and steppe regions (Pantelev, 1998). *C. migratorius* has a broad range associated mainly with deserts and semi-deserts, but also penetrating the steppe. Shenbrot et al. (1999) considered it a desert dweller.

1.3 Data collection

A system of 11 permanent 1-ha grids was established in spring 1997 to represent the main habitat types from non-stabilized dunes to clay depressions. Each grid was subdivided into 25 plots (20 by 20 m). Two folding live-traps made of wire (25 cm × 7 cm × 7 cm) were established in each plot within a circle of 5 m radius around a center of each plot marked by a 30 cm stake. Rodents were caught, marked by toe-clipping, weighed, sexed and released. Because only gerbils, social voles and mice entered the traps well enough, I used a variety of registration techniques. For *S. pygmaeus* and *Ellobius talpinus* I used indirect estimations, characterising spatial distribution and only relative abundance. Susliks were registered by the presence of actually used winter burrows within each 20 m × 20 m sample plot (presence = 1, absence = 0), and mole voles *Ellobius talpinus* were counted by the presence of groups of fresh mounds within a sample plot (presence = 1, absence = 0). Dipodids were caught at night with a hand-held net using a searchlight (20 W) with power supply from a rechargeable battery. Only points of first trapping (registration) were used in the analysis. Each grid was checked over a period of five nights: once in May – June 1997, once in May – June 1998 and once in June 1999. Soil samples (0.5 kg) were taken from the centers of the plots for laboratory estimation of clay content. The number of shrubs, tussocks of perennial grass and big annual succulents in each plot was counted (by species) in a circle around the plot center 5 m in radius. To determine a percentage cover of the vegetation I measured the height and diameter of crowns or tussocks (30 measurements within each 1 ha grid). The abundance of annual plants was evaluated by clipping plants in 0.5 m² sample plots (4 sample plots in each plot, taken at random around plot center). I also estimated the number of contours of plant associations and

the relative height of the microrelief within each plot. Total vegetation cover was estimated visually in each plot with the use of a 0.5 m² frame for sampling. For a more complete description of the data collection method, see Shenbrot (1992), Rogovin and Shenbrot (1995), Shenbrot and Rogovin (1995). Twenty two habitat variables were estimated in the field, including abundance of annual vegetation by species, cover of perennials by species, total cover of vegetation, relative height of microrelief, size of gaps in vegetation cover, and number of contours of plant associations.

1.4 Statistical analyses

Environmental data (habitat variables) were log-transformed before analysis to normalize them. Because One-way Analysis of Variance (ANOVA) did not reveal a significant influence of any plant species or genera separately on the distribution of rodent species excepting dominant microphyllous shrub *Artemisia lerchiana* and tussock grass *Agropiron fragile*, I combined plant species into ecological groups, supposed to be essential for rodents (annual grass of fam. Poaceae, succulents, ephemeral herbs, perennial tussock grass, microphyllous shrubs (Table 1). I also used cluster analysis (UPGMA algorithm), based on a correlation matrix of environmental variables for preliminary choice of presumably significant and relatively independent variables. The thirteen variables selected (Table 1) were then included into a Stepwise Multiple Regression Analysis (Zar, 1984) to reveal a set of environmental factors responsible for the observed pattern of spatial distribution of each rodent species. The same algorithm of cluster analysis was also used to classify grids by the environmental variables selected, and by rodent species distributed in the grids.

Table 1 Description of environmental variables measured for each sample plot and included in analysis

Acronims	Variable	Unit
REL	Relief (within grid difference from min to max height)	m
CLY	Content of clay in soil	%
ART	Abundance of <i>Artemisia</i> annuals	No m ²
AGR	Abundance of annual grasses	No m ²
AFRB	Abundance of annual forbs	No m ²
ASUC	Abundance of annual succulents	No m ²
TAK	Relative size of gaps in vegetation cover	%
PGR	Cover of perennial tussock grass	%
PMIC	Cover of microphyllous shrubs	%
PSUC	Cover of succulents	%
PPRN	Cover of perennial plants	%
PVEG	Cover of vegetation, including dry plants	%
NCNT	Within plot number of plant associations	No

used to describe the relative position of rodent species in the space of environmental variables (Green, 1974). To attain compatibility for different years, data for three years were pooled together in analyses to obtain a model of ecological (discriminant) space. Niche positions for individual species were calculated in this space separately for each year. Each niche center corresponded to the position of the centroid of each species in discriminant space. From year to year shifts in position of niche centers were estimated along each ordination axis. Shifts corresponded to changes in mean values in distribution of species registration points along each axis. Confidence ellipses for species occurrence in discriminant space were calculated based on the assumption of a bivariate normal distribution using coordinates of centroids, standard deviations by each axis and coefficients of correlation. Ordination axes were calculated based on groups of species which were recorded on >20 occasions.

A cluster analysis (UPGMA algorithm) based on the matrix of Euclidean distances between centroids was used to reveal spatially cohesive groups (spatial guilds) of rodent species in ecological space.

Niche overlap was evaluated by DFA by comparing the observation points of each pair of species separately. As a measure of niche overlap, I used the overlap in the probability of displacement along the discriminant axis (Green, 1974; Cody and Walter, 1976). To evaluate the pattern of niche overlap in discriminant space and its change from year to year, the method of "nearest-neighbor analysis" was used (Inger and Colwell, 1977; Winemiller and Pianka, 1990). Although some limitations of DFA have been suggested (see James and McCulloch, 1990 for review), they have little effect on the stability of results (Williams and Titus, 1988; Tabachnik and Fidell, 1996). Comparison of estimations of niche topological relationships within a community obtained by different ordination techniques (DFA, Principal Component Analysis and Correspondence Analysis) demonstrated that the results produced by discriminant analysis were the closest and most statistically similar to unbiased estimations (Krasnov and Shenbrot, 1998).

Niche breadth values can be calculated using plot scores obtained by the respective ordination technique as average deviation of species registration points from the center of its niche along each ordination axis (Carnes and Slade, 1982). To calculate niche breadth in a multidimensional space, I used the mean Euclidean distance in the space of ordination axes. I used scores obtained through Principal Component Analysis of environmental variables in all set of plots within 11 1-ha grids. In contrast to DFA where groups (species) are defined initially, PCA deals with one data set and evaluates a linear response model in which the abundance of species increases or decreases with the value of each environmental variable (Tabachnik and Fidell, 1996).

The model evaluated by PCA represents distribution of rodent species abundance in ordination space reflecting total variance of environmental characteristics described in the region. In contrast the ordination model in DFA represents only a fraction of the ecological space which is used by community members. In this respect niche breadth calculated through PCA is free of some distortions of DFA and seems preferable for estimation of annual changes.

To analyze the dependence of rodent species diversity on the productivity of vegetation and habitat structural complexity 12 square plots of 0.25 ha each were established in 1997, a year of high abundance of all rodent species. A sandy plain with sage-bush and grass was chosen as a landscape of relatively uniform vegetation with pronounced gradients of productivity and patchiness. As a measure of rodent species diversity in the plots, I used the Shannon index:

$H = - \sum p_i \log_2 p_i$, where p_i is relative abundance of the i -th species.

2 Results

2.1 Patterns of species abundance and habitat use

I recorded 10 rodent species on 11 grids during late spring-early summer of 1997 – 1999. There were 21 *Allactaga major* (13 in 1997, 4 in 1998, 4 in 1999), 32 *A. elater* (20, 6, 6), 42 *Pygeretmus pumilio* (16, 17, 9), 100 *Stylodipus telum* (68, 20, 12), 133 *Meriones meridianus* (60, 11, 62), 145 *M. tamariscinus* (74,

29, 42), 56 *Mus musculus* (13, 23, 20), 261 *Microtus socialis* (237, 14, 10). There were 23 square plots with used winter burrows of *Spermophilus pygmaeus* (20, 1, 2) and 30 square plots with active *Ellobius talpinus* (26, 1, 3). The distribution of species abundance over 1 ha grids is shown in Appendix 1. Comparison of results of cluster analysis of grids by environmental variables (Fig.1B) and by composition and abundance of rodents (Fig.1C) shows only partial conformity of dendrograms. The restricted conformity means that rodent species share an ecological space in some different way than can be expected in accordance with the visible macrohabitat structure of the region (Fig.1A).

