

NICHE CONVERGENCE IN THE DESERT RODENTS OF TWO GEOGRAPHICALLY ISOLATED COMMUNITIES

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RESUMEN

Usando el método de análisis de conglomerados se realizó una clasificación ecológica para dos comunidades de roedores geográficamente aislados, una en Asia Central (trans-Altai Gobi, República Popular de Mongolia) y la otra en Norte América (Desierto Chihuahuense, Mapimí, México). El espacio ecológico de cada una de las comunidades fue determinado por medio de la técnica de ordenación polar (Bray y Curtis, 1957). Para la determinación de la dieta de los roedores se analizaron contenidos estomacales tomando en cuenta, sólo grandes grupos de alimento. En la conduc-

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ta exploratoria se utilizó la técnica de "Open field" (Eisenberg, 1963, 1967). Estos tipos de conductas se relacionaron con el uso del espacio (microhábitat). Las especies geográficamente aisladas fueron en todos los casos agrupadas a un nivel de semejanza menor que las relacionadas geográficamente. Sin embargo, las especies asiáticas fueron más especializadas en el uso del microhábitat y en su alimentación. La distribución de especies en el espacio ecológico de Trans Altai Gobi fue generalmente más uniforme, tomando en cuenta que el espacio ocupado fue tan grande como en Mapimí. De los dos grupos de especies que se encontraron en la comunidad del Desierto Chihuahuense (Mapimí), uno estuvo integrado por Heterómidos y el otro por Cricétidos norteamericanos. La diferencia que se encontró en el espacio ecológico de las comunidades de Trans Altai Gobi y del Desierto Chihuahuense fue debido básicamente a un grado diferente de divergencia ecológica entre los roedores saltadores bipedos y cuadrúpedos. La riqueza específica en ambas comunidades fue similar. La comunidad de Trans Altai Gobi tiene una fuerte divergencia de especies y estuvo compuesta por nueve géneros y diez especies (*Euchoreutes naso*, *Salpingotus crassicauda*, *Allactaga sibirica*, *Allactaga taliae*, *Dipus sagitta*, *Mus musculus*, *Cricetulus migratorius*, *Rhodopus rovorovskii*, *Meriones meridianus*, *Rhombomys opimus*). En el Desierto Chihuahuense, estuvo compuesta por siete géneros y once especies (*Spermophilus spilosoma*, *Spermophilus variegatus*, *Perognathus pencillatus*, *P. flavus*, *P. nelsoni*, *Dipodomys merriami*, *D. nelsoni*, *Neotoma albigula*, *Onychomys torridus*, *Peromyscus eremicus* y *Sigmodon hispidus*). Los trabajos más recientes realizados por los ecólogos rusos sobre convergencia ecológica en roedores del desierto y estepas se han basado en el concepto de "formas de vida" (Kaskarov 1938, 1944; Formozov 1950, 1956; Khodashova 1953; Bannikov 1954). Este concepto refleja el fenómeno de evolución paralela (convergencia) de algunos caracteres en animales que se encuentran en condiciones ambientales similares. Para cada una de las "formas de vida", las características morfológicas, que tienen una significancia adaptativa fueron consideradas primordiales. Diferentes autores han llegado a conclusiones basándose en diferente caracteres, y consecuentemente la clasificación ecológica final ha sido frecuentemente un tanto subjetiva. La razón de estas diferencias es que el significado del término "forma de vida" ha sido tratado de manera diferente (Krivolutsky 1967). Con el desarrollo de la tecnología de Taxonomía Numérica (Sokal y Sneath 1963; Smirnov 1969; Jardine y Sibson 1971), las clasificaciones ecológicas pueden considerar al mismo tiempo un gran número de parámetros, más o menos relacionados ecológicamente, y una estimación numérica de cada parámetro (Fuji 1969). Cada una de las clasificaciones usualmente están basadas en la idea del nicho ecológico fundamental, tratado como una combinación de todos los recursos usados por las especies (Hutchinson 1957), o todas las interacciones de las actividades de las especies con esos recursos. El enfoque cuantitativo requiere una mayor evaluación objetiva, pero el problema es que aumenta la selección de parámetros por comparación. Si usamos un gran número de características morfológicas, es difícil evitar confusiones en algunas características de valores adaptativos diferentes. La posibilidad de reducir cada uno de los errores, es factible, siempre y cuando al clasificar, no se empleen sólo los factores morfológicos, sino también los ecológicos. Entre estos factores ecológi-

cos se consideran primordiales: los hábitos alimentarios; patrones de utilización de espacio, incluyendo conducta forrajera o de escape y el uso de refugio. Estas características en ecología y conducta han sido extensamente utilizadas para determinar nichos tróficos y espaciales (Pianka 1969; Brown 1975; Odum 1975). Este enfoque fue utilizado por Shenbrot (1980, 1982) en la clasificación morfológica de los jerbos de Asia menor. Este sistema se asemeja en gran parte a la clasificación morfológica de los jerbos adoptada en la taxonomía actual. Esta semejanza es difícilmente posible cuando se hace la comparación de caracteres ecológicos de formas filogenéticamente distantes e independientes y de comunidades geográficamente aisladas, debido a que la divergencia ecológica dentro de un grupo taxonómico puede exceder las diferencias entre representantes de diferentes taxa. En tales casos es posible entroncar los equivalentes ecológicos entre formas no relacionadas filogenéticamente, los cuales han evolucionado en ambientes físicos y geográficos similares. Tales trabajos pueden dar bases para la investigación de las peculiaridades estructurales de comunidades geográficamente aisladas. El grado de semejanza en formas ecológicas de diferentes comunidades nos conduce al uso del análisis de procesos de tales evoluciones. Esto se basa en el estudio de características de la estructura, condiciones ambientales y la historia de las comunidades geográficamente aisladas. En este trabajo intentamos crear una clasificación ecológica de roedores del desierto, para identificar formas ecológicas equivalentes, y analizar la estructura de las comunidades filogenéticamente independientes de los desiertos de Asia Central y Norte América. Los datos sobre la ecología y conducta de los roedores fueron colectados durante las expediciones de los autores al área de Trans Altai Gobi como parte de la expedición biológica Soviético-Mongola (verano 1980-1982), y durante la expedición al Desierto Chihuahuense (México) en la Reserva de la Biosfera de Mapimi, Dgo. (Sept.-Nov. 1981-1983).

ABSTRACT

An ecological classification of rodents from two geographically isolated communities; Central Asia (Trans-Altai Gobi, MPR) and North America (Central Chihuahuan Desert, Mexico) is proposed using the method of cluster analysis. The ecological space of each community was determined through the use of the polar ordination technique (Bray and Curtis, 1957). The criteria used were rodent diets (stomach contents analyzed in terms of main food items) and exploratory behavior in "open field" tests; this kind of behavior was related to space (microhabitat) use in nature. Geographically isolated species were in all cases clustered at a lower level of resemblance than geographically related ones. Both in microhabitat use and feeding the Asian species were most specialized. The distribution of species in the ecological space of Trans-altai Gobi community was more uniform and the occupied volume was larger than in Mapimi. There were two groups of species in the Mapimi community one was composed of Heteromyid rodents and another of North American Cricetidae. The differences in the volume of the

ecological space in the Gobian and in the Mapimi communities were basically due to the different degree of ecological divergence between the bipedal and quadrupedal ricochet rodents. The species richness in both communities are considered to be similar. The community of the Trans-Altai Gobi is composed of strongly divergent species of 9 genera and 10 species. In Mapimi, there are 7 genera and 11 species.

INTRODUCTION

The desert, as an habitat for animals, has focused the attention and interest of ecologists many times, providing them with a vast field of research on the convergence and parallel development of characters (Kashkarov 1933, 1938, 1944; Kashkarov and Korovin 1936; Formosov 1956, 1976; Eisenberg 1967, 1975; Dlusski 1981; Mares 1976, 1980, 1983). Due to extreme temperatures, droughts, and great weather fluctuations, life in the desert is shown in a rather limited way. Natural selection is particularly powerful under such conditions, and its trends coincide frequently in geographically insolated and faunistically independent arid regions.

It seems likely that the structural differences in rodent communities of the Trans-Altai Gobi and of Mapimi might have resulted from the different environments in the deserts of Central Asia and North America. The range of rodent macrohabitat variability in the Gobi was greater than that in the Chihuahuan Desert. Differences in the proportion of arid regions of the two continents could considerably affect the rates of ecological and morphological divergence in desert rodents.

