VERTEBRATE ECOLOGY IN ARID ZONES OF MEXICO AND ASIA

VLADIMIR SOKOLOV, GONZALO HALFFTER AND
ALFREDO ORTEGA
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INSTITUTO DE ECOLOGIA A. C., CENTRO DE INVESTIGACIONES
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CHAPTER 1

THE DESERT AS A HABITAT AND AN ARENA FOR EVOLUTION

Vladimir E. Sokolov and Gonzalo Halffter

The desert has long attracted the attention of researchers. It is not by accident that desert vertebrates became classical examples of convergent evolution (bibliographic quotes). Kangaroo rats (*Dipodomys*) of North America, extinct Argirolagidae of South America, jerboas (Dipodidae) of Eurasia and North Africa, Australian Kangaroo mice (*Notomys*) are brilliant examples of mammalian adaptation to life in open arid landscapes with sparse and patchy vegetation. No less known are subterranean forms of mammals, also typical of arid territories. These are for example Asian zokors (*Myospalax*) Eurasian molevoles (*Ellobius*), gophers (Geomyidae) of North America, tuco-tuco (Ctenomydae of South America, naked sand rats of Africa (Bathyergidae), and marsupial moles (Notoryctidae) of Australia. Virtually all big taxa of the animal and plant Kingdoms of deserts provide examples of convergent (of parallel) evolution. The reason is that desert conditions are very close to the extreme ones. Only few limiting factors operate in the deserts and for this cause the direction of their actions coincides with different places in such restrictive conditions. Desert animals have to change their structure, behavior and physiology due to the effects of the most stringent natural selection. Thus a desert is a unique arena for many evolutionary transformations whose understanding is promoted by a limited set of environmental factors. Up to date not a single definition of the concept "desert" exists. According to a unified UNESCO map compiled in 1977, the arid regions of the world include four bioclimatic zones as follows: 1) an extra arid zone, deprived of vegetation in flat interfluves, with precipitation levels of no more than 100 mm per year; 2) an arid zone with sparse and scant vegetation, represented by annual and perennial succulents with precipitation levels of 100-200 mm per year; 3) a semi-arid zone with shrubs and interrupted grass covered with precipitation level of 200-400 mm per year; 4) and, finally, the zone of insufficient humidification, including certain tropical savannas, chaparral communities and chernozem steppes with precipitation levels of 400-800 mm per year. According to this map the area of arid territories is almost of 48 mln square kilometers; about one third of the earth land surface. However, according to revised UNESCO and FAO data, about 23 per cent of the land surface is placed in the category of typical deserts (Babaev *et al.*, 1986). The most apt definition of a desert, from our point of view, is given by M. Petrov (1973), who defines a desert as a territory with an extremely dry climate (precipitation level less than 200-250 mm per year and with an irregular pattern, and with evaporation prevailing over precipitation) occasionally containing an extinct river network or rare transit rivers lacking a constant surface runoff, and with sulfides and chlorides predominating in saline soil with salt crystals. This is the territory where, plant and animal kingdoms are sparse, migration of salt solutions in soils prevails over biogenetic processes, and farming is possible only with irrigation.

Deserts are located in three climatic belts: moderate, subtropical and tropical. Despite differences in climate, mainly in the lower thresholds of temperature and the range of temperature differences, all deserts have many features in common. Currently there are five desert regions in our planet; namely: the Great desert belt in the Old World, the deserts of North America, the deserts of South America and those of South Africa and Australia.

The main limiting factors for all deserts in our planet are the following:

1.- Low level of humidification, extreme unevenness of precipitation across seasons and alternation of extremely dry years with years relatively favorable for vegetation growth and fruitage.

2. Extreme temperature conditions. Deserts are characterized by a huge gap between minimum and maximum temperatures on the land surface (58^{0}C at the Lybian desert; 54.7 ^{0}C at the Death Valley of California). Tremendous daily temperature drops occur the deserts. For instance in the Pamirs mountains desert temperature varies from 20^{0}C to - 20 ^{0}C in one day (Valter, 1975).

3. Lack of seasonal and spatial heterogeneity in the distribution of fodder resources. The phytomass of the richest saxaul forests (*Haloxilon ammodendron)* at the Middle Asia desert which constitutes 55 t/ha (Rodin, 1961); and of the poorest, extreme arid Gobi desert as little as 5.3-7.0 Kg/ha (Kazantzeva, 1986). The level of the vegetation cover in deserts even in the richest desert at Central Karakum (Turkmenia) does not exceed 45 percent (Nechaeva, 1970).