Capture rate of live-trapping differed from year to year. It was 19.4% in 1997, 4.0% in 1998, and 7.3% in 1999 (one capture per individual was considered). 1997 was a year of high abundance for all species except *Mus musculus*. *P. pumilio* was also abundant in 1998 and *M. meridianus* in 1999. Abundance of *Mus musculus* increased in 1998, whereas populations of most other species declined drastically after a humid winter with frost and ice crust after cold rain in February. Two species occurred in three grids, two in four, one in six, three in eight and two in nine grids. No species inhabited all grids (Appendix 1).

Stepwise Regression Analysis showed that spatial distribution of each species was only partly determined by environmental variables (from two to six variables) with significant regression coefficients (Table 2). Signs of

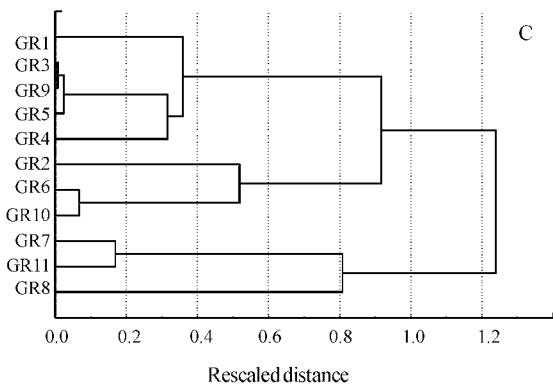
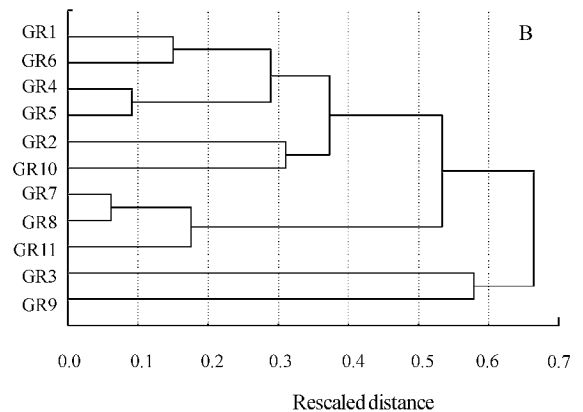
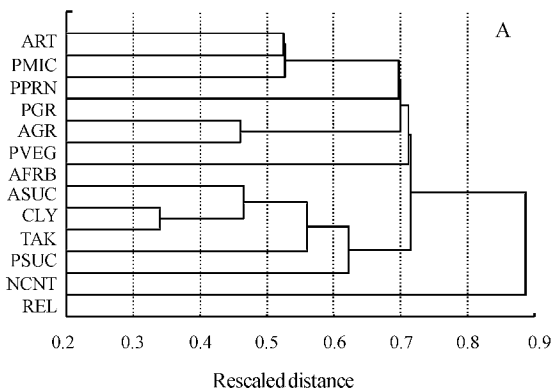


Fig.1 Dendrograms based on UPGMA cluster analyses, showing results of classification (A) of 13 environmental variables in all sets of plots within 11 grids, (B) of 11 grids by 13 environmental variables in all sets of sample plots within grids, (C) of 11 grids by rodent species composition and abundance in all sets of sample plots within grids

See full variable names in Table 1

coefficients reflected the direction of the relationship. Although the equations were strongly significant, the R^2 values were low, varying from 2% to 18%. The result was not improved after entering into analysis both values and square values of observed variables (on the theory that nonlinear relationships might exist).

Six species, *S. pygmaeus*, *A. major*, *A. elater*, *P. pumilio*, *S. telum*, and *M. meridianus*, were associated with habitat variables more common for desert and semi-desert (gaps in vegetation, succulents, microphyllous shrubs, structural complexity of the habitat regions). Four species, *M. socialis*, and to a lesser extent *E. talpinus*, *Mus musculus* and *M. tamariscinus*, were associated with conditions more common for a steppe-like landscape. Each species differed in the

combination of variables that significantly determines its spatial distribution. For instance, the social vole *Microtus socialis* was determined positively by perennial grass cover, *Artemisia* abundance, and negatively by abundance of succulents, being associated with steppe-like conditions. *Stylodipus telum*, inhabiting similar sandy plains, was determined positively by microrelief, presence of gaps in vegetation and negatively by abundance of succulents. A predictable decrease in the sizes of gaps in vegetation cover may lead to a decrease of abundance of this species in the long term.

There were no species with microhabitat affinities that characterized them as strictly desert (inhabitants of only open sands or only hard loam areas) or grassland (communities of tussock grass) inhabitants.

Table 2 Summary of multiple regression analyses of rodent species abundance on environmental parameters

Species	Equation ^a	R^2	F	df	P
<i>S. pygmaeus</i>	SPYG = 0.01PMIC - 0.04ASUC + 0.01TAK	0.03	5.35	4 820	<0.001
<i>A. major</i>	AMAJ = 0.01TAK + 0.02CLY	0.02	4.14	5 819	<0.01
<i>A. elater</i>	AELAT = 0.03TAK - 0.04PSUC + 0.01ASUC - 0.06NCNT	0.07	16.12	4 820	<0.001
<i>P. pumilio</i>	PPUM = 0.13 + 0.38ASUC - 0.30PPRN + 0.02TAK - 0.03PSUC - 0.05REL	0.18	18.28	10 814	<0.01
<i>S. telum</i>	STEL = -0.23 + 0.27REL + 0.07TAK - 0.04ASUC + 0.02AGR	0.09	5.96	13 811	<0.001
<i>M. meridianus</i>	MMER = 0.37 - 0.07TAK - 0.07PGR + 0.31NCNT - 0.09CLY - 0.03AFRB	0.14	16.52	8 816	<0.001
<i>M. tamariscinus</i>	MTAM = 0.53 - 0.10PMIC - 0.16PGR - 0.11CLY + 0.06PPRN - 0.05TAK + 0.03AGR	0.17	13.03	13 811	<0.001
<i>E. talpinus</i>	ETAL = 0.07 - 0.14CLY + 0.05REL - 0.07NCNT + 0.01AFRB + 0.01PPRN	0.08	10.53	7 817	<0.001
<i>Mus musculus</i>	MUS = 0.10REL + 0.03PPRN - 0.01ASUC	0.05	10.15	4 820	<0.001
<i>M. socialis</i>	MSOC = 0.07ART - 0.41ASUC + 0.09PGR	0.09	9.53	8 816	<0.001

^a See Table 1 for acronyms. Only variables with significant regression coefficients were included in equations ($P \leq 0.05$ for rare and $P < 0.01$ for abundant species).

2.2 Partitioning of resources

Discriminant Function Analysis was performed using data on 10 rodent species for all three years pooled together (Tables 3 and 4). The first three DF represent the component of between habitat variation (92.5% of variance) and only the first axis explains the most important contribution to the segregation of species (67.1%). Only this axis can be easily interpreted in accordance with landscape division. It reflects a general landscape gradient from sandy to clay soils; there is a parallel increase of abundance of succulents and in the size of gaps in vegetation that means the presence of takys (vegetation-free clay surfaces). This axis segregates three species of jerboas from the other group of species (Fig.2). Concomitantly, there was a strong arch effect along the second axis which indicates the mathematical artifact (Jongman et al., 1987). This axis practically repeats the segregation of species along the first one, and was omitted from further consideration. Within habitat component of species segregation was not well pronounced and appears in part along DF3 and more clearly along DF4 axes that can be interpreted

approximately as within habitat changes of conditions towards desert-like habitat (increase of habitat structural complexity and decrease of productivity). Only this axis segregates two species of gerbils and the mole vole, whereas the first and third DF axes provide segregation of jerboa species. There were no specific axes of the discriminant space that could explain the distribution of any one species.