STUDY AREAS

The desert of Central Asia and southern North America are located in different climatic belts. The former are in the temperate and the latter in the subtropical and tropical ones. They differ, essentially, in terms of precipitation, diurnal and seasonal changes of temperature and stability of climatic cycles. Despite these differences, there are some common physiognomic features (similar geomorphological parameters, aridity in climate, structure of plant communities) typical of the desert in the broad sense (Meigs 1957; Petrov 1973; Walter 1975).

The Trans-Altai Gobi in the territory of Mongolian Peoples Republic (between 43° - 45° N and 95° - 105° E) is characterized by a great variety and extreme variability of its environmental conditions. The climate is strongly continental. Precipitation occurs mainly during summer and annual precipitation fluctuates between 20 to 100 mm. Air temperature varies seasonally from -34°C in winter to + 40°C in summer (Gunin *et al.* 1980).

The Trans-Altai Gobi of the MPR was treated by Mannikov (1954) as an independent zoogeographic district of the Mongol-Tibet province of the Palearctic Region.

The Mapimi Reserve (Durango, México) lies in the northern part of the Mexican Plateau (26° 29' - 26° 52' N, 103° 32' - 103° 58' W). The climate is arid, subtropical, characterized by rather steady fluctuations. Mean annual precipitation is 230 mm and is distributed mainly during the summer. Mean monthly air temperatures fluctuate from 11°C in January-February to 28°C in June-August. Like in the Gobi Desert, this region lies at an altitude above 1000 m.

Geomorphologically, the region is characterized by parallel ranges of low mountains interrupted by alluvial valleys. The alluvial slope soil is mostly covered with gravel and stones, and, like the Gobi Desert, sands are rather rare and mainly represented by small fixed massifs. The alluvial valleys are typical for their patchy vegetation chiefly composed of herbs, while the flat interfluves are abundantly covered with low semi bushes, shrubs and prickly pears of the genus *Opuntia* (Martínez and Morello 1977).

Biogeographically, the Mapimi region belongs to the Chihuahuan province of the Sonoran subarea of the Nearctic Region. It can be treated as a special subprovince of the Chihuahuan Desert (Morafka 1977).

METHODS

Rodents of Central Asia were collected in the subzone of extra-arid deserts of the Trans-Altai Gobi (43° 10' - 43° 20' N and 99° 00' E) ten species are widely distributed belonging to the following families (Fig. 1):

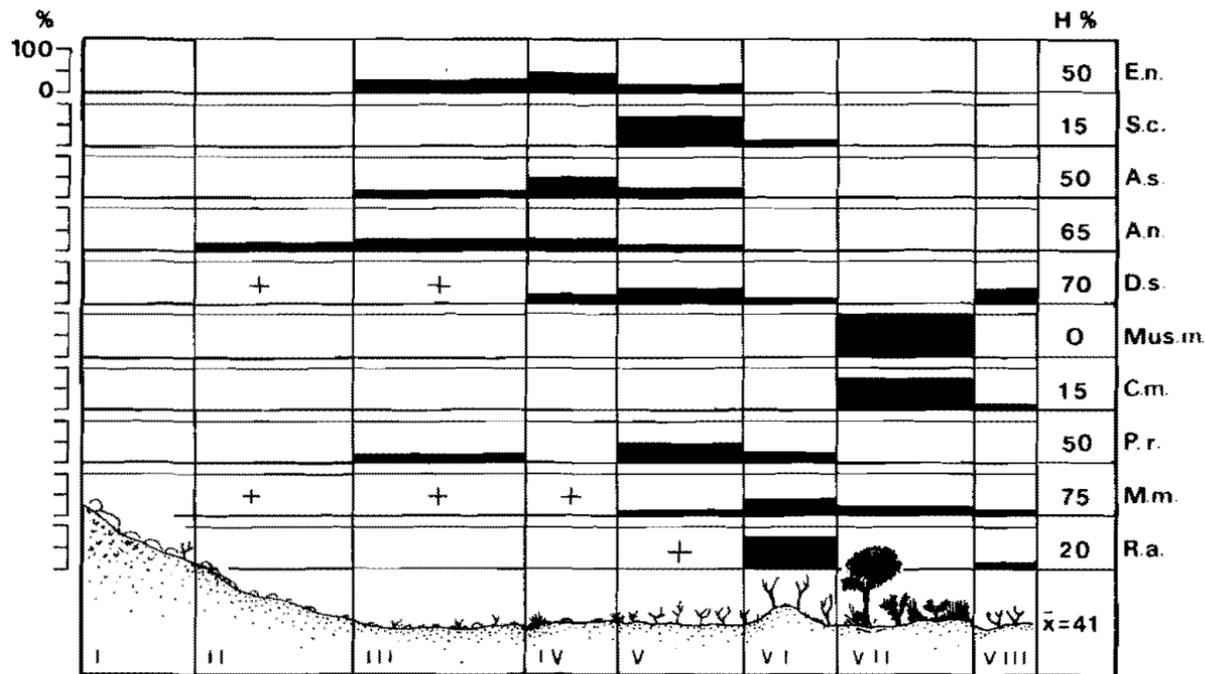


Figure 1

Rodent species distribution through the macrohabitats in the extreme arid subzone of Trans-Altai Gobi. H - measure of diversity of macrohabitates were utilized; "+" - under 10% registration of the species encountered; Rodent species: (see Table 1). I-VIII, see "Use of Macro-Habitats", in methods.

Dipodidae (5 species): *Euchoreutes naso* Sclater, *Salpingotus crassicauda* Vinogradov, *Allactaga sibirica* Foster, *A. natalie* Sokolov, *Dipus sagitta* Pallas;

Muridae (1 species): *Mus musculus* Linnaeus;

Cricetidae (4 species): *Cricetulus migratorius* Pallas, *Phodopus roborovskii* Satunin, *Meriones meridianus* Pallas, *Rhombomys opimus* Lichtenstein (Kulikov and Rogovin 1980).

Rodents of North America were collected in the Mapimi Reserve. In this zone there are 11 species of terrestrial rodents (Grenot and Serrano 1981) of the following families (Fig. 2):

Sciuridae (2 species): *Spermophilus variegatus* Erxleben, *S. spilosoma* Bennet;

Heteromyidae (5 species): *Perognathus flavus* Baird, *P. penicillatus* Woodhouse, *P. nelsoni* Merriam, *Dipodomys merriami* Mearns, *D. nelsoni* Merriam;

Cricetidae (4 species): *Neotoma albigula* Hartley, *Onychomys torridus* Coues, *Peromyscus eremicus* Baird and *Sigmodon hispidus* Say et Ord.

Of the two species of ground squirrels, *Spermophilus variegatus* is extremely rare. *Sigmodon hispidus* is also extremely rare. According to the new data *Spermophilus mexicanus* Erxleben and *Peromyscus maniculatus* Wagner are also found there, however these species are too rare to be important to community dynamics.

Rodents were captured with Sherman traps in areas of 1 ha in size. There were 25 traps per plot with 20 m distances between them. Densities were estimated through the Lincoln index during three days when most of rodents were marked. In the Trans-Altai Gobi plots were followed and 20 in Mapimi.

Trapping areas were selected to cover the entire range of environmental resources in the region.

Use of Macro-Habitats

In accordance with the floristic subdivisions of

the extra-arid subzone of the Trans-Altai Gobi (Feodorova 1980) we distinguished the following macrohabitats (Fig. 1):

- I. Large-stone slopes of the mountains with no plant and animal species.
- II. Medium-stone piedmonts with plant communities composed of *Ephedra przewalskii* Stapf. + *Zygophyllum xantoxylon* Maxim. + *Iljinia regelii* (Bunge) Korov.
- III. Roch plains with vegetation composed of *I. regelii* + *Haloxylon ammodendron* (C.A. Mey) Bunge.
- IV. Rock plains without vegetation and depressions covered by *E. przewalskii*, *Z. xantoxylon*, *Calligonum mongolicum* Turcz.
- V. Proluvial valleys crossed by dry river-beds with shrub communities - *H. ammodendron* + *C. mongolicum* + *E. przewalskii* and *Reaumuria songorica* (Pall.) Maxim. + *Artemisia scoparia* W. et K.
- VI. Sand dunes fixed by *H. ammodendron*.
- VII. Oases with azonal vegetation.
- VIII. Ecotones between oases and desert areas.

