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Source: Journal of Vertebrate Biology, 70(1)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.20091

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2021, 70(1): 20091 DOI: 10.25225/jvb.20091

RESEARCH PAPER

Microhabitat partitioning in a rodent community in the arid conditions of the South-western Caspian Lowland

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Received 25 August 2020; Accepted 26 January 2021; Published online 5 March 2021

Abstract. This article analyses the factors underlying the spatial distribution of a rodent community in the arid conditions of the Caspian Lowland. Based on a habitat selection model, we hypothesized that sympatric species would occupy and utilize species-specific environmental habitats and resources in common spaces and that niche overlap between species would be low. Thirteen environmental parameters were chosen for study. Nine parameters significantly discriminated interspecies differences (*Meriones meridianus* occurred in dry microhabitats, *Meriones tamariscinus* occurred in wetter microhabitats, and *Apodemus witherbyi* and *Cricetulus migratorius* showed eurybiotic spatial patterns). *Mus musculus* was predominantly found in wet environmental conditions. Thus, *A. witherbyi* and *C. migratorius* were characterized by the greatest range of spatial niches in the community, and *M. musculus* was characterized by the narrowest range of spatial niches. Pairwise comparisons of rodent spatial niches revealed low overlap values.

Key words: microhabitat using, spatial niche, spatial niche overlap, environmental parameters, rodents

Introduction

One goal of community ecology is to determine the mechanisms that enable species to coexist. Resource partitioning between ecologically similar and sympatric species has received ample attention in ecology (Ross 1986, Kronfeld-Schor & Dayan 2003, Neronov & Alexandrov 2004, Klenovšek et al. 2013, Magomedov 2017, 2019). Studies of this issue have helped in understanding the mechanisms of coexistence and the size and stability of communities (Pianka 1973, Schoener 1974, Bouchon-Navaro 1986, Bukvareva & Aleshchenko 2012, Klenovšek et al. 2013). According to niche theory, coexisting species must exhibit ecological differences in at least one niche dimension, such as space, food or time (Pianka 1973, Schoener 1974, Shenbrot 1987). Early studies of coexistence examined the possible roles of abiotic factors on species spatial patterns (Hardy 1945), but later studies have focused on the role of biotic factors (especially interspecific competition) as possible determinants of distributional patterns (Brown 1973, Schoener 1974, Shenbrot 1987, Rosenzweig 1995, Zhong et al. 2016).

According to the "microhabitat paradigm", sympatry among small mammal species is

enabled by many factors, including microhabitat partitioning (Rosenzweig & Winakur 1969, Price & Kramer 1984, Brown 1989, Jorgensen 2004, Kubiak et al. 2015). Spatial partitioning is thought to be the most efficient way to use resources that may allow coexistence between ecologically similar species in a common space. The spatial distribution of a species is determined by its adaptations to specific environmental conditions that allow it to survive. Abundance, behavioural and physiological indicators can indicate the degree of well-being of a species in an environment (Price 1978, Shenbrot 1987, Brown 1989, Scott & Dunstone 2000). The spatial patterns of rodents are far from stable. Their distribution can be determined by many environmental factors and resources. In particular, it is important to study the spatial pattern of sympatric species to understand the mechanisms that influence community structure. Rodent communities provide excellent models to reveal the mechanisms that enable species to coexist (Shenbrot 1987, Kotler et al. 1993, Ziv et al. 1993, Brown et al. 1994, Chabovsky & Alexandrov 1996, Williams et al. 2002, Stevens & Tello 2009).

Arid environments are not entirely suitable for the existence and coexistence of ecologically similar sympatric species. Therefore, interspecific competition is expected to be strong in these conditions. Moisture deficiency, low productivity, patchiness of resources and hot summers make these environments a unique platform for understanding the mechanisms underlying the coexistence of multispecies communities. Rodents from arid environments are often used to reveal the spatial dynamics of ecological communities. We are especially interested in understanding the microhabitat preferences of widespread rodents dwelling in the Caspian Lowland. We expected that species in this community would display spatial fluctuations in accordance with species-specific responses to environmental variability and species interactions. The aim of this work was to estimate the microhabitat distribution of the rodent species community in the Terek-Kuma Lowland and reveal how the species segregate environmental resources. We hypothesized that rodent species occurrence is related to the heterogeneity and complexity of the habitat and choice of microhabitats determined by environmental parameters and species-specific responses.