Table 3 Summary of Discriminant Function Analysis of rodent species positions in the resource space

Information	1997 - 1999			
	DF1	DF2	DF3	DF4
Eigenvalue	2.542	0.641	0.321	0.132
Chi-square test for significance	1 910.6	865.3	455.8	225.2
Degrees of freedom	120	99	80	63
% discriminant information	67.09	16.91	8.50	3.50
Probability	<0.001	<0.001	<0.001	<0.001

DF1 - DF4 are the first four discriminant functions accounting for a total 96% of the variance. Data from 1997 - 1999 were pooled.

Table 4 Linear correlation between each discriminant function and each environmental variable in the observation vector^a

Variable ^b	DF1	DF2	DF3	DF4
REL	-0.14	-0.09	0.26	-0.25
CLY	0.50	0.41	0.011	0.37
AGR	-0.08	0.06	0.24	-0.15
AFRB	-0.06	-0.18	-0.25	-0.50
ASUK	0.70	-0.47	-0.31	0.04
TAK	0.57	0.20	0.59	-0.08
PGR	-0.06	0.35	-0.40	-0.04
PMIC	0.00	0.45	-0.06	0.25
PPRN	-0.085	0.48	-0.28	-0.31
PVEG	-0.03	0.23	-0.31	-0.20
NCNT	0.11	0.016	0.19	0.47
PSUK	0.15	-0.00	0.09	-0.04

^a Data from 1997 – 1999 were pooled.

^b Acronyms of environmental variables are shown in Table 1.

All habitats in the region can be subdivided into two big groups. The first is represented by sandy plains and dunes at different stages of stabilization. The second, by depressions and dry river beds with more clay content in the soil.

The structure of the rodent community revealed by the results of DFA based on use of habitat variables only at sites where rodents were caught/registered reflects the general landscape structure and is associate with two clusters of environmental variables in Fig.1A. It indicates the existence of two spatial guilds of rodent species that can be considered at a first estimate as psammophylous and sclerophylous (Fig.3).

The last group is represented by only three species of jerboas from which only *Pygeretmus pumilio* is strictly sclerophilous (Fig.2). Most species are associated with sandy habitats.

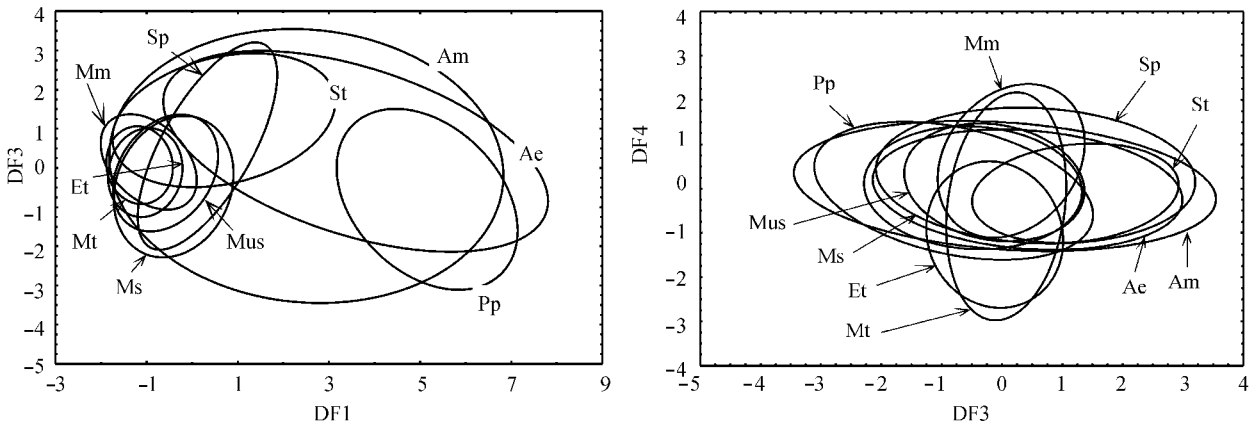


Fig.2 Ninety percent confidence ellipses for rodent species in ordination space of DF1 and DF3, and DF3 and DF4
Full species names for this and subsequent figures see in the legend for Appendix 1.

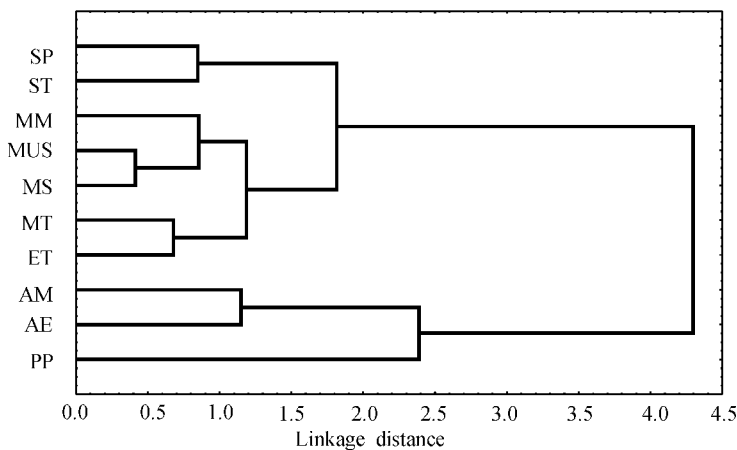


Fig.3 Dendrogram based on UPGMA cluster analyses of Euclidean distances between niche centroids in DF ordination space

2.3 Variation of niche parameters

The position of niches was not constant from year to year (Fig.4.) Significant from year to year shifts of niche centers were evaluated for four species (*A. elater*,

S. telum, *M. tamariscinus* and *Mus musculus*) along DF1 and for three species (*P. pumilio*, *S. telum*, *M. meridianus*) along DF3 (Table 5). Shifts along DF1 reflect mainly between habitat variation, whereas shifts