Patchy distribution is an specific feature of the vegetation in a desert. Heterogeneity of the resulting environment is an important condition for the adaptation of many species of desert ground vertebrates just like small mammals and lizards.

Fodder reserves in deserts have pronounced seasonal variations. Plant growth is timed by the humid season. The season of precipitation in deserts varies geographically. In Central Asia occurs in the spring and autumn while in the deserts in Mongolia and México it occurs in the summer. The humid season rarely lasts two months a year. The majority of the vertebrates breeds during this short period of vegetative growth. Hoarding and hibernation are common in small desert mammals as an adaptation to the absence of fodder in dry periods which are frequently accompanied by low temperatures. Hibernation is also characteristic of majority of desert reptiles and amphibians. Mobile animals (birds and ungulates) have seasonal migrations during dry periods. Hoarding is characterized by complex forms of behavior with an occasional division of labor, including foraging (*Rhombomys opimus*), construction of complex burrows with chambers for fodder reserves and preliminary drying and shorting of fodder. Foraging in open landscapes with a high risk of attack by predators requires an effective system of communication. Diurnal small mammals of arid regions use acoustic signals to warn conspecifics of danger (Nikolsky, 1984).

Desert animals have diverse forms of territorial behavior, from rigid territoriality to complete nomadism which is a result of fodder shortage and brevity of the breeding period. In all cases various forms of scent marking activity are of great importance for desert mammals. Specific features of the environment promote the development of some specialized forms of scent marking behavior in desert rodents and are used to transmit the information that the burrow or the territory is occupied. These include signal hills at the burrows of great gerbils (Rhombomys opimus), and scent holes at dust-bathing or sand -bathing sites at the burrows of Kangaroo rats (*Dipodomys*). Specific sebaceous glands are hypertrophied in many desert rodents. Active marking behavior in their home range can be explained by the poor preservation of excreta in arid climate.

Hibernation is a typical phenomenon widely spread among desert animals. The duration of hibernation in some rodents and lizards ranges from 8 to 9 months. Summer hibernation is common during the dry periods. Hibernation may be interrupted in the case of the growth of autumn vegetation, for instance in a little suslik (*Citellus pigmaeus*) or lasts until the next year (Kalabukhov, 1985). The physiology of hibernation (which requires preliminary accumulation of large fat reserves) disagrees with the specific functional features of the reproductive system. Winter hibernating species of mammals breed for shorter periods show a diminished fecundity, take more time to become mature and also take care of their offspring. When comparing the population of rodents in different zones, K-selected species are most widely represented in the desert communities. These are the species with a relatively constant oriented density dependent mortality and show no sharp drops in abundance. The size of their population is close to the carrying capacity of the environment and the individual life span is relatively long (more than a year). The breeding strategy of desert species operates on the principle of high effectiveness rather than productivity (Pianka, 1970).

Desert species are characterized by increased competitive abilities. Competition for resources in the desert (including fodder and shelter) is an established fact (Munger and Rown, 1981; Harris, 1984; Lemen and Freeman, 1987). Apparently in the conditions of limited resources, even in a climax equilibrated community, the competition can play the role of the structural homeostasis mechanism, promoting differentiation of animals into intra and interpopulation level in the space of conditions and resources of the environment. Competition becomes particularly acute during the most unfavorable periods, in terms of resources, and plays the role of the factor of ecological differentiation. All this is determined not only by high level of the constant nature or predictability of climate for a short-term period, but mainly by the age-long extreme effect for the most important climatic and climate-induced factors on animals.

Desert landscapes are the most ancient ones in our planet. For instance, imprints of xerophilous plants are known from deposits of the upper Paleozoic (Markov, 1956). The formation of modern deserts began in the upper Cretaceous and continued at a different places in Paleocene. The gradual formation of a subarid region with precipitation levels of 500-800 mm per year took place at that time in the territory of modern Eurasia south of 55^0 NL. This region was formed on the area of the tropical Gelenden botanic-geographical province and included the territories of modern Central Europe, Arabia, Kazakhstan, Middle and Central Asia. (Sinitzung, 1967). During the Paleocene-Oligocene the Poltava floristic region was formed on the basis of the Gelenden province with a great diversity of the evergreen xerophytic flora as *Ephedra* and *Welwitshia* which have survived to the present. Besides the Great Basin desert and those of South Europe deserts of the Paleocene are known in the USA, Peru, Colombia, South America and Central Australia (Shvartsbakh, 1955). The process of the period of aridization was replaced by the period of relative humidification of the climate. In the Neogene (Miocene and Pliocene) the rapid development of desert landscapes was related to dramatic orogenic changes which further cooled and dried the climate (Axerold, 1950, 1958, 1967, 1972,; Sinitzung, 1967; Vuilleumier, 1971; Bailey *et al.*, 1977). In the Miocene dry grass steppes with autochthonous vegetation were formed in the territory of the Great Basin desert and the deserts of North America (Krishtofovich, 1955). At the same time an adaptive radiation of rodents (Dipodidae, Cricetidae, Heteromyidae, and Sciuridae) occurred and has formed an important part of the contemporary fauna of deserts (Shevyreva, 1983).