In accordance with the floristic subdivisions of Mapimí (Martínez and Morello 1977) the following macrohabitats were distinguished (Fig. 2):

- I. Large-stone slopes of the mountains with sparse cactus-shrub vegetation and yuccas.
- II. Medium-stone slopes with flat surfaces covered by *Agave asperrima* Jacobi + *Larrea divaricata* (D.C.) Coville + *Euphorbia antisyphilitica* Zucc.
- III. Small-rock and gravel piedmonts with cac-

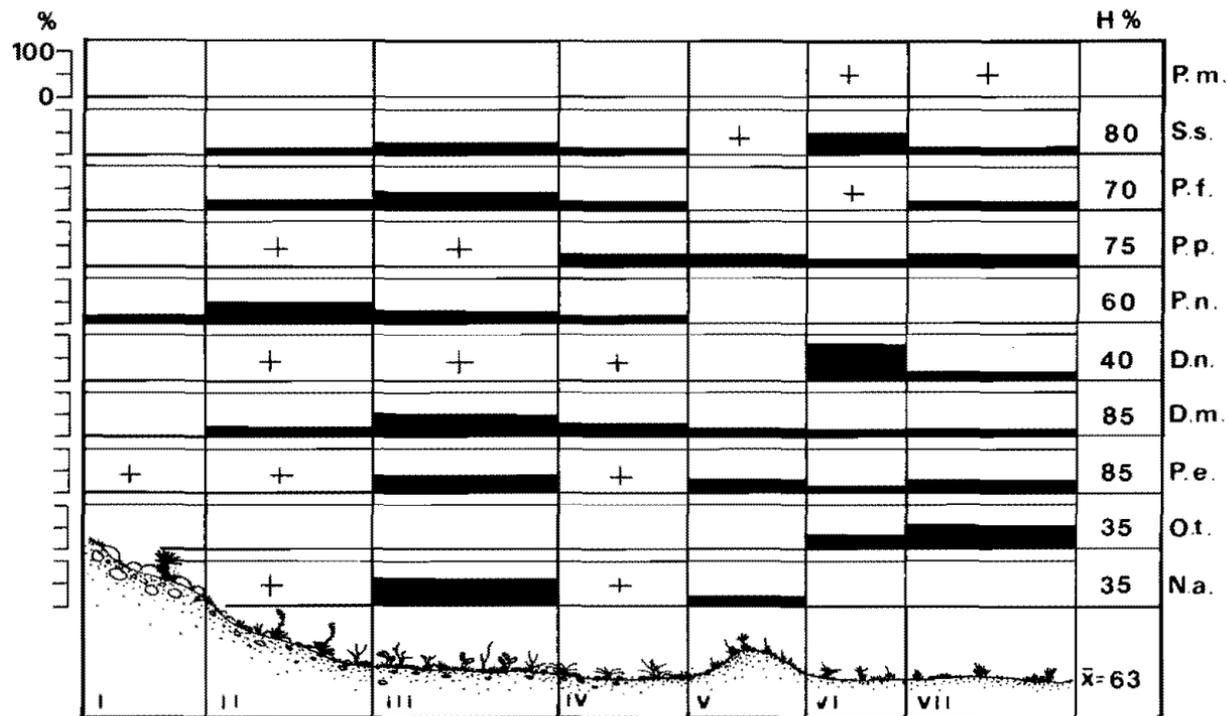


Figure 2

Rodent species distribution through the macrohabitats in the Mapimi desert. Rodent species (see Table 1). Types of macrohabitats: I - VII, see "Use of Macro-Habitats" in methods. Other designations the same as in Fig. 1.

- tus-shrub vegetation: *Opuntia rastrera* Weber + *K. divaricata* + *A. asperrima* + *Fouquieria splendens* Engelm.
- IV. Gravel plains with sparse shrub vegetation of *L. divaricata*.
 - V. Sand dunes with shrub communities: *L. divaricata* + *Jatropha dioica* Cerv. + *Yucca* sp. and herbs.
 - VI. Alluvial valleys covered by *Prosopis glandulosa* and herbs (*Hilaria mutica* (Buck) Benth).
 - VII. Alluvial valleys with shrubs (*Suaeda nigrescens* Johnston) and herbs (*H. mutica*).

Within-Macrohabitat Distribution

In order to estimate the correlation between rodent locomotion activities and within-macrohabitat species distribution, foot tracks were registered on squares of smoky foil glued to small boards, 30 x 30 cm in size. Sunflower seeds and oat flakes were used as baits. An area of 2 ha was selected at the nopalera of Mapimi (*Opuntia rastrera* + *Larrea divaricata*), and 50 boards with baits were placed in a grid system of 20 m distances between them. We recorded 579 visits of 4 nocturnal rodent species on these boards.

Exploratory Behavior

Individual exploratory behavior of an unknown new territory was studied under laboratory conditions. Animals were kept in individual cages to be tested later in plastic boxes (1x1x1 m) by using the "open field" technique (Eisenberg 1963, 1967). Sifted sand was used as the substrate. Each species was tested 10 times, during 10 min each time, the number of males and females being equal.

The following patterns of activity were recorded: number of different gate transversals over the box, patterns of freezing and sniffing postures, jumps, and substrate digging. It was proposed that

all these patterns of activity relate to the use of food resources scattered in the space, avoidance of predators, and shelter-building. Over 40 years ago bird behavior in food gathering was successfully used by Shulpin (1939-1940), he identified the so-called "adaptative types" of birds. As found in the experiments of the "open field" type, the level of activity in rodents and some forms of their behavior were directly connected with their mode of life (Wilson *et al.* 1976, Dewsbury *et al.* 1980, Vigorov 1980).

Types of locomotion were specified in accordance with the classification of gaits offered by Gambarian (1972): 1) symmetrical (diagonal) gaits - a) diagonal quadrupedal run, b) symmetrical bipedal run; 2) asymmetrical gaits - a) four-legged ricochet jumps (quadrupedal ricochet, b) hind feet ricochet jumps (bipedal ricochet).

Food Habits

Food habits were determined by the ratio of volumes of basic food types, i.e., seeds and fruits, green parts of plants, and invertebrates, contained in the stomach (visual estimation with an error of not more than 10%). We examined 469 stomach contents from Trans-Altai Gobi and 122 stomach contents from Mapimi. Rodents were collected during the wet season of intensive vegetation, flowering and ripening of plants.

Data Analysis

The species were compared in terms of their peculiar ecology and behavior by using the coefficient of percentage resemblance:

$$Y_{ih} = 1 - \frac{1}{2} \sum_j |P_{ij} - P_{hj}|$$

where P_{ij} and P_{hj} are the frequencies of the j resource use by the species or the frequency of their behavior j (Shoener 1968, 1970). The resemblance coefficients were employed to classify the species by their ecological and/or behavioral features. Dendograms were based on the

data of the unweighed pair-group method of cluster analysis (Sokal and Sneath 1963).

The species were ordinated in the system of three axes of ecological space by using the Bray and Curtis method (1957) (Beals 1960). The least similar species were at the ends of the X axis (the first axis of coordinates) at the maximum distance from one another. The position of all other species on the X axis was calculated by the formula of Pythagorean distances:

$$X_i = \frac{a^2 + c^2 - b^2}{2c}$$

where X_i is the position of the species "i" on the axis X, "a" is the distance from the first end of the axis to the point X_i , "b" is the distance from the second end of the axis to the point X_i , and "c" is the distance between the ends of the axis X. The terminal points of the axis Y (the second axis) represented a pair of species closely situated on the axis X but with low coefficients of resemblance. Then the position of all species on the second axis was found. After that, using the same principle, the third axis was drawn. In this technique, the polar ordination axes do not show any actual measurements of ecological space. The models of polar ordination graphically reflect the interposition of species in the integral space of the investigated ecological (ecologoethological characters).

The position of species in the structure of the community in each desert was analyzed by the pattern of the regression curves of the ecological resemblance coefficients. This method was used by Inger and Colwell (1977) in their analysis of the community structure of amphibians and reptiles. To draw these curves, the resemblance coefficients of each species were ranked on the principle of nearest neighbour. Each rank yielded the mean value of the resemblance coefficients. The number of ranks was equal to that of species in the community minus 1. The curves were compared by their relative sizes, and their lack of parallels (*geumetric incongruence*) (Plokhinsky 1970).

The mean values were compared by the standard criterion of Student.

The variety of rodents' diets and their use of macrohabitats were assessed by using the information index of variety offered by Shannon (Shannon and Weaver 1949):

$$H = \sum_j P_{ij} \log P_{ij}$$

where H is the variety index (entropy) P_{ij} the frequency of use of the resource "j" by the species "i".