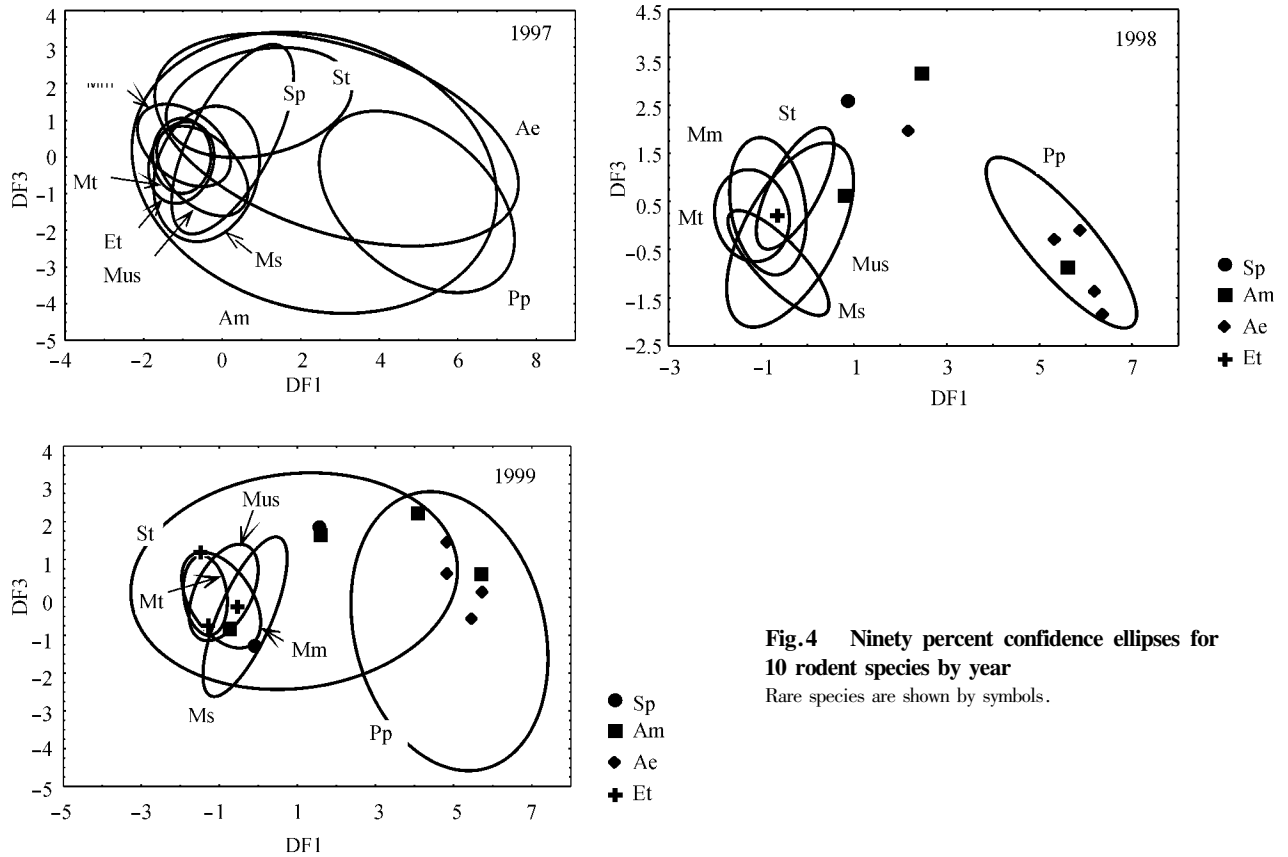


Fig.4 Ninety percent confidence ellipses for 10 rodent species by year

Rare species are shown by symbols.

Table 5 Annual variation in positions of species centroids along first (DF1) and third (DF3) axes of discriminant space

Species	Year	Mean \pm SE		Student's <i>t</i> values		
		1997	1998	1997 - 1998	1997 - 1999	1998 - 1999
		<i>N</i> ₉₇	<i>N</i> ₉₈			
<i>S. pygmaeus</i>	1997	20	1	1997 - 1998	1997 - 1999	1998 - 1999
	DF1	0.27 \pm 0.19	0.88	-	0.55 ^{ns}	-
<i>A. major</i>	1997	13	3	0.38 ^{ns}	0.2 ^{ns}	0.14
	DF1	2.35 \pm 0.67	2.95 \pm 1.41			
<i>A. elater</i>	1997	20	6	1.81 ^{ns}	2.09*	0
	DF1	2.92 \pm 0.56	4.70 \pm 0.81			
<i>P. pumilio</i>	1997	16	17	1.52 ^{ns}	0.13 ^{ns}	1.43 ^{ns}
	DF1	4.96 \pm 0.33	5.47 \pm 0.05			
<i>S. telum</i>	1997	68	20	6.08***	0.05 ^{ns}	1.89 ^{ns}
	DF1	0.94 \pm 0.17	-0.26 \pm 0.10			
<i>M. meridianus</i>	1997	60	11	0.8 ^{ns}	0.17 ^{ns}	0.69 ^{ns}
	DF1	-0.97 \pm 0.09	-0.85 \pm 0.12			
<i>M. tamariscinus</i>	1997	74	28	1.69 ^{ns}	4.67***	1.80 ^{ns}
	DF1	-1.03 \pm 0.05	-1.19 \pm 0.08			
<i>E. talpinus</i>	1997	26	1	-	0.20 ^{ns}	-
	DF1	-1.04 \pm 0.09	-0.63			
<i>Mus musculus</i>	1997	13	23	0.55 ^{ns}	1.92 ^{ns}	2.67*
	DF1	-0.50 \pm 0.17	-0.37 \pm 0.16			
<i>M. socialis</i>	1997	237	14	1.45 ^{ns}	0.28 ^{ns}	-
	DF1	-0.39 \pm 0.05	-0.62 \pm 0.15			
		<i>N</i> ₉₇	<i>N</i> ₉₈			
		DF3	DF3			
<i>S. pygmaeus</i>	1997	20	1	1997 - 1998	1997 - 1999	1998 - 1999
	DF3	0.49 \pm 0.31	2.58	-	0.13 ^{ns}	-
<i>A. major</i>	1997	13	3	0.36 ^{ns}	0.59 ^{ns}	0.03 ^{ns}
	DF3	-0.43 \pm 0.55	0.96 \pm 1.18			
<i>A. elater</i>	1997	20	6	0.57 ^{ns}	0.35 ^{ns}	0.81 ^{ns}
	DF3	0.47 \pm 0.36	0.04 \pm 0.66			
<i>P. pumilio</i>	1997	16	17	2.14*	0.49 ^{ns}	0.84 ^{ns}
	DF3	-1.22 \pm 0.33	-0.36 \pm 0.23			
<i>S. telum</i>	1997	68	20	3.61***	2.42*	0.78 ^{ns}
	DF3	1.48 \pm 0.11	0.78 \pm 0.16			
<i>M. meridianus</i>	1997	60	11	0.34 ^{ns}	2.89**	1.94 ^{ns}
	DF3	0.32 \pm 0.09	0.40 \pm 0.22			
<i>M. tamariscinus</i>	1997	74	28	1.39 ^{ns}	0.18 ^{ns}	0.82 ^{ns}
	DF3	0.03 \pm 0.07	0.20 \pm 0.10			
<i>E. talpinus</i>	1997	26	1	-	0.36 ^{ns}	-
	DF3	-0.15 \pm 0.12	0.19			
<i>Mus musculus</i>	1997	13	23	0.63 ^{ns}	1.36 ^{ns}	1.48 ^{ns}
	DF3	-0.38 \pm 0.18	-0.20 \pm 0.22			
<i>M. socialis</i>	1997	237	14	1.87 ^{ns}	0.15 ^{ns}	0.72 ^{ns}
	DF3	-0.46 \pm 0.07	-0.77 \pm 0.15			

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ^{ns} Differences are not significant.

Table 6 Results of PCA of environmental variables in 11 grid areas^a

Information	1997 – 1999 ^b			
	PC1	PC2	PC3	PC4
Eigenvalue	3.26	2.41	1.84	1.63
% total variance	21.76	16.11	12.30	10.84
% cumulative	21.76	37.87	50.17	61.02
Factor loadings ^c : ASUC ^d	0.69			
CLY	0.83			
PSUC	0.56			
TAK	0.81			
NCNT	0.53			
PPRN		0.74		
PMIC		0.69		0.52
PVEG		0.60		
REL		-0.52		
AGR			0.73	
ART				0.57
PGR				-0.55

^a PC1 – PC4 are the first four principal components accounting in total 61% of variance. ^b Data from 1997 – 1999 were pooled. ^c Linear correlations ($r > 50\%$) between each PC and each environmental variable. ^d Acronyms of environmental variables are shown in Table 1.

along DF3 reflect both between and within habitat variation. No significant correlation was found between relative change in abundance and in niche position along DF1 ($R^2_{1997-1998} = 0.08$, ns, $R^2_{1998-1999} = 0.07$, ns) and DF3 ($R^2_{1997-1998} = 0.10$, ns, $R^2_{1998-1999} = 0.08$, ns; *S. pygmaeus* and *E. talpinus* were omitted as rare in 1998 – 1999). A significant shift of niche center characterized *Mus musculus*, a species with relatively stable abundance, but not *Microtus socialis*, a species

characterized by a drastic decline in abundance after 1997. There was no pronounced correlation between shifts in niche position and annual changes in species abundance ($R^2 = 0.04$, $n = 8$, ns).