Contemporary desert landscapes finally formed at the end of the Pliocene (Sinitzung, 1967). However, the desert boundaries during the Quaternary period changed substantially. The climate was by far more humid in the deserts of North America in the glacial periods (Petrov, 1973). In south west North America, in the territory of what is now known as the Sonora desert, there were patches of forests in the Pleistocene and Holocene (Martin and Mehringer, 1965; van Devender, 1977). Nevertheless, the status of arid regions in the Quaternary period was similar to that of the preset.

The paleoclimatology data show that the arid regions of our planet were for a long time divided by land with humid climate or by oceans. This is also supported by the high level of endemism of desert flora and fauna of different continents (Formozov, 1964; Vlater, 1975; Mares, 1980; Dlussky, 1981). An exchange of flora and fauna generally occurred between deserts of the same continent. In the Eurasian deserts the dispersion of species proceeded westward of the Central Asian desert and to the East from the deserts located in the territoryof the contemporary Middle and Frontal Asia (Geptner, 1945). The similarity of the psammophilous fauna in the deserts of South Africa and North Africa is apparently explained by settling of species along the regions with sand dunes. However, because they are divided by vast areas with humid climates, deserts may preserve a high level of fauna endemism even with the presence of continental ties. For instance, the rocky deserts of South Africa are typically highly endemism (Petrov, 1973). The formation of the isthmus between North and South America during the Pliocene did not similarly affect the vertebrate fauna in the desert of either continent. The formation of the Pliocene bridge resulted in South America in a dramatic wave the settlement of North American species of mammals, among which the Cricitinae displayed a particularly broad adaptive radiation. The adaptation to life in a desert habitat among the Cricetinae could not have happened earlier than the late Pliocene or early Pleistocene. At this time the typical south american desert marsupial, Argirolagidae became extinct. During that period, the arid region rodents of the continent were represented only by caviomorphous rodents (Simpson, 1983). A broad radiation of the Cricetidae in the south american desert was, on the one hand, prevented by the shortage of area and low diversity of desert territories, and, on the other, by a powerful buffer from the tropical areas with humid climate (also essentially limiting the settlement from South America to the north). The Cricetidae of South America failed to become adapted to the life style in arid climates (Mares, 1980).

Thus the deserts in our planet represent a natural experiment on a global scale. The formation of similar landscapes of desert took place in geographically isolated regions under conditions of gradual aridization of climates. Coadapted complexes of species were formed on these landscapes under the effect of very stringent selection. The comparison of these communities, as well as of constituent species, can provide extensive information for the study of the regularities of the evolution, genesis of adaptations (orientation of evolution, coadaptation and pre-adaptation), and the problems of the structural organization of communities (elucidation of the reasons for the combination of species in communities, mechanisms of their stability, etc.). Desert animals including insects, reptiles and mammals are extremely convenient models for the study of those problems.

This collection of papers is the result of a joint research project carried out by specialists of the Institute of Evolutionary Morphology and Ecology of Animals of the USSR Academy of Sciences (Moscow) and the Mexican Institute of Ecology (México) implemented in compliance with the program of international cooperation the MAB (UNESCO). Parallel with traditional comparative studies of the morphofunctional and behavioral adaptation of species, this publication contributes to the development of standard quantitative approaches to the study of species of small vertebrates of ecologically organized in geographically separated zonal complexes.

These studies conducted in both the Sovietic Union and México in accordance with the agreement. The desert, a landscapes-climatic zone common to both countries, provided an ecosystem model which inspires the thought and research for our scholars. In addition to information about the deserts of Middle Asia and Kazakhstan and the deserts in the north of central and western México, the book relies on information on the deserts of Central Asia, located in the Mongolian People's Republic. Data on the Central Asia desert were obtained during the study of nature in Mongolia within the framework of the permanent Soviet-Mongolian Integrated Biological Expedition.