RESULTS AND DISCUSSION

Use of Macrohabitats

Rodent species distribution along an altitudinal gradient of macrohabitats is shown in Fig. 1 and Fig. 2. The species of Mapimí use a larger range of macroconditions. The average Shannons index for macrohabitats occupied in Mapimí is 63%, in the Trans-Altai Gobi it is 41%. The most specialized forms live in Mongolia, but the most plastic (eurytopic) ones - Mexico. The limits of similarity of species in their use of macrohabitats are equal in both communities: in the Trans-Altai Gobi from 9 to 67%, in Mapimí from 0 to 66%. But, because of the higher number of eurytope species in Mapimí, the average overlaps in spatial rodent niches differ: in the Trans-Altai Gobi - $17 \pm 3\%$ (the number of pairs compared (n) is 45, 10 species), in Mapimí - $31 \pm 3\%$ (n = 36, 10 species); $P < 0,01$. We shall differ discussion of these differences to the last section.

Exploratory Behavior and Use of Microhabitats

Peculiar rodents' exploratory behavior reflect their use of the local microconditions. The distribution of 4 species of nocturnal rodents living in the cactus-shrub (nopalera) plant community of Mapimí illustrate this correlation.

It is characteristic of *P. nelsoni*, when exploring an unfamiliar territory, to move by ricochet quadrupedal jumps, even in slow locomotion. This species has typical horizontal orientation postures and its fossorial activity is very intense. *D. merriami* moves by quadrupedal and also by bipedal ricochet jumps. Its frequency of orientation postures and substrate-digging is lower than in *P. nelsoni*. The scheme of these species behavior shows their ability to overcome places within vegetation

and to recover scattered food from the surface soil. In case of any danger, these animals can change to quick bipedal and quadrupedal ricochet, seeking the protection of shrubs or hiding in their intricate burrows. Under natural conditions, as we found, these species gather their food from sites covered with thick bushes and cacti and from those with thin vegetation.

Gambarian (1972) states that the primitive ricochet jump is typical for most rodents. However, this type of locomotion is differently fixed in different species. A more progressive improvement of the quadrupedal ricochet saltation reflects higher mobility and better adaptation to life in deserts with patchy vegetation. The next step is a transition to bipedal locomotion which is best developed in Afro-Asian jerboas (Fokin 1978). In American *Dipodomys* this mode of locomotion is still primitive (simultaneous bipedal ricochet with the jerk effected simultaneously by both feet). When moving slowly, the animals often bear upon their front feet. Their activity outside burrows is highly limited in time (Reichman 1983).

There are numerous publications on the problem of spatial and trophic resources partitioning by representatives of desert Heteromyd rodents (the latest reviews by Reichman 1983; Price and Brown 1983). The hypothesis that bipedalism of *Dipodomys* was a kind of morphological adaptation for more effective use of desert environment with patchy distributed resources of food (Reichman and Obershtein 1977; Price 1978; Reichman 1979) seems to be verified by visual observation of the feeding behavior of *Dipodomys* and *Peronathus* (Bowers 1982; Thompson 1982), as well as by experiments (Price 1983).

In case of *N. albigula* its exploration of an unfamiliar territory is characterized by numerous symmetric gaits, long horizontal and vertical orientation postures with sniffing, freezing postures, while its jumps, quick motions and soil-digging are rather infrequent. The behavior of *N. albigula* describes it as a dweller of well-protected sites with dense vegetation cover, as a good and careful scout-explorer ready to escape to the thick bushes or to any other kind of shelter at any time, in case of danger. The symmetric diagonal locomotion helps to diminish the height of the trajectory of the animal body during its movement; this kind of locomotion is more efficient energetically in habitats with thick grasses and shrubs (Fokin 1978). In Mapimí, *N. albigula* lives in thickets of prickly pear and agaves, where it builds its vast nests and actively gathered dry materials, prickles, fruits and stalks of near-by cactuses which to

store. The mobility of this rather large animal (it weighs up to 250 g) is limited to some hundred square meters. Wood rats move only along paths and are extremely cautious.

As compared with *N. albigula*, *Peromyscus eremicus* is more mobile and subtle (up to 20 g in weight); its diagonal locomotion is similar to the former one. The animals make frequent jumps, their freezing are rather rare; like in wood rats, their fossorial activity is relatively poor, they gather up their food on the soil surface. Under natural conditions of cactus-shrub desert these animals were encountered on sites abundant in dry materials, such as dry boughs, dry agave peduncles, dead cacti. The animals can easily jump over stones and dried-up trees, they can well climb up high branches or shrubs.

As our data show, species with similar forms of behavior (Tabl. 1) were frequently found in similar places on our experimental site (Fig. 3). Any direct competition between these species for spatial resources seems to be low or absent, because they are rather distant phylogenetically from one another (different genera) and also differ in terms of size and appearance.

Exploratory Behavior General Comparison

The peculiarities of behavior of 20 rodent species during their exploration of an unfamiliar territory (Tabl. 1) were used to make a special classification of these rodents in terms of their relation to spatial resources (Fig. 4). Species with most similar forms of behavior in some cases have similar morphology and are related phylogenetically (*P. eremicus* - *P. maniculatus*, *P. penicillatus* - *P. nelsoni*, etc.). In other cases, judged by the features of maximum similarity in behavior, species of more distant phylogeny were clustered together (*S. spilosoma* - *O. torridus*, *S. crassicauda* - *E. naso*).

There are 3 large groups of species:

The first group (from *Mus* to *Onychomys*) is composed of slowly running, symmetrically locomoting forms which do not build deep and intricate burrows (except *S. spilosoma*). They should gather food mainly from the surface soil.

The second group (from *Rhombomys* to *Dipo-*

Table 1 – Part I

Frequencies of the patterns of exploratory behavior of the rodent species in the "open field" tests.

*** SPECIES**

Patterns of behavior	P.f	P.p	P.n	D.m	D.n	P.m	P.e
Diagonal quadrupedal locomotion	–	–	–	–	–	0.68± 0.04	0.61± 0.2
Quadrupedal ricochet	0.63± 0.03	0.63± 0.02	0.60± 0.03	0.58± 0.02	0.46± 0.02	0.05± 0.02	0.06± 0.00
Bipedal ricochet	–	–	–	0.18± 0.02	0.16± 0.02	–	–
Diagonal bipedal locomotion	–	–	–	–	–	–	–
Jumping	0.03± 0.01	0.02± 0.00	0.02± 0.00	0.02± 0.01	0.02± 0.01	0.06± 0.02	0.14± 0.01
Hind feet orientation (vertical)	0.04± 0.01	0.06± 0.01	0.04± 0.01	0.06± 0.01	0.22± 0.02	0.04± 0.02	0.06± 0.01
Four limb orientation (horizontal)	0.07± 0.02	0.06± 0.01	0.10± 0.02	0.02± 0.01	0.03± 0.01	0.12± 0.03	0.09± 0.01
Freezing postures	0.15± 0.02	0.01± 0.01	0.01± 0.01	0.03± 0.01	0.01± 0.00	0.01± 0.01	0.01± 0.00
Digging	0.09± 0.02	0.23± 0.02	0.22± 0.02	0.12± 0.02	0.10± 0.01	0.05± 0.02	0.04± 0.01
Sum of acts per 1 Test	23.5	41.9	39.4	48.8	56.7	78.0	68.9

*P.f - *Perognathus flavus* – P.p - *P. penicillatus* – P.n - *P. nelsoni* – D.m - *Dipodomys merriami* – D.n - *D. nelsoni* – P.m - *Peromyscus maniculatus* – P.e - *P. eremicus*

Table 1 – Part II

Frequencies of the patterns of exploratory behavior of the rodent species in the "open field" tests.