Niche breadth values were calculated using scores obtained through Principal Component Analysis of environmental variables regardless of rodents' distribution (Table 6). The first four PC were most informative, accounting for 61% of total variance; values of niche breadth were estimated within the space of these components (Table 7). During the period of my observations spatial niche breadth changed significantly in five species out of (*A. elater*, *S. telum*, *M. meridianus*, *M. tamariscinus*, *Mus musculus*). No significant correlation was found between annual shifts in species abundance and in niche breadth ($R^2_{1997-1998} = 0.00$, ns, $R^2_{1998-1999} = 0.06$, ns—I considered only abundant species; *A. major*, *A. elater*, *S. pygmaeus*, *E. talpinus* were omitted as rare in 1998 – 1999). The niche breadth of abundant species changed independently ($R^2_{1997-1998} = 0.04$, ns, $R^2_{1998-1999} = 0.04$, ns). Yearly changes in species abundance did not correlate with shifts in niche breadth when only significant shifts were considered ($R^2 = 0.04$, $n = 7$, ns). There were no pronounced positive relationships between the abundance of a single species and its niche breadth (Fig.5). Even *M. socialis*, a species with the most pronounced change in abundance, did not extend its spatial niche significantly. A threefold decrease in the abundance of *S. telum*, from 1997 to 1998 was associated with the highly significant narrowing of its niche, whereas a slight decrease in its abundance from 1998 to 1999 was associated with a significant increase of species niche breadth.

Table 7 Niche breadth values of rodent species in different years

Year	1997		1998		1999		Student's <i>t</i>		
	<i>N</i> ₉₇	Mean ± SE	<i>N</i> ₉₈	Mean ± SE	<i>N</i> ₉₉	Mean ± SE	1997 – 1998	1997 – 1999	1998 – 1999
<i>S. pygmaeus</i>	20	1.2 ± 0.1	1		2				
<i>A. major</i>	13	1.9 ± 0.2	4	1.8 ± 0.4	4	1.8 ± 0.4	0.22 ^{ns}	0.22 ^{ns}	0.00 ^{ns}
<i>A. elater</i>	20	1.4 ± 0.1	6	0.8 ± 0.2	6	1.2 ± 0.2	2.68*	0.89 ^{ns}	1.41 ^{ns}
<i>P. pumilio</i>	16	1.1 ± 0.1	17	1.1 ± 0.1	9	1.2 ± 0.1	0.00 ^{ns}	0.71 ^{ns}	0.71 ^{ns}
<i>S. telum</i>	68	2.7 ± 0.3	20	0.9 ± 0.2	12	2.0 ± 0.2	4.99 ^{***}	1.94 ^{ns}	3.88 ^{***}
<i>M. meridianus</i>	60	1.7 ± 0.1	11	2.1 ± 0.2	62	1.6 ± 0.1	1.78 ^{ns}	0.71 ^{ns}	2.23*
<i>M. tamariscinus</i>	74	1.1 ± 0.1	29	1.3 ± 0.1	42	1.4 ± 0.1	1.41 ^{ns}	2.12*	0.71 ^{ns}
<i>E. talpinus</i>	26	2.2 ± 0.1	1		3				
<i>Mus musculus</i>	13	1.6 ± 0.1	23	1.7 ± 0.1	20	1.0 ± 0.1	0.71 ^{ns}	4.24 ^{***}	4.95 ^{***}
<i>M. socialis</i>	237	1.8 ± 0.04	14	1.6 ± 0.1	10	1.8 ± 0.1	1.85 ^{ns}	0.00 ^{ns}	1.41 ^{ns}

* $P < 0.05$, *** $P < 0.001$, ^{ns}: differences are not significant.

Niche breadth was calculated as mean Euclidean distance in space of PC1 – PC4.

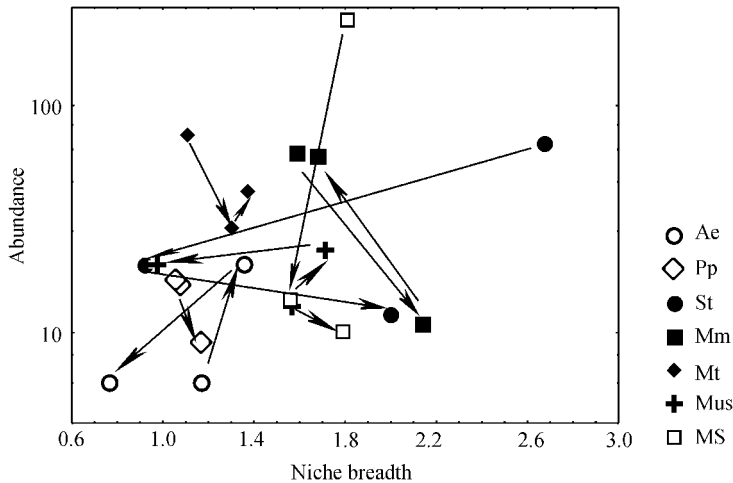


Fig.5 Relationship between abundance and niche breadth of each rodent species in different years as indicated by arrows

Each arrow shows the direction of annual shift. Abundance is represented on logarithmically scaled axis.

2.4 Niche overlap and changes of spatial community structure

Most pairs of species were characterized by low values of niche overlap (Appendix 2 and 3). Seven of 45 values in 1997, one of 28 values in 1998 and five of 28 values in 1999 exceeded 20 per cent. There were twelve, five and two values respectively, varying from 10 to 20 per cent. The mean overlap was 0.10 in 1997, 0.06 in 1998, and 0.09 in 1999 (Mann-Whitney U : $Z_{1997-1998} = 2.27$, $P < 0.05$, $Z_{1997-1999} = 1.05$, ns, $Z_{1998-1999} = 1.05$, ns).

The results of analyses of community organization based on niche overlap values indicate a partial destruction of the community guild structure in years of rodents' low abundance (Fig.6). The reason for guild destruction consists both in a decrease of overlap values (owing to a decrease in the abundance of some species) and in the disappearance of some other species. The hump-shaped form of the curve of standard deviation of niche overlap values existed only in a year of high rodent abundance. This pattern was associated with the more low-grade line of mean overlap in 1997 that exceeded lines for 1998 and 1999 at parts corresponding to a lower order of proximity. The values of overlap among a group of nearest neighbors in overlap were similar from year to year, varying non-significantly (Mann-Whitney U) from 0.24 ± 0.003 in 1997 to 0.19 ± 0.03 in 1998 and to 0.26 ± 0.03 in 1999.

2.5 Steppe expansion and rodents diversity

Steppe expansion in the region of my study leads in the first place to within habitat changes. Productivity tends to increase whereas habitat heterogeneity decreases. An analysis of relationships between these variables and rodent species diversity was conducted within one habitat type, the sagebrush with grass plain, in a set of 12 0.25-ha grids (Fig.7). Rodents diversity linearly increased

with an increase of diversity of microhabitats ($R^2 = 0.38$, $P < 0.05$, $Y = 0.37 + 0.76X$), and decreased with an increase of productivity of ephemeral plants represented mainly by two genera of Poaceae, *Anisantha* and *Poa* ($R^2 = 0.59$, $P < 0.05$, $Y = 1.87 - 0.002X$), and of cover of vegetation ($R^2 = 0.60$, $P < 0.05$, $Y = 3.15 - 0.06X$).

3 Discussion

One objective of this study was to examine the rodent community of southern Kalmykia ("Chernie Zemli") in order to understand the responses of rodent species to environmental variables, based on data obtained during three years of intensive recovery and succession of vegetation after a ten-fold decrease in live-stock. I supposed that I would be able to predict abundance and distribution of rodent species in the future, if steppe expansion continues in the region.

Steppe expansion in Kalmykia has been well documented process since the beginning of 1990 (Vinogradov and Kulik, 1996; Neronov, 1997a, b). Over ten years there were no pronounced changes in the species composition of rodent fauna (Shilova et al., 2000). During this study the community was represented mostly by rodent species with ranges of desert and semidesert type. Only *A. major* is a species widely distributed in steppe, and *E. talpinus* is a species, inhabiting steppe, semi-desert and some desert habitats. The abundance of some species (*S. pygmaeus*, *M. meridianus*, *M. tamariscinus*, *M. socialis*) changed in comparison with the period of intense anthropogenic disturbance in the 1980s, and these changes were discussed with respect to the recent steppe expansion (Shilova et al., 2000). For other species, comparative data were absent.