Material and Methods

Species and study area

Five species were included in the study: *Meriones tamariscinus* (78.1 ± 5.1 g), *Meriones meridianus* (46.2 ± 1.38 g), *Cricetulus migratorius* (23.3 ± 1.13 g), *Apodemus witherbyi* (24.6 ± 1.51 g) and *Mus musculus* (17.1 ± 1.03 g). The study was performed in the Terek-Kuma Lowland in the Republic of Daghestan, Russia, at 44°41′ N, 46°24′ E and 44°53′ N, 45°38′ E, with an arid continental climate. The study material was collected from 2012-2013. The Terek-Kuma Lowland is a typical semidesert with areas of meadow-bog-steppe and dry-steppe. The landscapes consist of longitudinal sand dunes, systems of ridges and interridge depressions with stable, semi-stable, and shifting sand dunes. The soils are sandy, light chestnut, and alkaline (Akaev et al. 1996). The climate is dry continental with a mild winter and hot summer. The mean temperature in January is –2.9 °C, the mean temperature in July is 22.5 °C. The precipitation rate reaches 350 mm. The snow cover is sparse and unstable (Akaev et al. 1996).

The study area is composed of steppe vegetation (L´vov & Abachev 1984), consisting of mixed grass-wormwood and wormwood-saltwort associations, xerophytic shrubs, Jerusalem thorn (*Paliurus spina-christi*) and buckthorn (*Rhamnus pallasii*). The herbage is dominated by feather-grass (*Stipa capillata*), brome grass (*Bromus squarrosus*), timothy grass (*Phleum phleoides*), wormwood Taurian (*Artemisia taurica*), saltwort (*Salsola dendroides*), etc. (L´vov & Abachev 1984).

Sampling design and data collection

Four plots were selected to represent the main substrate and vegetation components. Each plot was characterized by three features: degree of sand mobility (bare, semi-stabilized and stabilized), state of shrubs and microrelief. Plot 1 consisted of barchans with bare and semi-stabilized sands (square, 2.8 ha). Plot 2 consisted of sagebrush-grass steppe formations and small sandy hills (< 1.5 m) with varying degrees of stabilized sands (square, 3.1 ha). Plot 3 consisted of shrub associations (*Cotinus coggygria*, *Crataegus pentagyna)* with complex ridges, interridge depressions and stabilized sands (square, 2.9 ha). Plot 4 consisted of *Juniperus oblonga* associations with slightly hilly relief and stabilized sands (square, 2.6 ha). Distances between plots

Table 1. Soil and vegetation characteristics of microhabitats in study area (X ± SE).

	Environmental parameters			
	Soil bulk density	Soil water content	Total herb phytomass	Shrubs density
Microhabitats	g/cm^3	%	kg/ha	ind/ha
Bare sands and barchans	0.95 ± 0.02	5.47 ± 0.14	2.61 ± 0.14	1.40 ± 0.09
Semi stabilized sands	1.01 ± 0.03	7.04 ± 0.38	4.33 ± 0.21	26.40 ± 3.84
Stabilized sands	1.08 ± 0.03	8.57 ± 0.41	5.14 ± 0.25	40.52 ± 5.38
Inter-ridge depressions	1.07 ± 0.03	9.11 ± 0.32	4.96 ± 0.21	31.62 ± 4.11
Shrubby associations	1.16 ± 0.02	10.17 ± 0.35	5.35 ± 0.28	87.36 ± 5.62

were two to four kilometres. Five typical arid land microhabitats were present on all plots: bare sands and barchans (28%), semi-stabilized sands (37%), stabilized sands (18%), interridge depressions (10%) and shrubby associations (7%). Plots were subdivided into squares, which were classified according to microhabitat. Total herb phytomass and soil parameter values were highest in the shrub association and lowest in the bare sands and barchans. Shrubby associations and interridge depressions were relatively wetter microhabitats (Table 1).

The line transect survey technique was used to estimate the abundance of rodent species and microhabitat distribution. Rodents were trapped in spring (15-20 May), summer (8-12 July) and autumn (3-7 October) using Shipanov live traps (250 × 13 × 10 mm). Traps remained for three nights in each plot and were activated in the evening and checked early in the morning and. Live traps were baited with sunflower seeds. In total, 3,510 trap nights were included in the study period, and 358 individuals were captured. There were 12 transects altogether, three per plot, each containing 45-50 traps. The distance between transects in each plot was 120-200 m and traps were placed 4-6 m apart. An index of rodent abundance was calculated as the number of captures per 100 trap nights. Each trapped animal was sexed, weighed, marked by toe-clipping and released at the point of capture. Recaptured animals were excluded from analysis.