*** SPECIES**

Patterns of behavior	N.a.	O.t.	S.s.	C.m.	P.r.	R.o.	M.m.
Diagonal quadrupedal locomotion	0.59± 0.02	0.50± 0.03	0.54± 0.02	0.69± 0.02	0.72± 0.02	0.01± 0.00	0.01± 0.00
Quadrupedal ricochet	0.05± 0.00	0.02± 0.01	–	–	–	0.48± 0.02	0.54± 0.02
Bipedal ricochet	–	–	–	–	–	–	–
Diagonal bipedal locomotion	–	–	–	–	–	–	–
Jumping	0.01± 0.01	0.06± 0.01	0.01± 0.00	0.02± 0.01	–	0.01± 0.00	0.02± 0.01
Hind feet orientation (vertical)	0.09± 0.01	0.12± 0.02	0.24± 0.02	0.02± 0.00	0.02± 0.00	0.10± 0.01	0.06± 0.01
Four limb orientation (horizontal)	0.12± 0.02	0.16± 0.02	0.08± 0.01	0.06± 0.01	0.14± 0.01	0.16± 0.01	0.15± 0.01
Freezing postures	0.18± 0.02	0.02± 0.01	0.01± 0.00	0.03± 0.01	0.02± 0.01	0.01± 0.00	0.01± 0.00
Digging	0.02± 0.01	0.12± 0.02	0.13± 0.01	0.18± 0.02	0.10± 0.01	0.23± 0.02	0.21± 0.04
Sum of acts per 1 Test	46.7	68.3	72.5	66.2	77.6	68.8	83.3

*N.a. - *Neotoma albigula* – O.t. - *Onychomys torridus* – S.s. - *Spermophilus spilosoma* – C.m. - *Cricetulus migratorius* – P.r. - *Phodopus roborovskii* – R.o. - *Rhombomys opimus* – M.m. - *Meriones meridianus*

Table 1 – Part III

Frequencies of the patterns of exploratory behavior of the rodent species in the "open field" tests.

Patterns of behavior	* SPECIES					
	E.n.	S.c.	A.n.	A.s.	D.S.	Mus. m.
Diagonal quadrupedal locomotion	–	–	–	–	–	0.69± 0.02
Quadrupedal ricochet	0.04± 0.01	–	0.29± 0.02	0.28± 0.01	0.01± 0.00	0.03± 0.01
Bipedal ricochet	0.57± 0.02	0.69± 0.01	0.37± 0.02	0.38± 0.02	0.07± 0.01	–
Diagonal bipedal locomotion	–	–	–	0.01± 0.00±	0.46± 0.02±	–
Jumping	0.09± 0.01	0.12± 0.01	0.04± 0.01	0.03± 0.01	0.02± 0.01	–
Hind feet orientation (vertical)	0.16± 0.01	0.03± 0.01	0.17± 0.01	0.15± 0.01	0.31± 0.02	0.03± 0.01
Four limb orientation (horizontal)	–	0.01± 0.00	–	–	–	0.04± 0.00
Freezing postures	–	0.03 0.00				0.05± 0.01
Digging	0.13± 0.01	0.13± 0.01	0.14± 0.01	0.15± 0.01	0.13± 0.01	0.15± 0.01
Sum of acts per 1 Test	79.6	122.0	90.4	37.0	79.3	75.3

*E.n. - *Euchoreutes naso* – S.c. - *Salpingotus crassicauda* – A.n. - *Allactaga nataliae* – A.s. - *Allactaga sibirica* – D.s. - *Dipus sagitta* – Mus. m. - *Mus musculus*

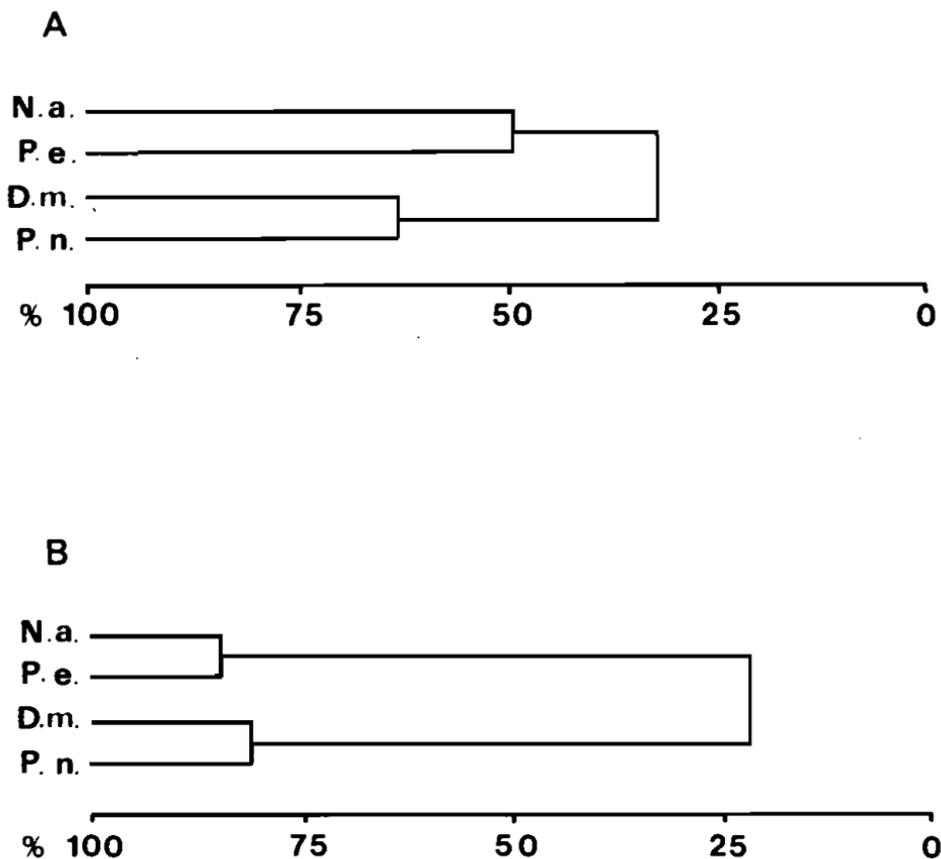


Figure 3

Classification of 4 nocturnal rodent species a) in their relations to microhabitates in the cactus-shrub (Nopalera) desert of Mapimi, b) in exploratory behavior in the "open field" tests.

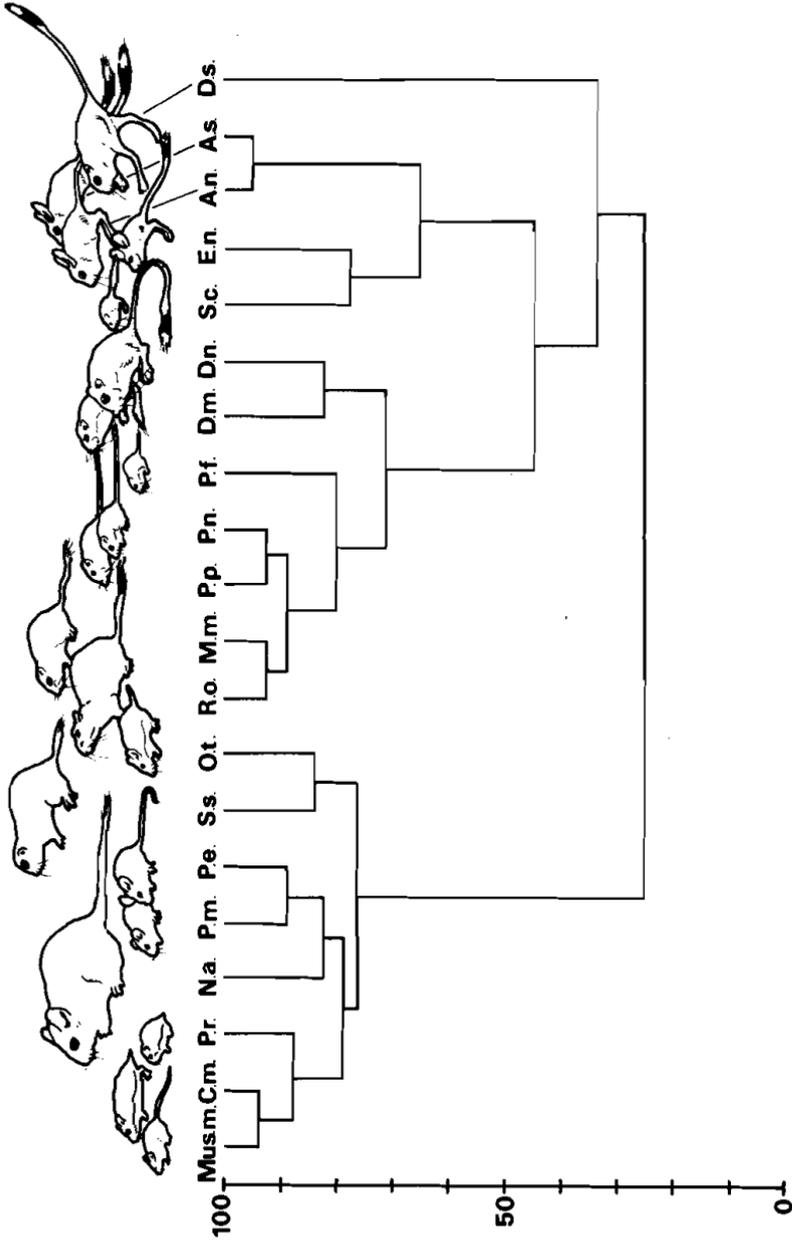


Figure 4
Classification of the desert rodents in behavior when they explore an unfamiliar territory.

domys) is composed of active quadrupedal ricochet rodents which can gather food from the soil surface and from its surface layer, and dig deep burrows.