Stepwise Regression Analysis demonstrated that

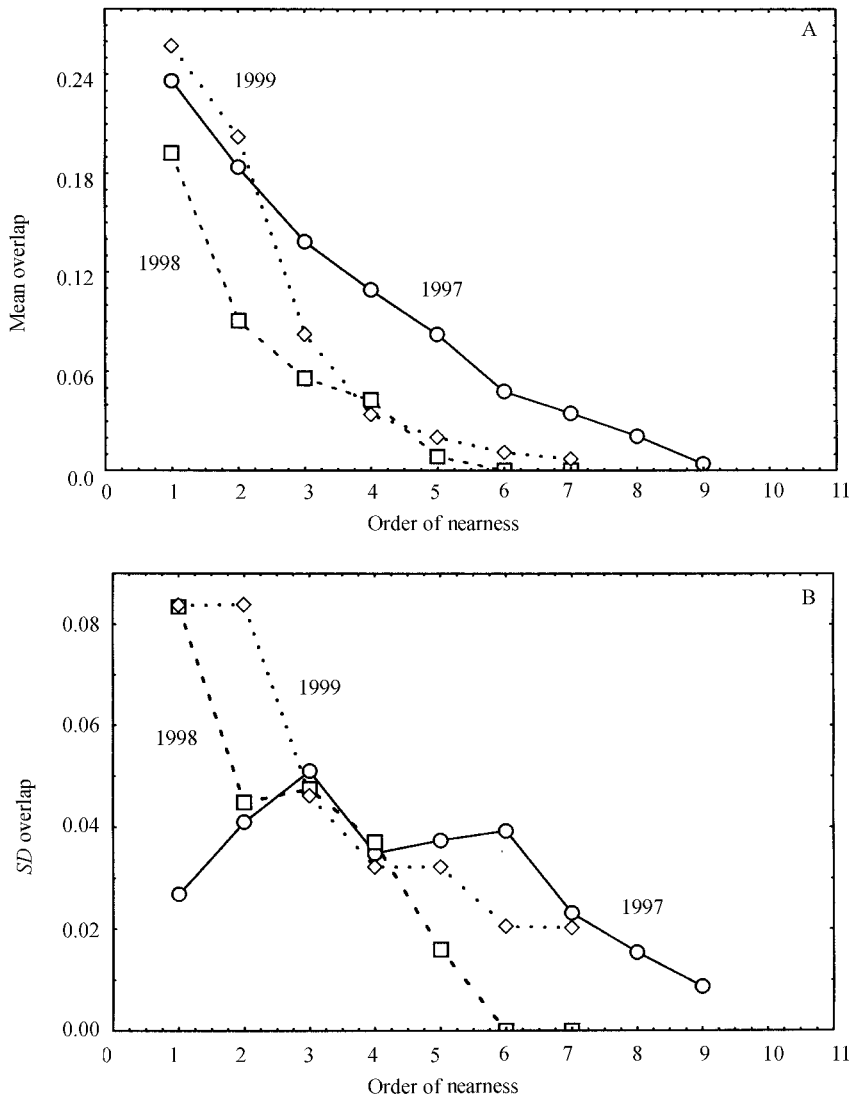


Fig.6 Mean (A) and standard deviation (B) of niche overlap against rank of niche neighbor for a rodent species community in 1997, 1998, and 1999

environmental variables in grids only partially explain the habitat occupancy of each species. Coefficients of determination (R^2) did not exceed 18%, and were noticeably lower than in similar analyses provided for the rodent community in a real desert in Israel (Shenbrot and Krasnov, personal communication). For most species this result seems unconnected with the lack of data. The reason may have to do with the specific situation in the region, i. e. with changing environmental conditions. The recent steppe expansion has decreased habitat heterogeneity; both components of within- and between-habitat variation decreased from year to year. The apparently low level of selectivity shown by each species, relating to habitat variables, may be the result of some inertia in species' responses to environmental changes. Nevertheless, the results of the analyses allow us to ascribe most rodent species in their requirements to desert or semi-desert forms. I may predict, for instance, a decrease in the abundance of *S. telum* with the

overgrowing of gaps in vegetation in sandy, sage-bush and grass areas. *M. socialis* in a similar habitat type will be favored by the further growth of tussock grass and sagebrush (*Artemisia*).

My second objective was to determine temporal changes in the spatial organization of the rodent community using uniform methods of data collection and analysis. Discriminant Function Analysis and Principal Component Analysis show that community structure, as well as niche parameters of concrete species, varied from year to year. The results of the analyses show that the spatial guild structure was well expressed in a year of high species abundance when niche overlap was higher in pairs of species with moderate and low overlap. This pattern was similar to that obtained for the South Bukhara Desert (Shenbrot, 1992) and for the Kyzylkum Desert (Shenbrot and Rogovin, 1995). At low density, the guild structure became inconspicuous because of the disappearance of some species, mostly two jerboa species from the

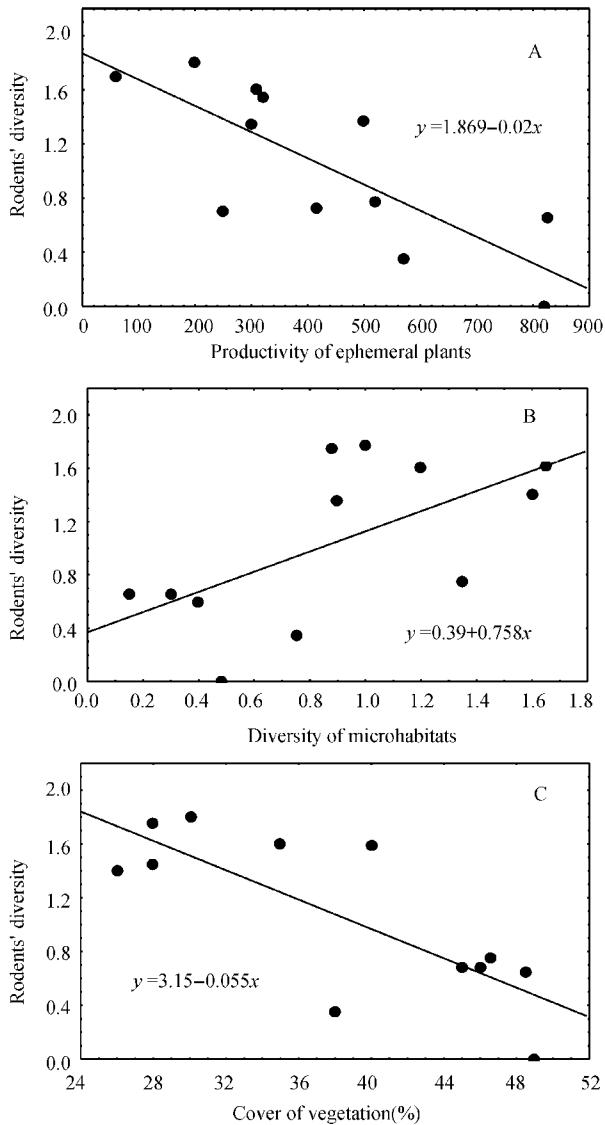


Fig. 7 Dependence of rodents' α -diversity (A) on productivity of ephemeral plants, (B) on diversity of microhabitats, and (C) on percent cover of vegetation in twelve 0.25 ha plots distributed within one habitat type, sagebrush with grass plain

sclerophyllous guild. At the same time, the relative stability of the position of niches of some psammophilous species or shifts within the group of related sandy habitats indicates a temporal stability of the psammophilous guild with some changes of within-guild structure.

Three years is too short period for conclusions about trends in rodent community dynamics. In three years it seems impossible to separate particular components of the rodent population dynamic from those challenged by direct changes in the environment. Short-term local fluctuations in temperature and humidity (mostly in a cold period) can influence rodent populations. The rate of recovery and succession also differs in different habitat types. The process is fast in anthropogenic habitats and in sandy plains (Neronov, 1997a; Neronov et al., 1977), and

seems to go slower in habitats with clay loam soils. Thus, the responses can differ among species adapted for habitats with sandy and clay loam soils.