Microhabitat parameters

A critical objective of this research was to associate the characteristics of rodents and the environmental parameters in the study area. To assess the association of the rodent species with microhabitats rather than whole biotopes, vegetation and soil characteristics were quantified at the points of animal capture (four measurements at each point in a 2 m radius) using standard methods of field botany and soil science. Terrestrial phytomass was determined by mowing 1 m^2 plots. Then, we identified the plant species, divided them into two groups (cereals, forbs) and dried the samples at 40 °C. We also measured the projective cover of herbaceous vegetation in 1 m^2 plots. Shrubs were characterized using the K-nearest neighbours' method. Two soil characteristics were measured: soil bulk density (g/cm^3) and soil water content (%). Soil bulk density was measured with a coring method during the same time period as the vegetation survey. A volumetric cylinder was pressed into the soil to a depth of 0.1 m to take a core sample. The soil water content was measured with the gravimetric method, which involves collecting soil samples, weighing them before and after drying and calculating the soil's original moisture content as a percentage (%). The following environmental parameters were evaluated: soil water content (%) – SWC, soil bulk density (at 0.3 m depth, g/cm^3) – SBD, phytomass of cereals in open areas (kg/ha) – PCO, phytomass of forbs in open areas (kg/ha) – PFO, protective cover cereals in open areas (%) – PCCO, protective cover forbs in open areas (%) – PCFO, shrub density (hectare) – SD, height of shrubs (m) – HS, crown cover of shrubs (%) – CCS, phytomass of cereals in shrubs (kg/ha) – PCS, phytomass of forbs in shrubs (kg/ha) – PFS, protective cover of cereals in shrubs (%) – PCCS, and protective cover of forbs in shrubs (%) – PCFS. Differences in microhabitat parameters were tested with a one-way analysis of variance (see below). To avoid interseasonal differences in the state of some environmental parameters (phytomass, soil water content, etc.), the data from one season (summer) was used to analyse the microhabitat distribution pattern. However, data on the abundance of rodent species are shown seasonally, except for winter.

Statistical analysis

Discriminant analysis is considered an appropriate method for describing the spatial structure

of ecological communities and topological interrelations of species centroids and ellipsoids, whereas principal component analysis is the most suitable for calculating the relative sizes of clusters of data points (e.g. niche breadth: Rogovin & Shenbrot 1993, Krasnov et al. 1996). Discriminant analysis was used to describe the distribution of the spatial niches of the studied rodent species using environmental spatial parameters (habitat space) and to reduce the dimensionality of this space. In the framework of this approach, species abundance and environmental variables were considered simultaneously (see above). Discriminant axes were calculated based on the pooled dataset consisting of the values of microhabitat variables for each point of registration of a rodent. The position of a species in a microhabitat was estimated as the coordinates of the species ellipsoid along each of the discriminant axes for each trapping session separately (Shenbrot 1987, Rogovin & Shenbrot 1993). We used environmental parameters that characterized the relationship of rodent species to the microhabitats (vegetation and soil characteristics). Thus, environmental parameters characterized the species-specific use by every rodent species of the microhabitats where they were captured (see above). Additionally, characteristics of environmental parameters where rodents were captured established a spatial niche. To estimate the values of habitat breadth, the dataset consisting of the values of habitat variables for each plot was subjected to principal component analysis, and scores of the principal component axes were obtained for each plot. Coordinates of species ellipsoids along each axis were calculated using projections of registration points on the component axes separately for each trapping session. Habitat breadth was measured as the standard deviation of observation points from the ellipsoid for a given species in a given trapping session in the space of the principal component axes (Rogovin & Shenbrot 1993, Shenbrot & Krasnov 2004). Spatial niche overlap was calculated separately for each pair of species. A separate discriminant function was calculated in each case based on paired comparisons of the observation points of two species. As a measure of niche overlap, we used the probability of displacement along the discriminant axis, i.e. the percentage of incorrectly classified cases (Cody & Walter 1976). Overlap values in the range 0-0.25 were considered low, 0.25-0.5 were considered moderate, 0.5-0.75 were considered high and from 0.75 up were considered very high. Statistica 6.0 (Statsoft Inc. 2002) was used for all empirical analyses.