The third group (from *Salpingotus* to *Allactaga*) is composed of sprinter bipedal ricochet jerboas which dig deep burrows and look for food as the species of the second group do. *D. sagitta*, which represents tridactyl jerboas, is close to the last two groups. It is characterized by symmetrical bipedal run. When this animal is quiet, it moves only by pace, which seems to enable it to gather food at low energetical cost and to hide behind and under shrubs or to climb over branches. At the same time, when crossing sites covered with extremely thin vegetation, *D. sagitta* can readily take to rapid ricochet saltation on its hind feet.

The symmetrical uniform rhythmic form of locomotion in *D. sagitta* and in some other species of jerboas seems to have provided these species with an ability to widen the area of spatial resources use.

All jerboas use open areas and actively escape those with thick vegetation. Quadrupedal ricochet rodents require well protected environments which can be either their intricate burrows or thick bushes. Species with predominant symmetrical type of locomotion correlate in their distribution with thickets of bushes and herbs.

No Gobian jerboas has similar exploratory behavior forms among Mapimi's rodents. American *Perognathus* and *Dipodomys* are grouped together with Asian *Meriones* and *Rhombomys*, but not with the bipedal Dipodidae. The first genus is more similar to gerbils, as it was also found by Mares (1980) when he analyzed the morphoecological characters.

Food Habits

The classification of 20 species in terms of their food habits, as presented in the dendrogram in Fig. 5, is based on the comparison of their diets.

Among species which are mainly herbivorous (green plant eaters) (group 1 in Fig. 5) the percentage of herbaceous plant material in the stomach contents increases in the following order: *D. sagitta* - *D. nelsoni* - *N. algibula* - *R. opimus*.

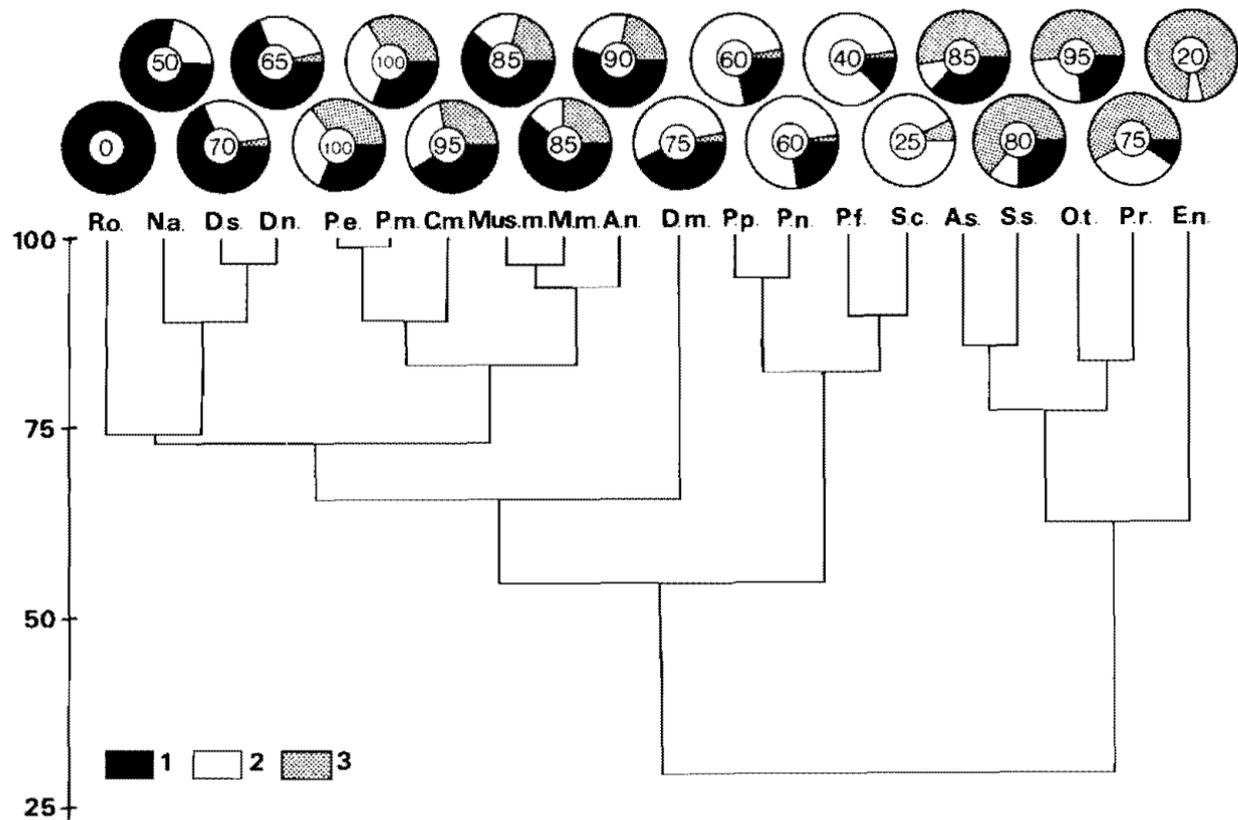


Figure 5

The composition of desert rodent diets and classification of species in feeding. Designations: 1 - green parts of plants, 2 - seeds and fruits, 3 - invertebrates. Digits within the circular diagrams - indexes of the diet diversity H.

Peromyscus species to *A. nataliae*, used mixed food, green parts of plants, seeds and insects (approximately in equal proportions) are included in the second groups.

The next group embraces granivorous species. The proportion of seeds in diets increases in the row: *P. penicillatus* - *P. nelsoni* - *P. flavus* - *S. crassicauda*.

The kangaroo rat *D. merriami* is situated between the second third groups.

At last, there are species which consume more animal food (insects and other invertebrates), and these are included in the fourth group. The rate of diet specialization increases in the row: *A. si-birica* - *O. torridus* - *P. roborovskii* - *S. spilosoma* - *E. naso*.

In all comparisons, the most specialized are the Asian species. Shannon's indexes are minimal in Asian *R. opimus*, *E. Naso* and *S. crassicauda* (Fig. 5). However, there are exceptions. Several species among Gobian forms which consume a wide spectrum of food. On the whole, the average index of diet diversity in Mexican rodents is 70%, exceeding that in the Asian species (60%).

Four trophic groups are represented in each community. The average overlap in diets of species in the Mapimí community is $60 \pm 3\%$ ($n=45$, 10 species), in the Trans-Altai Gobi it is $51 \pm 4\%$ ($n = 45$, 10 species). The differences are not significant, ($p>0.05$).

Ecological Classification and Structure of Communities

The generalized ecological classification of desert rodents, represented in Fig. 6, shows graphically the results of multiplication of pair-wise similarity indexes in terms of the animals' exploratory behavior and feeding. We found such an approach possible, because the positive correlation between trophical and behavioral indexes of similarity is rather low ($r = 0,16$, with $n = 180$ $P < 0,05$). Based on the above data, we believe that the food type and the way in which the animals use the space (in our case it is their exploratory behavior) are independent variables (Gody 1974).