The results of the analyses of abundance, niche position and niche breadth show that species tend to respond to fluctuating conditions and resources in accordance with their own individualistic manner. In general, these results signify that rodent community organization is more associated with a Gleasonian vision of the community (Gleason, 1926) as an opportunistic collection of species, than with the Clementsian view (Clements, 1949) on the community as a well organized co-adapted system. The approach used in this study was derived from the Hutchinsonian niche concept that assumes highly individualistic species responses in a spatially heterogeneous environment (Brown, 1995). Independent temporal variations of niche parameters appears as another reflection of highly individualistic, species-specific ecological adaptations. At the same time, the fluctuations of abundance and other niche parameters as well as an absence of pronounced trends in changes of rodent abundance along main environmental gradients may indicate a non-equilibrium state in the community. The present steppe-like landscape represents transition stages of the succession. The observed plant and animal communities appear to be unstable systems lacking strong self-organizing patterns (Neronov, 1997b; Shilova et al., 2000).

A highly pronounced individualism of species in their responses to the environmental dynamics may lead to the predictable (non-random) changes of some general community characteristics, such as total biomass, species richness, and species diversity. The results of analyses in a limited spatial scale show that rodent species diversity correlates positively with habitat structural complexity and negatively with characteristics of productivity. This result was obtained in areas with fast recovery and succession of vegetation. Steppe expansion there leads to an increase in primary productivity and to a decrease in habitat heterogeneity. The inverse relationship between habitat structural heterogeneity and primary productivity was discussed as a possible explanation for the hump-shaped form of dependence of rodent diversity on productivity of vegetation in an Israeli desert (Abramsky and Rosenzweig, 1984; Rosenzweig and Abramsky, 1993). The most patchy habitat structure coincides there with moderate conditions of productivity. Steppe expansion in Kalmykia may lead in time to a decrease in species abundance and diversity of rodents of desert and semi-desert origin. An analysis of the history of the exploitation of the Caspian lowlands by man in the 19th and early 20th centuries (Neronov, 1997b) shows the positive role of moderate grazing (both different kinds of livestock and wild saiga antelope) in maintaining semi-desert landscape structure and as a consequence of the rich and unique rodent

fauna. Now it is difficult to predict to what extent steppe rodents from the north can compensate for the decrease in species diversity. During the period of this study a common steppe component of the fauna was weakly pronounced. The only typical steppe species, *Sicista subtilis* Pallas, 1773, which had been registered in the region earlier, continued to be a rare representative, and was caught outside of my grids.

Acknowledgements I am very grateful for help in collecting data to all participants of the Complex Kalmykian Expedition of the A.N. Severtzov Institute of Ecology and Evolution (RAS), and especially to Dmitry Alexandrov, Andrew Chabovsky, Vladimir Neronov, Ludmila Savinetskaya, and Prof. Svetlana Alexandrovna Shilova. I am greatly indebted to my friends and colleagues Jan A. Randall and Joanne Turnbull who kindly agreed to look through the manuscript and to correct the English.

References

- Abramsky Z, Rosenzweig M, 1984. Tilman's predicted productivity-diversity relationship shown by desert rodents. *Nature* 309: 150 – 151.
- Brown JH, 1995. *Macroecology*. Chicago: University of Chicago Press, 269.
- Carnes BA, Slade NA, 1982. Some comments on niche analysis in canonical space. *Ecology* 63: 888 – 893.
- Clements FE, 1949. *Dynamics of Vegetation*. New York: Hafner Press, 500.
- Cody ML, Walter H, 1976. Habitat selection and interspecific interactions among Mediterranean sylviid warblers. *Oikos* 27: 210 – 238.
- Gleason HA, 1926. The individualistic concept of plant associations. *Bulletin of the Torrey Botanical Club* 53: 7 – 26.
- Green RH, 1974. Multivariate niche analysis with temporally varying environmental factors. *Ecology* 52: 73 – 83.
- Heptner VG, 1945. Desert-steppe fauna of the Palaearctic and centers of its origin. *Bull. Mosc. Soc. Natur: Ser. Biol.* 50: 17 – 38 (In Russian).
- Inger RF, Colwell RK, 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecological Monographs* 47: 229 – 253.
- James FC, McCulloch CE, 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review in Ecology and Systematics* 21: 129 – 166.
- Jongman RHG, Ter Braak CJF, Van Tongeren OFR, 1987. *Data Analysis in Community and Landscape Ecology*. Wageningen, Netherlands: Pudoc, 301.
- Kotenkova EV, Bulatova NS, 1994. *The House Mouse*. Moscow: Nauka Press, 267 (In Russian).
- Krasnov BR, Shenbrot GI, 1998. Structure of communities of ground-dwelling animals at the junction of two phytogeographic zones. *Journal of Biogeography* 25: 1 115 – 1 131.
- Kutcheruk VV, 1994. The area of superspecies complex *Mus musculus* s. lato. In: Kotenkova EV, Bulatova NS ed. *The House Mouse*. Moscow: Nauka Press, 267 (In Russian).
- Neronov V, 1997a. Age old dynamics of Caspean semi-deserts. *Nature and People* 4: 49 – 51 (In Russian).
- Neronov VV, 1997b. On the history of mass dispersion and phytocenology of tyrsa grass (*Stipa capillata* L.) in Kalmykia. *Arid Ecosystems* 3 (5): 82 – 92 (In Russian).
- Neronov VV, 1997. Spatial distribution of rodents in conditions of an anthropogenic dynamic of vegetation in southern Kalmykia. *Ekologia* 5: 369 – 376 (In Russian).
- Panteleev PA, 1998. *Rodents of the Palaearctic. Composition and areas*. Moscow: A.N. Severtzov Institute of Ecology and Evolution Publ., 116.
- Popov NV, Survillo AV, Knyazeva TV, Varshavskii BS, Podsvirov AV, Sadzhiyev VB, Yakovlev SA, 1995. Biocenotic effects of anthropogenic landscape transformation of Chernye Zemli. In: Zonn IS, Neronov VM ed. *Biota and Environment of the Kalmykia Republic*. Moscow, Elista: Korkis Publ., 211 – 221 (In Russian).
- Rosenzweig M, Abramsky Z, 1993. How are diversity and productivity related? In: Ricklefs RE, Schluter D ed. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. Chicago: University of Chicago Press, 52 – 65.
- Rogovin KA, Shenbrot GI, 1995. Geographical ecology of Mongolian desert rodent communities. *Journal of Biogeography* 22: 111 – 128.
- Schoener TW, 1986. Resource partitioning. In: Kikkawa J, Anderson DJ ed. *Pattern and Process*. California: Blackwell Scientific Publications, 91 – 126.
- Schoener TW, 1989. The ecological niche. In: Cherratt JM ed. *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World*. Oxford: Blackwell, 79 – 113.
- Shenbrot GI, 1992. Spatial structure and niche patterns of a rodent community in the south Bukhara desert (Middle Asia). *Ecography* 15: 347 – 357.
- Shenbrot G, Krasnov B, 2004. Temporal dynamics in spatial organization of a rodent community in the Negev Highlands (Israel). *Journal of Zoology Lond.* 263: 207 – 218.
- Shenbrot GI, Rogovin KA, 1995. Temporal variation in the spatial organization of a rodent community in the southwestern Kyzylkum Desert (Central Asia). *Ecography* 18: 370 – 383.
- Shenbrot GI, Sokolov VE, Heptner VG, Kovalskaya YM, 1995. *Mammals of Russia and adjacent regions. Dipodid rodents*. Moscow: Nauka Press, 573 (In Russian).
- Shenbrot GI, Krasnov BR, Rogovin KA, 1999. *Spatial ecology of desert rodent communities*. Berlin, Heidelberg, New York: Springer-Verlag, 292.
- Shilova SA, Chabovskii AV, Isaev SI, Neronov VV, 2000. Dynamics of the rodent community and populations in Kalmyk semi-deserts under conditions of decreasing pastoral load and increasing humidity. *Proceedings of Russian Academy of Sciences. Biological Series* 3: 332 – 344 (In Russian).
- Tabachnik BG, Fidell LS, 1996. *Using multivariate statistics*. 3 rd edn. New York: Harper Collins College Publications.
- Tupikova NV, 1995. Map of rodent population in Kalmykia and adjacent areas. In: Zonn IS, Neronov VM ed. *Biota and Environment of the Kalmykia Republic*. Moscow, Elista: Korkis Publ., 196 – 210 (In Russian).
- Vinogradov BV, Kulik KN, 1996. Cartography of dynamic of lands' desertification using aero- and space snapshots. *Proceedings of Russian Academy of Sciences. Geological Series* 2: 140 – 149 (In Russian).
- Wiens JA, 1989. *The Ecology of Bird Communities, Vol. 1. Foundations and Patterns*. Cambridge: Cambridge University Press, 520.
- Williams B, Titus K, 1988. Assessment of sampling stability in ecological applications of discriminant analysis. *Ecology* 69: 1 275 – 1 285.
- Winemiller KO, Pianka ER, 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60: 27 – 55.
- Zar JH, 1984. *Biostatistical Analysis*, 2nd edn. London: Prentice-Hall.
- Zonn SV, 1995. Desertification of natural resources of agrarian production of Kalmykia in the last 70 years and measures of its control. In: Zonn IS, Neronov VM ed. *Biota and Environment of the Kalmykia Rpublic*. Moscow, Elista: Korkis Publ., 19 – 52 (In Russian).