Biosphere reserves have become the bases for conducting research in field conditions. A developing network of MAB reserves has created more favorable conditions for coordination of the efforts of scientists in different countries, not only in solving the practical issues of conservation and rational management of nature, but also in solving theoretical problems of biology. In Mexico research was carried out at the Mapimí Biosphere Reserve (Durango) and in the Pinacate proposed Reserve (Sonora); in the USSR, the search was conducted at the Repetek Biosphere Reserve (Turkmenia) and in Mongolia, at Great Gobi Biosphere Reserve (Bayan-Hongor aimak). This book also reports the findings of scientists of the Institute Evolutionary Morphology and Ecology of Animals obtained during field tours to the Republics of Middle Asia and Kazakhstan.

We entertain the hope that this book will be an example of the embodiment of the idea of international cooperation of scientists and coordination of research on theoretical problems on the biology of desert animals.

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CHAPTER 2

FACTORS OF MORPHO-ECOLOGICAL DIVERGENCE OF SPECIES IN COMMUNITIES OF DESERT RODENTS.

Konstantin A. Rogovin and Alexey V. Surov

Abstract

This review covers the literature and the author's own data on the role of predators and interspecific competition in the evolution of desert rodent communities. Predators and competition for limited resources are viewed as the fundamental factors that promote the morpho-ecological divergence of species in communities. This review analyzes feasible ways of testing hypotheses on the role of each of these factors. It probes into the possibility of interaction between factors. The problem of compatibility of social systems of coexisting species is given due consideration. Special attention is paid to Heteromyidae and Dipodidae communities. The evolution of bipedal locomotion in desert rodents is discussed using these groups as examples. Based on the results of observations, the following possibility is viewed as the most likely: climate aridization results in the impoverishment of the habitat and its transformation into a patchy one. In these conditions the most simple way to preserve the particular level of adaptation unchanged is by the expansion of the area of resources used by a species. The evolution of bipedal locomotion takes place initially through the intensive use of the home range and its even assimilation. In the patchy desert environment the appearance of bipedal gait is explained by a high risk of falling prey to predators in open unsheltered areas. The transition to an extensive use of space in jerboas (vast, overlapping home ranges) is a secondary phenomenon, related to the formation of vast, low productivity Palearctic deserts.

Introduction

The main objective of community ecology is to explain the variety, distribution and abundance of organisms at any place and time.

What is community structure, and what are the forces which determine it? These questions still present in spite of a huge amount of research performed during the last three decades. Empirical data recently collected provide the basis for comparative analysis of the organization of communities for a number of groups of animals, indicating insufficiency and contradiction of generalizations pertaining within the framework of the competitive community paradigm. Even the explanatory significance of the community structure concept has been questioned (Wiens, 1977; Connor and Simberloff, 1979; Roth, 1981; Simberloff and Boecklen, 1981; Simberloff, 1982;).

It has become clear that a number of factors such as adaptation to environmental conditions in allopatric populations, predation and extinction have been underestimated (Simberloff, 1982; Wiens, 1982; Case, 1983;).This may be partially explained by the absence of precise distinction when explaining the causes and results of specific factors and also by the insufficient development of a comparative approach and by the weaknesses in the experimental approach in research on community structure (Roth, 1981; Simberloff and Boecklen, 1981; Bowers and Brown, 1982; Brown *et al.*, 1986; Diamond, 1986; Price, 1986). Research into the structure of communities is conducted mainly to elucidate the rules in the combination of species. A contribution could be made both by a comparative formalized description of a number of genetically related communities, with a different number of species and by testing these communities with respect to hypothetical groups, formed by a random unification of species.

The existence of rules in the organization of communities, revealed during the first stage of research allows the formulation of hypotheses on the causes of the present type of species packing, that is the second stage: research into the functional aspects of organization. Testing these hypotheses is the most interesting, but the most difficult stage too. A successful researcher must have, first of all, a wide range of interests and to be a talented naturalist, besides the skills to perform an accurate experiment.

It is difficult to assess the role of possible factors in structuring of communities due to the fact that they are interactive very often or could function differently at different stages of the evolution of a community. In these conditions it would be expedient to replace the question "Which of the possible factors determine the structure of a community?" by the question: "What is the relative role of this or a number of other possible factors?" (Price and Brown, 1983).

At the same time the new outlook in research on mammalian communities can be outlined.