In the dendrogram, the species, which are geographically related, are clustered together by the principle of maximum

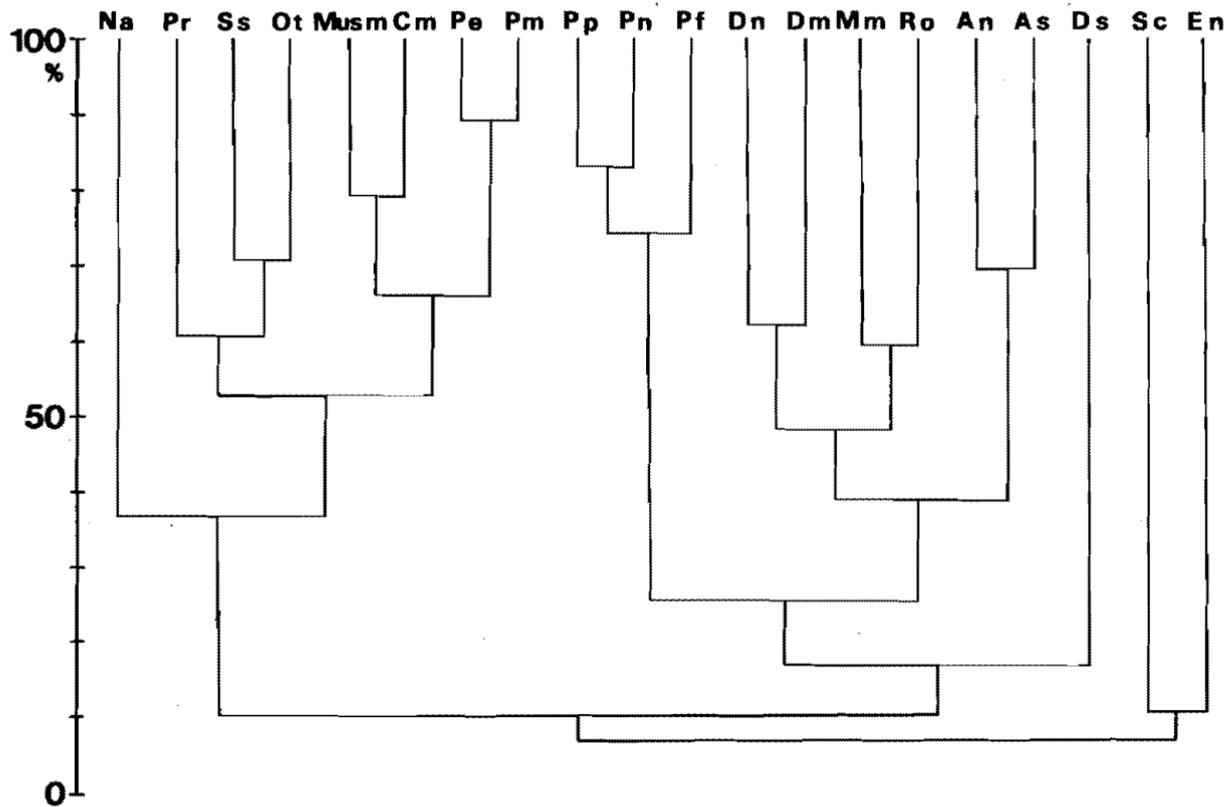


Figure 6
General classification of desert rodents in exploratory
behavior and feeding.

similarity (Fig. 6). Geographically separated forms are in all cases grouped at a lower level of resemblance. It testifies to low level relationship between ecological forms representing different communities. It is not easy to specify ecological groups of distinct characteristics. Nevertheless, some correlations are interesting. The American kangaroo rats (genus *Dipodomys*) are closer to the Asian gerbils (genus *Meriones* and g. *Rhombomys*). The American deer mice (g. *Peromyscus*) are grouped together with the Asian *C. migratorius* and *Mus musculus*. The Gobian *P. roborovskii* is closest in its ecology and behavior to *O. torridus* and *S. pilosoma* from Mapimí.

In the system we have accepted for measuring the ecological space, some Gobian jerboas (genera *Euchoreutes*, *Salpingotus*, *Dipus*) have no close ecological forms in the community of Mapimí. A reciprocal situation is found in Mapimí's *Perognathus* which are trophically more specialized for seed-eating than the Gobian ricochet rodents.

The position of species in the system of two parameters of ecological space (the trophics and the pattern of territory use) was analyzed by using the technique of polar ordination of species on the basis of reverse coefficients of similarity between each species and other members of the community (Fig. 7, a, b). The species' ordination in the three dimensional space was established for the Trans-Altai Gobian and Mapimí communities separately.

The distribution of species in the community of the Trans-Altai Gobi is more uniform, and the occupied hypervolume of the ecological space there is larger than in Mapimí. The species with specialized locomotion or/and diet (*E. naso*, *S. crassicauda*, *D. sagitta* and *R. Opimus*) lie in the periphery of the model. In the Mapimí community there are two groups of species, one of which is composed of seed-eating and seed-herbaceous plant-eating ricochet rodents of the heteromyidae family. The second group is made of North American Cricetidae. The squirrel *S. pilosoma* belongs to the same group.

The mean value of generalized coefficients of rodent similarity in the community of the Trans-Altai Gobi is $19.9 \pm 2.7\%$, with extreme values from 0 to 79% ($n=45$). The generalized coefficients of rodent similarity in Mapimí vary from 8 to 69% ($n=45$), with their mean value of $31.7 \pm 3.7\%$. The differences are reliable in terms of Student's test criterion ($P<0.05$).

In case of the Mapimí community, the dispersion

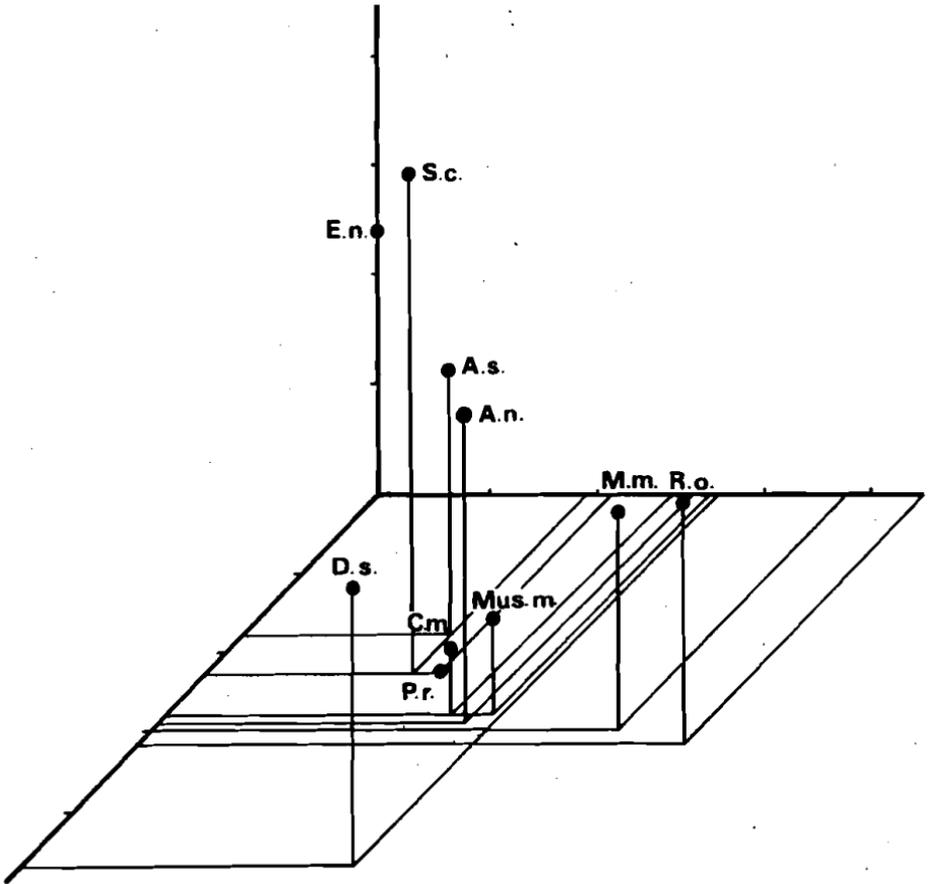
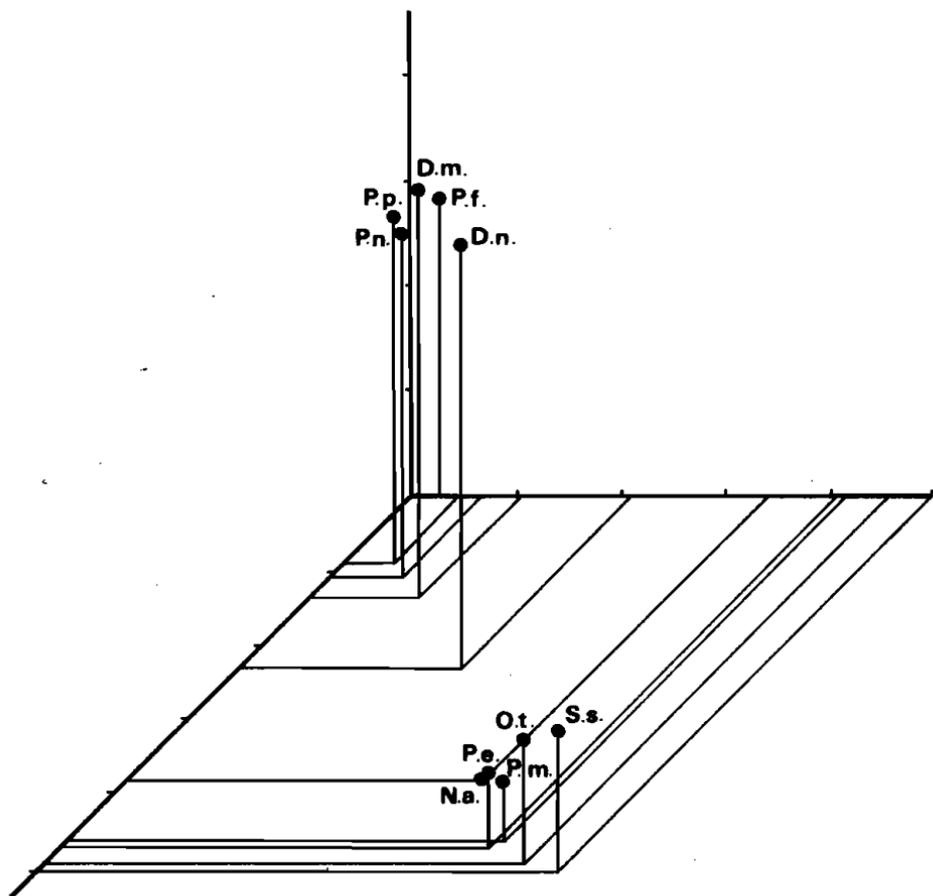