Table 2. Abundance of rodent individuals captured in the study area, a/b: "a" is abundance on 100 traps nights, "b" is the number of captured individuals.

	Season		
Species	Spring	Summer	Autumn
M. tamariscinus	1.70/18	2.72/34	5.17/62
M. meridianus	2.73/29	4.72/59	6.75/81
C. migratorius	0.38/4	1.04/13	0.67/8
A. witherbyi	0.47/5	1.28/16	0.83/10
M. musculus	0.28/3	0.88/11	0.42/5
Traps nights/n individuals	1,060/59	1,250/133	1,200/166

Table 3. Summer microhabitat distribution of rodents (individual/100 traps nights) and species diversity in the study area. *M.t. – Meriones tamariscinus, M.m. – Meriones meridianus, C.m. – Cricetulus migratorius, A.w. – Apodemus witherbyi, M.mus. – Mus musculus.*

	Species						
Microhabitats	*M.t.*	*M.m.*	*C.m.*	*A.w.*	*M.mus.*	Species richness	Diversity
Bare sands and barchans	0.07	1.87	0.19	0.26	0.00	4	1.51/30
Semi stabilized sands	0.27	1.42	0.29	0.43	0.22	5	2.97/59
Stabilized sands	0.65	1.03	0.33	0.30	0.32	5	3.94/79
Inter-ridge depressions	0.81	0.00	0.00	0.05	0.00	2	1.13/23
Shrubby association	0.92	0.40	0.23	0.24	0.34	5	3.72/74
Abundance of rodents	2.72	4.72	1.04	1.28	0.88		
Spatial niche breadth	3.70	3.33	3.85	4.07	1.88		

Results

During the study period, 358 rodent individuals were captured. The abundance and characteristics of the microhabitat distributions of model rodent species in the study area are presented in Tables 2 and 3. The most abundant species were *M. tamariscinus* and *M. meridianus*, other species had low abundance both annually and seasonally. The microhabitat distribution showed that *M. meridianus* is found in open, dry areas with minimal protective vegetation cover, and occurs both in flat areas and at elevation. In contrast, *M. tamariscinus* was found in wetter microhabitats with well-developed vegetation. *C. migratorius* and *A. witherbyi* were habitat generalists. *M. musculus* occurred in relatively wetter microhabitats. Three microhabitats were occupied by all rodent species (semi-stabilized sands, stabilized sands, shrubby association). The interridge depression microhabitat was occupied by *M. tamariscinus* and *A. witherbyi*. The broadest habitat niches (average values across all trapping sessions) were recorded in *A. witherbyi* and *C. migratorius*, whereas *M.*

Table 4. Results of One-way ANOVA of significant differences of environmental parameters among plots, Bonferroni correction value was 0.0039.

Parameters	Plot 1	Plot 2	Plot 3	Plot 4	F	*P*
Soil water content, %	8.64 ± 0.24	8.70 ± 0.30	10.49 ± 0.47	10.88 ± 0.54	2.67	0.039
Soil bulk density, g/cm^3	1.04 ± 0.02	1.07 ± 0.03	1.10 ± 0.03	1.17 ± 0.02	7.29	0.0001
Phytomass of cereals in open areas, kg/ha	3.06 ± 0.36	2.70 ± 0.44	1.14 ± 0.51	0.71 ± 0.48	4.65	0.002
Phytomass of forbs in open areas, kg/ha	3.71 ± 0.44	3.40 ± 0.56	1.54 ± 0.69	1.01 ± 0.68	3.85	0.007
Projective cover cereals in open areas, %	19.30 ± 2.34	18.65 ± 2.74	7.56 ± 3.42	4.58 ± 3.10	4.72	0.001
Projective cover forbs in open area, %	20.94 ± 2.47	20.80 ± 3.00	6.69 ± 3.02	4.75 ± 3.22	6.26	0.0002
Shrubs density, ha	16.78 ± 7.40	19.30 ± 7.60	80.10 ± 11.80	100.20 ± 8.10	15.74	0.0001
Height of shrubs, m	0.85 ± 0.28	1.21 ± 0.25	3.04 ± 0.32	3.89 ± 0.28	17.04	0.0001
Crown cover of shrubs, %	16.90 ± 5.37	26.10 ± 5.48	56.00 ± 5.65	57.70 ± 7.57	8.99	0.0001
Phytomass of cereals in shrubs, kg/ha	1.10 ± 0.40	1.39 ± 0.44	3.16 ± 0.56	3.69 ± 0.51	5.07	0.001
Phytomass of forbs in shrubs, kg/ha	1.36 ± 0.50	1.98 ± 0.63	4.63 ± 0.70	5.05 ± 0.69	8.36	0.0002
Projective cover of cereals in shrubs, %	6.84 ± 2.50	10.20 ± 3.32	29.06 ± 4.40	34.30 ± 4.90	10.13	0.0001
Projective cover of forbs in shrubs, %	8.00 ± 2.94	11.04 ± 3.53	28.50 ± 4.33	32.60 ± 4.57	7.68	0.0001