American heteromyid rodents (Heteromyidae) are a group of mammals permitting the use of the above mentioned approach. These rodents, widespread in North America, conform regular size series of forms in different types of deserts. Among rodents it is the wellknown group that forms communities, structured by size (weight) (Brown, 1973, 1975; Bowers and Brown, 1982).

Representatives of Heteromyidae are mainly granivourus forms that are capable of feeding on dry seeds. The ability to store seeds from the soil surface in burrows and shelters leads to the fact that in many cases the resources of seed are fully utilized from the soil surface (Lockard and Lockard, 1971; Price and Brown, 1983).

The original view of the primary role of interspecific competition in forming heteromyid communities and particularly their differentiation into quadrupedal and bipedal forms (Brown and Liberman, 1973; Brown, 1973; Reichman and Oberstein, 1977;Reichman, 1981;) is constantly questioned.

Predators are viewed as a possible factor, capable of determining the regularity in organization of communities of heteromyids by size (Price, 1981,1983,1984; Thompson, 1982b; Kotler, 1984a,b, 1985a). The theoretical substantiation of the "Predation" hypothesis is the view that in the heterogeneous environment (a desert for instance, with a patch distribution of vegetation) where cannot be a single strategy for avoiding danger (Rosenzweig, 1973; Thompson, 1982a,b). A patch-like distribution of vegetation in deserts enables the coexistence of different morpho-ecological forms with similar relations of costs to benefits in predator-avoidance behavior.

The primary adaptation of a population to environmental conditions during the period of isolation can beviewed as a factor which promotes the structural organization of the community. Some findings reveal that the possibilities for coevolution of species in communities of rodents are greatly exaggerated (Brown and Kurzius, 1987). The heterogeneity of the environment (distribution of resources) may order the distribution of species in a way which could easily be explained by competition (Tilman, 1982). As it is noted by Simberloff (1982), the hypothesis of adaptation to the conditions of habitat is, in fact, an alternative to the hypothesis of competition and was consigned to oblivion for many years.

Nevertheless two hypotheses have been established in the literature on the study of communities of desert rodents: 1) predators, and 2) interspecific competition. The need to evaluate the relative role of these factors caused vital interest in the analysis of the individual behavior of different species of the community in situations with preset and controlled parameters (Price and Brown, 1983; Price, 1986; Rogovin, 1988a). There are no data at present on the structure of communities of desert rodents from other continents. The analysis of the distribution of species by size (weight) in communities of Central Asia and Middle Asia rodents (essentially gerbils and jerboas) in the first approximation points to the absence of regularity in the distributions are indicative of the rodents communities of North America (Fig. 1). Our comparison of the morphological organization of rodents communities in the deserts of Mongolia and México by a set of metric factors indicates some patterns of regularity on the packing of species in the Central Asian desert community (see the article in this collection). Meanwhile, the nature of factors of structural organization in the community remains obscure. We can only assume that in the conditions of central Asia the role of predators or climate are relatively greater compared to interspecific competition. For a more distinct identification of factors involved in the formation of communities of desert rodents and for designing unequivocally interpretable experiments, we considered that the review of the available data in favouring the separate effects of predators and interspecific competition could be useful. Based on numerous data concerning the communities of American desert rodents of the Heteromyidae family, we attempted to present the literature and our own data on insufficiently studied communities of rodents in Middle and Central Asia (Mongolia), collected in 1979-1986, and also to compare them with the results of our surveys in the southern deserts of North America (México) in 1981, 1983 and 1987.

Some of our results are fragmentary and mainly illustrative, however, their use is justified by the application of a single design with which these data have been collected. The methods used in particular cases are given along the text or in captions to illustrations, or there is reference to a corresponding source. Since this study is a review and essentially debatable, we view it expedient not to discuss the methods used under a separate Chapter.