Appendix 1 Relative densities of rodent species on 1-ha grids in 1997 – 1999

Grid	Year	Species of rodents									
		Sp*	Am	Ae	Pp	St	Mm	Mt	Et**	Ms	Mus
1	1997	1				15	7	10	9	41	4
	1998					18	3	5		4	6
	1999					2	10	14	1	1	15
2	1997					1	6	31	14	13	
	1998					1		12	1	3	1
	1999					1	4	17	2		1
3	1997		2							40	1
	1998										1
	1999					2	2			3	
4	1997	11	2	6		32				33	
	1998	1				1				1	3
	1999		1			4	3			3	
5	1997	3	1	1		10	2			49	
	1998		1							2	5
	1999	1				1	1			1	1
6	1997	2	1	2		3	20	31		23	6
	1998						5			1	4
	1999						26	4			3
7	1997		3	8	4	1				3	
	1998		1	1	4						
	1999		1	3	5						
8	1997		1	2	1	6					
	1998		1								
	1999		1	1							
9	1997	3	1							31	1
	1998									3	2
	1999	1					1			2	
10	1997						25	2		4	1
	1998						3	12			1
	1999						15	7			
11	1997		2	1	11				3		
	1998		1	5	13						
	1999		1	2	4	2					
Total	1997	20	13	20	16	68	60	74	26	237	13
	1998	1	4	6	17	20	11	29	1	14	23
	1999	2	4	6	9	12	62	42	3	10	20

Sp: *Spermophilus pygmaeus*; Am: *Allactaga major*; Ae: *A. elater*; Pp: *Pygeretmus pumilio*; St: *Stylodipus telum*; Mm: *Meriones meridianus*; Mt: *M. tamariscinus*; Et: *Ellobius talpinus*; Ms: *Microtus socialis*; Mus: *Mus musculus*. * *S. pygmaeus* were registered by the presence of actually used winter burrows within each 20 × 20 m sample plot (presence = 1, absence = 0). ** *E. talpinus* were registered by the presence of groups of fresh mounds within each plot (presence = 1, absence = 0).

1: Sandy banks at the site of a sheep-fold abandoned 40 years ago with complex mosaic of vegetation dominated by *Eremopyron triticeum*, *Anisantha tectorum*, *Ceratocarpus arenarius*, summer vegetated *Portulaca oleracea*, and with sagebush (*Artemisia lerchiana*, *A. scoparia*), tussock grass (*Agropiron fragile*) and herbs in hollows. 2: Sandy plain with tussock grass, *Stipa capillata*, *Agropiron fragile* and sparse *Artemisia lerchiana* with ephemeral *Poa bulbosa*, *Anisantha tectorum*, *Carex stenophylla*. 3: Low stabilized sand ridges covered by small shrubs (*Artemisia lerchiana*, *Artemisia csoparia*, *Kochia prostrata*, *Tanacetum achilleifolium*), grass vegetation (*Agropiron fragile*, *Stipa capillata*, *S. lessingiana*) and ephemeral herbs (*Alyssum turkestanicum*, *Anisantha tectorum*, *Veronica verna*, *V. triphyllus* etc.). 4: Low sandy-loess sagebush (*Artemisia lerchiana* + *Artemisia austriaca*) plain with ephemeral grass (*Anisantha tectorum*, *Poa bulbosa*) and gaps of hard surface free of vegetation. 5: The same habitat type with higher productivity of vegetation and few gaps. 6: Area around a sheep-fold abandoned 15 years ago with complex mosaic of vegetation of early stages of restoration succession dominated by *Eremopyron triticeum*, *Anisantha tectorum*, *Ceratocarpus arenarius*, *Atriplex* sp., summer vegetated succulents, etc. 7: Clay depression associated with an ancient stream bed of the Manyich River and covered with sparse vegetation of succulents, *Haloenemum strobilaceum*, *Anabasis* sp., *Salsola* sp., and grass *Puccinellia distans*. 8: Low clay loam plain vegetated by *Anabasis* sp., *Salsola* sp., *Compharosma* sp., *Artemisia santorica*, and grass *Puccinellia distans* and *Stipa capillata*. Non-vegetated hard surfaces associated with abandoned roads. 9: Sandy loess sagebush *Artemisia lerchiana* plain of upper exposition with participation of *Stipa capillata* and annuals, *Anisantha tectorum*, *Alyssum desertorum* etc. 10: Semi-stabilized sand dunes at the edge of sandy sagebush plain with dense grass *Poa bulbosa*. Dunes are covered by annual plants (*Agriophyllum* sp., *Xanthium strumarium*, *Climacoptera crassa*). Grid also includes areas of open sands. 11: Clay loam area around artesian wells with alluvial saline sandy shield and mosaic of vegetation of *Atriplex* sp., *Salsola* sp., grass (*Eremopyron orientale*, *E. triticeum*, *Puccinellia distans*), suppressed sagebrush (*Artemisia* sp.) and gaps of hard clay surface (takyr).

Appendix 2 Niche overlap values in 1997 (above diagonal) and in 1998 (below diagonal)

	Sp	Am	Ae	Pp	St	Mm	Mt	Et	Ms	Mus
Sp	–	0.121	0.250	0.000	0.205	0.037	0.032	0.000	0.214	0.061
Am		–	0.182	0.207	0.099	0.027	0.023	0.000	0.032	0.116
Ae			–	0.111	0.136	0.037	0.032	0.000	0.070	0.061
Pp				–	0.024	0.000	0.000	0.000	0.016	0.000
St					–	0.094	0.113	0.054	0.148	0.037
Mm						–	0.261	0.151	0.131	0.192
Mt							–	0.270	0.180	0.115
Et								–	0.126	0.103
Ms									–	0.220
Mus										–

Mnemonics as in Appendix 1.

Appendix 3 Niche overlap values in 1999

	Sp	Am	Ae	Pp	St	Mm	Mt	Et	Ms	Mus
Sp	–									
Am		–	0.200	0.077	0.250	0.015	0.022		0.000	0.042
Ae			–	0.067	0.267	0.000	0.000		0.000	0.000
Pp				–	0.095	0.015	0.000		0.000	0.000
St					–	0.059	0.057		0.188	0.094
Mm						–	0.298		0.076	0.347
Mt							–		0.000	0.258
Et								–		
Ms									–	0.033
Mus										–

Mnemonics as in Appendix 1.