Table 5. Results of discriminant analysis for environment parameters (Lambda Wilkes: 0.0054, F (52.24) = 13.09370, *P* < 0.0001, in bold type is significant values).

Parameters	Wilkes Lambda	Partial Lambda	Fisher`s criteria	*P*	df1	df2	df3	df4
Soil water content, %	0.008	0.655	8.04	0.0001	**–0.59**	0.23	**0.42**	0.18
Soil bulk density, g/cm^3	0.012	0.465	17.53	0.0001	–0.33	0.27	–0.21	–0.04
Phytomass of cereals in open areas, kg/ha	0.009	0.625	9.17	0.0001	–0.32	0.32	**0.57**	0.06
Phytomass of forbs in open areas, kg/ha	0.011	0.504	14.98	0.0001	**0.92**	–0.25	**–0.13**	–0.46
Projective cover cereals in open areas, %	0.006	0.865	2.37	0.062	–0.76	–0.09	–0.46	–0.52
Projective cover forbs in open area, %	0.006	0.933	1.10	0.365	–0.04	–0.15	0.22	–0.29
Shrubs density, ha	0.013	0.418	21.23	0.0001	**–0.81**	**–0.66**	0.20	0.10
Height of shrubs, m	0.009	0.598	8.24	0.0001	0.31	0.07	–0.32	**–0.52**
Crown cover of shrubs, %	0.010	0.534	13.29	0.0001	**–0.76**	0.54	–0.30	0.32
Phytomass of cereals in shrubs, kg/ha	0.006	0.890	1.89	0.124	–0.03	0.76	0.35	–0.76
Phytomass of forbs in shrubs, kg/ha	0.010	0.551	12.44	0.0001	–0.15	–0.38	**–0.62**	**0.78**
Projective cover of cereals in shrubs, %	0.007	0.783	4.22	0.004	0.20	0.29	**0.79**	–0.11
Projective cover of forbs in shrubs, %	0.006	0.858	2.53	0.050	**0.92**	**–0.92**	0.46	–0.07
Eigenvalue					17.95	2.12	1.06	0.52
Cumulative percentage of variance					0.829	0.93	0.98	1.000