Figure 1. Distribution of species of rodents by size (weight) in desert rodent assemblages of North America and Asia. 1-5 - heteromiyd communitiesof U.S. deserts; from Price and Brown (1983): 1-2 - Great Basin (Fishlake Valley and Mono Lake), 3 - Mojave (Kelso), 4-5 - Sonora (Santa Rita Range and Rodeo); 6-10 - our data for Mexican deserts : 6 - Sonora (Pinacate), sandy river valleys; 7 - Sonora (Pinacate), rocky foot of mountains and plateau; 8 - Chihuahua (Bolsón de Mapimí), rocky foot of mountains and plateau; 9 - Chihuahua (Bolsón de Mapimí), clay proluvial valleys, ancient hollows of lakes; 10 - Chihuahua (Bolsón de Mapimí), sands; 11-20 - Our data for deserts of Central and Middle Asia, our data : 11 - Trans Altai Gobi, sands; 12 - Kyzylkum, sands; 13 - western Kazakhstan (Taisugan), sands; 14 - south of Trans Altai Gobi, rocky foot of mountains and mesoplacoras; 15 - north of Trans Altai Gobi, the same; 16 - Central Kyzylkum, rocky foot of mountains and tertiary plateau; 17 - south of Trans Altai Gobi, mountain valleys, hollows of wind erosion and outflow; 18 - north of Trans Altai Gobi, the same; 19 - northern Kyzylkum, ancient dry river valleys and deltas; 20 - western Kazakhstan clay flatland, ancient lake hollows. Species of rodents : PL- Perognathus longimembris, Pf- P. flavus Pa- P. amplus; Pp- P. penicillatus; Ppa- P. parvus; Pn- P. nelsoni; Pi P. intermedius; Pb- P. baileyi; Mm- Microdipodops megacephalus; Mp- M. pallidus; Dm- Dipodomys merriami; Do- D. ordii; Dp- D. panamintinus; Dd- D. deserti; Ds- D. spectabilis; Dn- D. nelsoni; Per- Peromyscus eremicus; Pm- P. maniculatus; Ot- Onichomys torridus; Na- Neotoma albigula; Nl- N. lepida; En- Euchoreutes naso; Sc- Salpingotus crassicauda; Sh- S.heptneri; Sk- S. kozlivi; Cp- Cardiocranius paradoxus; Aj- Allactaga jaculus; Asv- A. severtzovi; As- A. sibirica; Ae- A. elater; An- A. nataliae (balikunica); Ab- A. bullata; Alb- Allactodipus brobrinskii; Ppg- Pygerethmus pygmaeus; Ppl- P. platiurus; Dsg- Dipus sagitta; St- Stilodipus telum; Sa- S. andrewsi; Pct- Paradipus ctenodactilus; Jt- Jaculus turcmenicus; El- Eremodipus lichtensteini; Crm- Cricetulus migratorius; Ale- Allocricetulus eversmani; Alc- A. curtatus; Phr- Phodoppus roborovskii; Ml- Meriones libicus; Mm- M. meridianus; Rho- Rhombomys opimus; Elt- Eolaglurus luteus.