Figure 7

Ordination of desert rodent species in three axes of ecological space: a) community of Trans-Altai Gobi, b) community of Mapimí.



of the rodent similarity coefficients here is somewhat higher (δ Mapimí = 25, δ Gobi = 18).

The same conclusion can be drawn when analyzing the regression curves of the ecological similarity coefficients (Fig. 8). The curves were drawn by ranking the similarity coefficients of each species; in both communities the curves were descending. The curve for the Mapimí community is above that for the Trans-Altai Gobi. The differences are reliable in terms of one row excess over the other ($P < 0.01$). However, the differences mainly involve forms of similar ecology.

On their terminal ends the curves converge closely. It can be attributed to the fact that in both communities the maximal distance between species in the ecological space is close. The existence of two groups of species in the Mapimí community is reflected in the step-like pattern of the curve. At the same time the curve for the Trans-Altai Gobi community is descending more smoothly, reflecting a more uniform distribution of species in the ecological space there. Both curves are significantly, nonunparallel ($P < 0.01$).

Discussing the structural difference of the communities under consideration, one should pay attention to the differences in the taxonomic distances between species in each of these communities. The community of the Trans-Altai Gobi is composed of strongly diverged, representatives of 10 species relating to 9 genera. In Mapimí, there are rodents only of 10 species representing 7 genera; there are also 3 pairs of close species of one genus. There is only one pair of close species of one genus in the Gobian community.

The differences in the volume of ecological space in the Gobian and in the Mapimí communities (Fig. 7 a,b) are basically due to the different degree of ecological divergence of the bipedal and quadrupedal ricochet rodents. As noted by Mares (1980, 1983), such ecological groups are characteristic of all typical desert faunas of long evolutionary history. Both communities reveal all trophic groups of species, including those specialized for seed eating, and hence, for living on waterless diet.

The desert rodent faunas of North America and Asia were developing independently from each other since the later Miocene; their phylogenetic similarity is relatively low (Simpson 1945; Hall and Kelson 1959; Walker 1964).

Finds of ricochet rodent fossils are related to

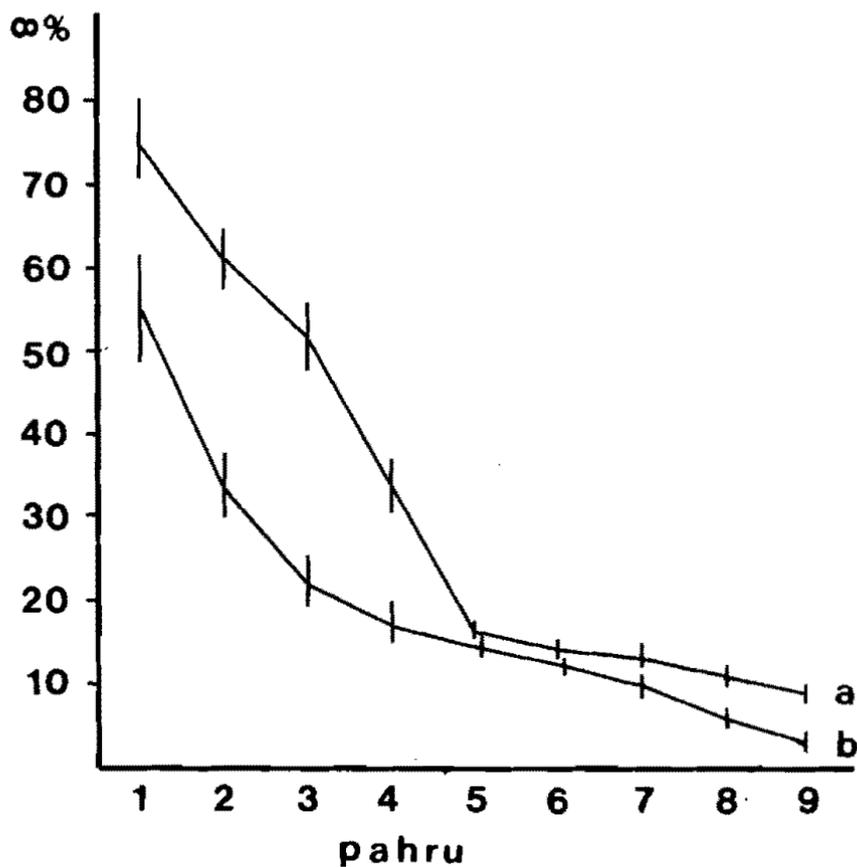


Figure 8

Regression curves of generalized coefficients of the ecological similarity of the rodents a) in Trans-Altai Gobi, b) in Mapimf.

Miocene. Jerboa of recent habit are known from the Early Miocene deposits of Central Asia, though it seems most likely that they became separated from the general *Dipodoid* stalk as far back as in lower Oligocene. Gerbils are of African origin, they appear in Central Asia during Late Miocene (Shevyreva 1983). The Heteromyidae differentiated in North America during Miocene-Pliocene adapting the increasing landscape aridization (Lindsay 1972; Hafner 1978; Patton et al 1981; Hafner and Hafner 1983). The family was became distinct much earlier, as Wood claims (1935), in the Middle Oligocene. The recent subfamilies Perognathinae and Dipodomysinae were already in existence in North America during Late Oligocene (Hafner 1978). During Middle Miocene, Heteromyidae were so widely spread in North America that some of their forms penetrated even into Central Asia (Shevyreva 1983).

In this way, paleontological data do support a relatively modern development of the ricochet rodents of North America.

In terms of their abundance in species, the communities under consideration can representatively characterize the faunas of the large desert of both continents. The deserts in Magnolia are most severe climatically. They are situated much northward than the deserts in Mexico which are more humid and warmer. On the whole, rodent habitat variability (variation) in the Gobi is greater than that in the Chihuahuan Desert.

The latter's phytocoenoses are more productive and include more plant species. Association of abundantly fruiting bushes (brushes) and cacti occupy a larger space there. Vegetation-free areas are rare. It is more difficult to identify floristic units geobotanic subdivisions here than in the Gobi where communities are not so rich in species and the boundaries between them are strictly correlated with the geomorphological local characters. The greater ecological plasticity of the American rodents in their macrohabitats use shown in our example (Fig. 1, Fig. 2) may be due to the peculiarities of environments in Mapimi.

North American deserts seem never to have been developed as much as those of Asia did. During glaciations, the Sonora desert, for example, was covered by individual patchy arid refuges alternated with humid areas (Martin and Mehringer, 1965). This structure of environment could have accelerated the rate of speciation but it did not influence the scale of ecological divergence of the species. The diversity of environment in different desert refuges was similar and restricted. It

seems likely that the structural differences observed by the authors in the communities of the Trans-Altai Gobi and in Mapimí might have resulted from the different environment in the deserts of Central Asia and North America. Involving large arid regions of the two continents, these differences could considerably affect the rates of ecological and morphological divergence in desert rodents.

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