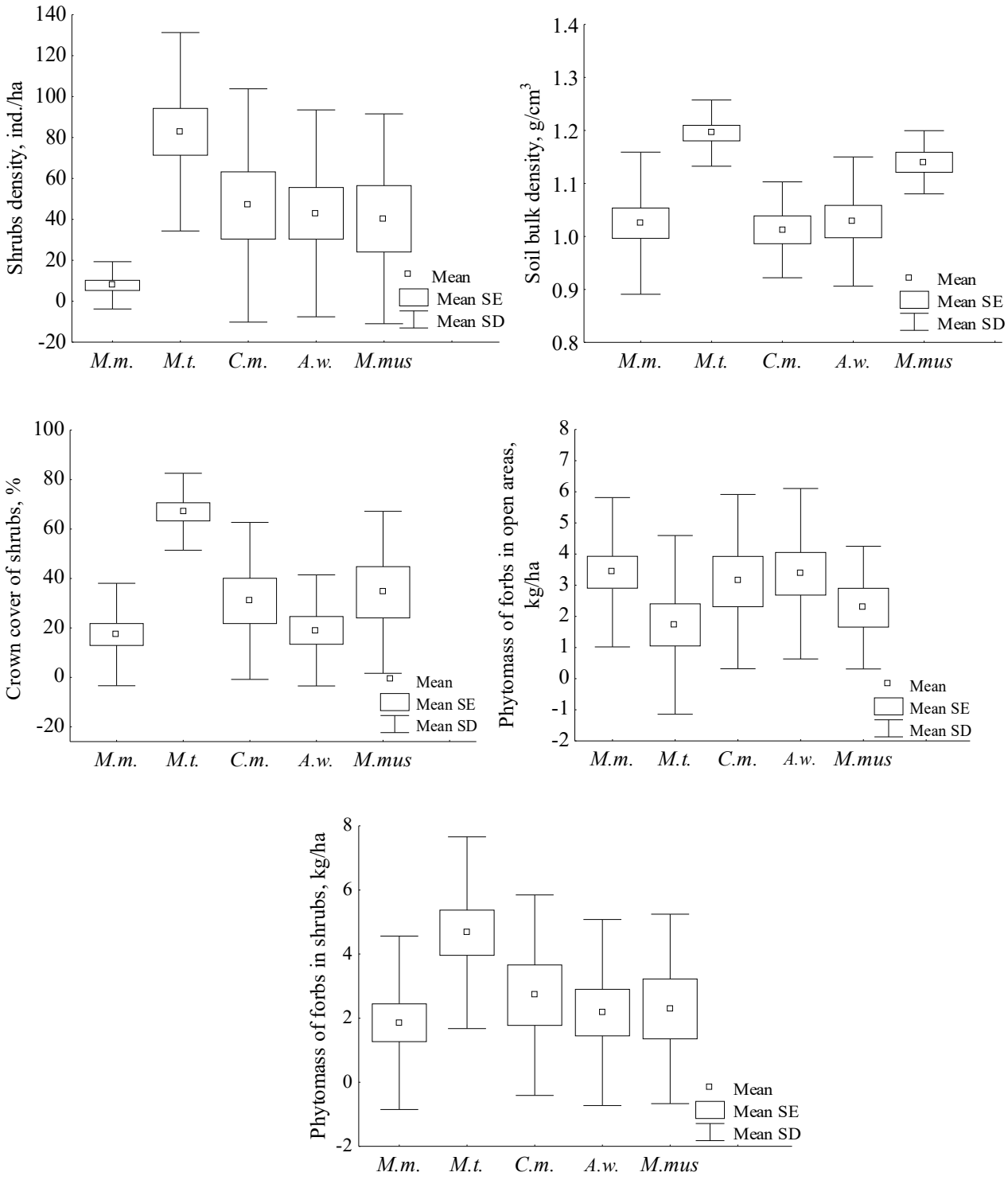

Fig. 1. Distribution of rodent species on the axes of main environmental parameters in 2D box plots (mean – arithmetic mean value of environmental parameter, SE – standard error, SD – standard deviation). *M.t. – Meriones tamariscinus, M.m. – Meriones meridianus, C.m. – Cricetulus migratorius, A.w. – Apodemus witherbyi, M.mus. – Mus musculus.* MANOVA F = 2.569, *P* = 0.006.

musculus had the narrowest habitat niches. Both gerbil species had intermediate habitat niche values (Table 3). Species diversity was highest in stabilized sands and shrubby association microhabitats, lowest in interridge depressions, bare sands and barchans, and intermediate in the semi-stabilized sands microhabitat (Table 3).

Habitat characteristics and partitioning of the rodent community

A one-way ANOVA of all microhabitat parameters showed significant differences. The Bonferroni corrected value was 0.0039 (Table 4). The results of the principal component analysis showed that the space of habitat variables had two significant