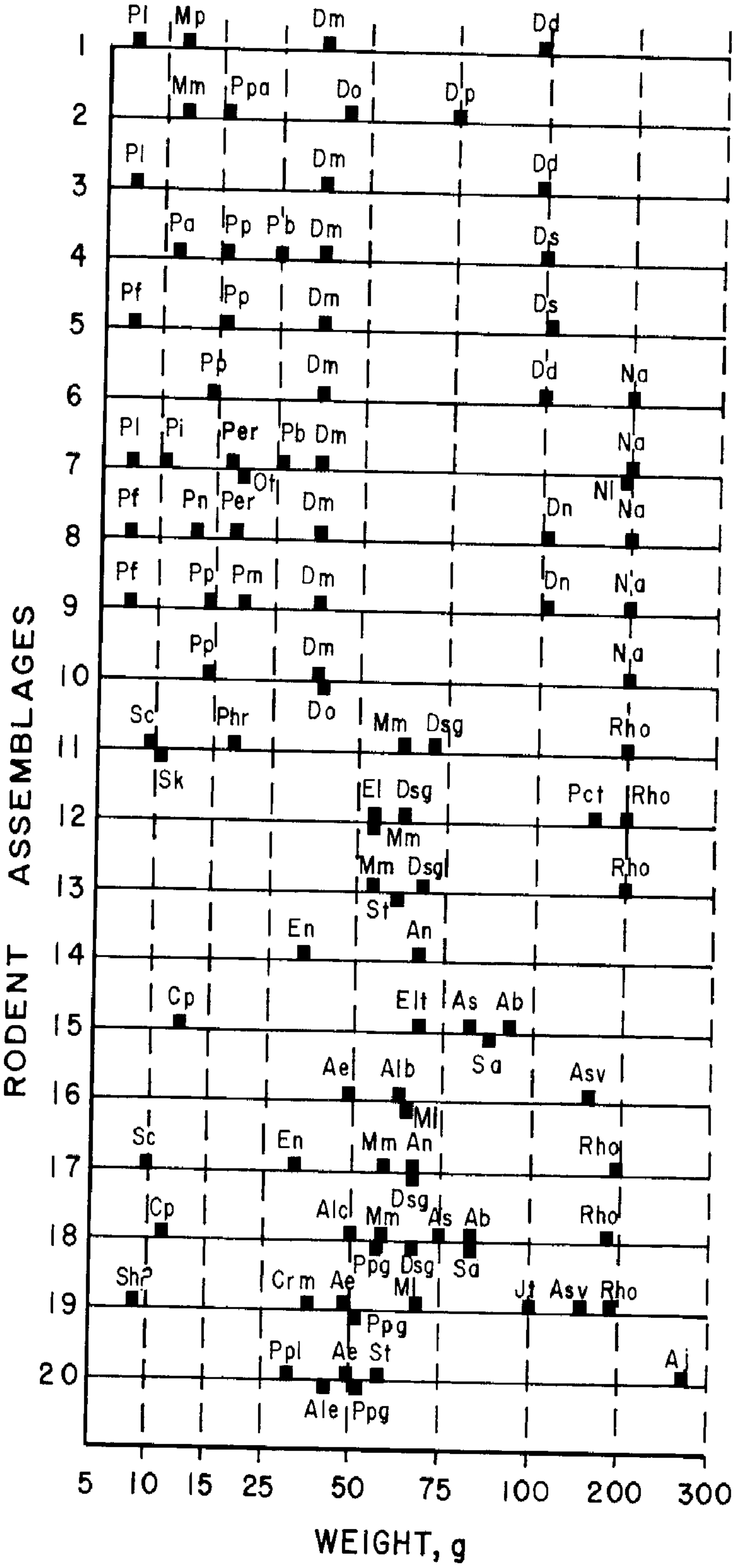

RODENT ASSEMBLAGES
1 Pl Mp Dm Dd
2 Mm Ppa Do Dp
3 Pl Dm Dd
4 Pa Pp Pb Dm Ds
5 Pf Pp Dm Ds
6 Pb Dm Dd Na
7 Pl Pi Per Ot Pb Dm Na Nl
8 Pf Pn Per Dm Dn Na
9 Pf Pp Pm Dm Dn Na
10 Pp Dm Na
11 Sc Sk Phr Do Mm Dsg Rho
12 El Dsg Mm Pct Rho
13 Mm Dsg St Rho
14 En An
15 Cp Elt As Ab Sa
16 Ae Alb Ml Sa Asv
17 Sc En Mm An Rho
18 Cp Alc Mm Dsg As Ab Rho
19 Sh? Crm Ae Ppg Dsg Ml Sa Jt Asv Rho
20 Ppl Ae St Ale Ppg Aj
5 10 15 25 50 75 100 200 300
WEIGHT, g

Figure 1.

THE ROLE OF PREDATORS IN MORPHO-ECOLOGICAL DIVERGENCE OF SPECIES IN COMMUNITIES OF DESERT RODENTS

1.Natural pressure of predators.

No quantitative assessments of the pressure of predators in communities of desert rodents have been made. Such assessments should include a parallel inventory of the number of rodents and remains of corresponding species among the prey structure of predators. Data on the pressure of predators in communities of other landscape zones show significant variation in the effect of predators in different conditions. In the East African savanna, with a relatively constant level of the number of rodents, birds of prey destroy in all about 10 per cent of prey populations (Brown, 1963). According to Pearson (1964) land predators removed in all from 5 to 26 per cent of the population of *Microtus californicus* in an area of 16 hectares, depending on the stage of their population dynamics. Similar data are given by Fitzgerald (1977) for the interrelationship between *Microtus montanus* and the ermine (*Mustela erminea*) in California. According to Bashenina (1977) one brood of the weasel (*Mustela nivalis)* was capable of completely destroy the population of *Microtus arvalis* in an area of 5.7 hectares of ploughed land. However, even in cases where the pressure of a predator does not essentially affect the population size of the prey, the predator plays the role of a selective factor. We shall not present numerous data on the selective catching of prey by predators, distinguished by age, physiology of the organism,traumas, etc. Most interesting is the evaluation of the role of predators as a leading factor to morpho-ecological differentiation of species. For this respect, an estimator of the role of predators in the survival of different morpho-ecological types of prey is quite undesirable. Kotler (1985a) assessed the success of hunting of a long-eared owl on bipedal and quadrupedal forms of heteromyid rodents in the Great Basin desert (*Asiootus*). Selectivity for a particular morpho-ecological type of prey pointed to a greater chance of catching quadrupedal pocket mice (*Perognathus)* as compared to bipedal kangaroo rats (*Dipodomys)* although the number of the latter species in nature was substantially higher.