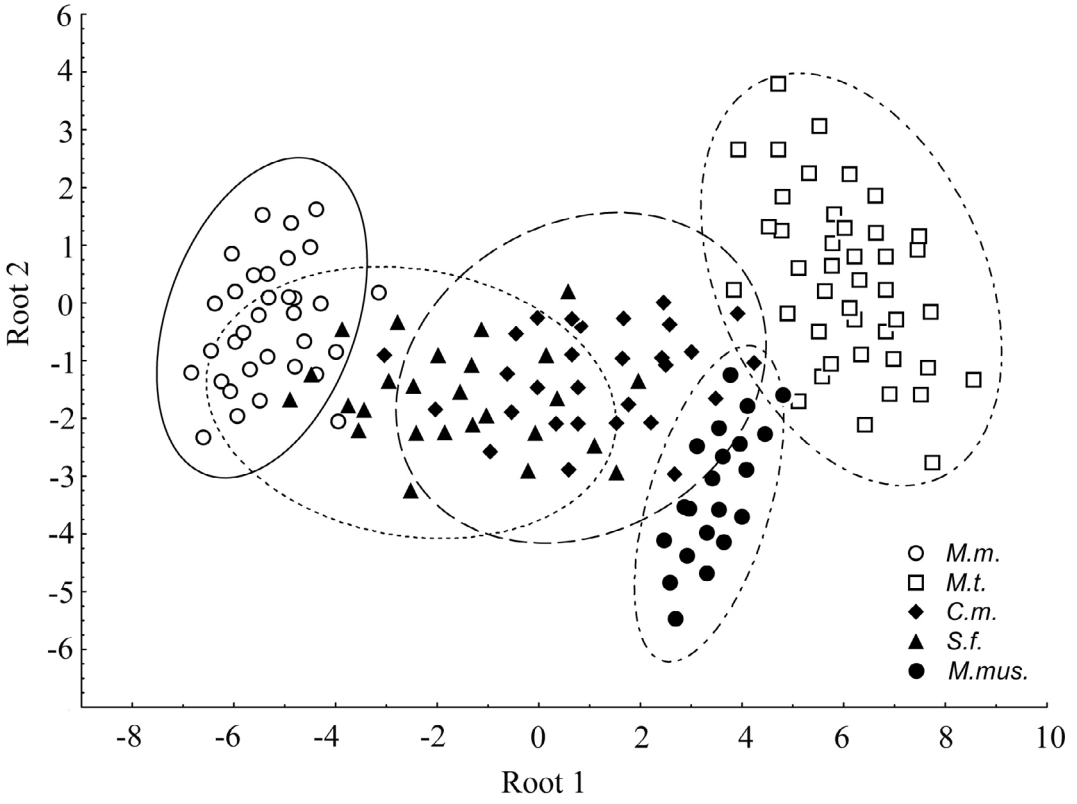

Fig. 2. Graphic pattern of rodents spatial niches concerning 13 environment parameters in the space of the first two discriminant axes (95% confidence ellipsoids). *M.t. – Meriones tamariscinus, M.m. – Meriones meridianus, C.m. – Cricetulus migratorius, A.w. – Apodemus witherbyi, M.mus. – Mus musculus.*

dimensions ($P < 0.001$), which accounted for 86.62% of the variance. The first axis represented soil parameters while the second axis reflected vegetation abundance.

The results of the discriminant analysis showed that nine of 13 environmental parameters displayed significant interspecific differences (Table 5). The largest contribution (by Fisher's criterion) in interspecific differences was from five environmental parameters (SD, SBD, PFO, CCS and PFS). Reducing habitat spatial dimensionality also showed that the division of this space by the rodent community occurred along the first two axes, which accounted for 83% of the variance.

Figure 1 presents data on the species-specific usage of the target rodent species for the five environmental parameters with the largest contributions to interspecific differences and confirms the microhabitat distribution shown in Table 3. Figure 2 shows the habitat partitioning of model rodents among the environmental parameters that represented the 13-dimensional spatial niche. Ellipsoids of *M. tamariscinus* and *M. meridianus* were characterized by relatively isolated positions from other species. Their ellipsoids confirmed species-specific ecological requirements, *M. tamariscinus* dwelt in more humid microhabitats with well-developed vegetation, and *M. meridianus* dwelt in dry microhabitats with bare sands. *A. witherbyi* and *C. migratorius*, which occurred in all microhabitats relatively equally, were characterized by the largest distribution range among the environmental parameters, with their ellipsoids located between two jird habitats. *M. musculus* inhabits human-constructed buildings and areas with well-developed vegetation and was

Table 6. Values of pairwise habitat niche overlap. *M.t. – Meriones tamariscinus, M.m. – Meriones meridianus, C.m. – Cricetulus migratorius, A.w. – Apodemus witherbyi, M.mus. – Mus musculus.*

Species	*M.t.*	*M.m.*	*C.m.*	*S.f.*	*M.mus.*
M. tamariscinus	0.00	0.13	0.21	0.16	0.23
M. meridianus		0.00	0.29	0.21	0.09
C. migratorius			0.00	0.25	0.20
A. witherbyi				0.00	0.12
M. musculus					0.00

characterized by the narrowest distribution range among the environmental parameters (Fig. 2).

The geographic pattern of the model rodent spatial distribution in multidimensional space is approximate and cannot precisely estimate the degree of overlap between species (Shenbrot 1987, Rogovin & Shenbrot 1993). Therefore, the values of pairwise habitat niche overlap were calculated (Table 6). There were no zero-overlap values between model rodent pairs. All pairs of rodents had minimal overlapping values. The largest overlapping value was in the pair *M. meridianus* – *C. migratorius*. Taxonomically more closely related gerbils had lower overlap values.

Discussion

Microhabitat characteristics are used to understand variation in the abundance of species and to identify important quantifiable niche dimensions. Particular microhabitat characteristics that are correlated with variation in abundance have been shown to reflect important decisions made by individuals to maximize fitness (Rosenzweig 1981, Stevens & Tello 2009). Our data support the hypothesis that environmental parameters underlie the microhabitat partitioning of rodent species in the Terek-Kuma Lowland. Discriminant analysis allowed us to describe the distribution of rodent species relative to 13 environmental parameters, revealing that these parameters significantly affected the distribution of rodents. The results indicate that the microhabitat partitioning of model rodents was mainly determined by vegetation state and soil water content. Shrub characteristics contribute the most to interspecific microhabitat partitioning of the rodent community. Vegetation is widely recognised as a key microhabitat determinant (Bouchon-Navaro 1986, Abramsky 1988, Wasserberg et al. 2005, Corbalán 2006, Boryakova & Lyamina 2013). Shrub belts are one of the main vegetation components of arid lands and contribute to the heterogeneity and complexity of the habitats and microhabitats (Magomedov et al. 2012). First, small quadrupedal rodents mainly use midgrass and shrubs to reduce the risk of predation. Second, in open areas, shrubs may represent patches of concentrated food resources by aggregating seeds and insects. A previous investigation showed that both gerbil and migratory hamster diets consist of seeds in late spring and summer (Magomedov 2017).

In earlier studies, low overlap values of spatial niches were shown in areas with a high number of both gerbil species (Chabovsky & Aleksandrov 1996, Matrosov et al. 1996, Kubiak et al. 2015). Populations of *M. tamariscinus* and *M. meridianus* showed both partial integration and spatial isolation in the steppes of Kalmykia (Chabovsky & Alexandrov 1996). We believe this result was due to the patchy distribution of microhabitats suitable for these species. Habitat use associated with vegetation structure is an important factor in the determination of the community structure of mammals. Most previous studies on the relationships among mammal communities, habitat structure and microclimate conditions have found that vegetation is a good predictor of community composition (Ivanter 1975, Ross 1986, Rosenzweig 1995, Abramsky et al. 2001, Kalcounis-Ruppell & Millar 2002, Williams et al. 2002, Boryakova & Lamina 2013, Zhong et al. 2016).

Habitat selection theories are based mainly on the concept of the ideal free distribution (Fretwell & Lucas 1970), which predicts that individuals distribute themselves among patches of differing quality according to the expected net gain in resources and intraspecific densities relative to other patches. Considerable debate about the value of the concept of ideal free distribution remains, but this concept forms the basis of the two prevailing models used to describe habitat selection of small mammals: IsoDAR analysis and the distribution method. Because of the logistical difficulties in measuring habitat use of small animals, habitat selection is assessed indirectly in both approaches by comparing patterns of local abundance among qualitatively distinct habitat patches (Stapp 1996). In the case of sympatric rodent species, the determinants of coexistence may be described on the basis of habitat selection patterns on different scales (Rosenzweig 1981, Morris 1987, 2003, Abramsky et al. 2001). Habitat selection is considered the active process by which a species chooses among distinct available resources (Johnson 1980). It is a multiscale process, ranging from the macrohabitat level to the microhabitat. On the macrohabitat scale, the main factors (vegetation and substrate type) have been described (Corbalán & Ojeda 2004, Tabeni & Ojeda 2005). On the microhabitat scale, the key role of vegetation cover has been described, with rodent feeding activity occurring under plant cover, where predation risk is reduced (Taraborelli

et al. 2003, Corbalán & Ojeda 2004, Kubiak et al. 2015). The importance of soil characteristics has also been common in studies of rodent community structure (Krasnov et al. 1996, Scott & Dunstone 2000, Corbalán 2006 etc.).

Using a large number of environmental parameters allowed the detailed characterization of the spatial components of ecological niches of ecologically similar and sympatric rodents and revealed the microhabitat partitioning patterns. Moreover, a previous analysis of the model rodent species' diets showed low values of overlapping trophic niches (Magomedov 2017). Under conditions of low overlapping of spatial niches and moderate overlapping of the trophic niche, there is no reason for competition in the rodent community in arid environments.

Acknowledgements

This work was supported by Russian Foundation for Basic Research (13-04-00022).

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