Numerous data on the feeding habits of birds of prey through analysis of pellets show the selectivity of feeding of different species of predators, however they can give us just tentative information on the amount of pressure on different species or life forms of rodents. The selectivity of the catch of different morpho-ecological types of prey by a predator can be identified precisely only in the case when two potential prey are put into similar conditions of safety, which could hardly be done in heterogeneous environment. It can be assumed that rodent species adapted to life in desert areas with a low number of natural shelters, such as jerboas and kangaroo rats, will have an advantage over the species adapted to life in areas with dense vegetation, forced to live in the open and vice versa. In fact, it has been shown that deer mice (*Peromyscus)* are more often consumed by the owl than kangaroo rats and gerbils (*Meriones*) (Dice, 1947; Lay, 1972; Kaufman, 1974; Webster and Webster, 1971).

Several guidelines concerning the importance of the role of adequate conditions for the survival of prey are given by observations of the hunting of owls for rodents, familiar and unfamiliar with the habitat area, in experimental conditions (Smirin, 1975). This author showed that the behavior of bank voles (*Clethrionomys glareolus*) and wood mice (*Apodemus sylvaticus*) is more secretive under the impact of a predator (Smirin, 1977, 1984). The experiment can hardly be precise due to the fact that predators, whether birds or mammals, are specialized in hunting a certain type of a prey (Osmolovskaya, 1948). Large predators, such as eagle owl (*Bubo bubo),* hunt large rodents, whereas small predators (little owls) prey on small species (Osmolovskaya, 1953; Formozov and Osmolovskaya, 1953; Soletskiy, 1961). Small predators are more specialized in selecting prey, since they are unable to hunt big prey.

The patchiness of desert environment suggests the coexistence not only of different strategies of predator avoidance but also of different strategies of hunting. Our observations at the semidesert of western Kazakhstan show that hunting foxes (*Vulpes vulpes*) never changed their hunting method after the prey is discovered depending on its species, gerbils or jerboas, for instance. The main method of hunting is skulking at a burrow or starting the prey from behind a bush. Foxes virtually never pursue jerboas. Apparently, they find the prey by their smell in protective burrows (jerboas) or by the smell and the rustle in a bush (gerbils) or moving lice shuttling from one bush to another. We observed a fox hunting by tourchlight on a plot with marked *Pygerethmus pygmaeus* at the semi-desert of western Kazakhstan. However we have registered only one case when the fox caught the marked rodent, although we have seen numerous attempts to catch a jerboa in a plot.

According to our observations, steppe polecats (*Mustela eversmanni*) catch rodents by actively penetrating into burrows. Apparently jerboas can be caught in a protective burrow with a sufficiently big entrance. The presence of an emergency exit in such burrows (old daytime rest burrows) allows *Pygerethmus pygmaeus* to leave through an opening, closed by a crust of earth.

We have seen coyotes (*Canis latrans*) hunting in packsstartling rodents from under the bushes in Bolsón de Mapimí (México). Coyotes run in a rank 10-15 m from each other,(thoroughly) combing out the bush covered desert (pastizal). The selectivity of the catch remains unknown. We may just assume that this method of hunting, of special importance for a prey, is its ability to locate the predator in advance and make short-distance spurts. Coyotes do not normally pursue their prey. There is another alternative for the prey when using this method of hunting, to stay into thick vegetation. The former decision gives selective advantage to the most reactive species which flee at the slightest danger, whereas the latter decisionis taken by species capable of sustain a high intensity of internal stimuli (sounds steps, rustle, signals of alarm, etc.).

The role of predators and particularly, of birds of prey, as a selective factor is diminishing due to reduction in their number. Predators, as a factor of the morpho-ecological differentiation of rodents in communities, have played an important role in the past. It is necessary to carry out additional quantitative evaluation of the survival success of different morpho-ecological types of prey under the influence of predators in controlled conditions. Apparently such direct evaluation alone can give support to the hypothesis of the role of predators in the structural organization of communities.

2. Morphological evidence of the role of predators as a factor of morpho-ecological divergence of species in communities of desert rodents.

Among the morphological peculiarities of species, the protective coloration is an important indicative of the role of predators as a selective factor. It is a well known fact that fur coloration fits the color of the substrate even in nocturnal species of desert rodents (Benson,1933; Dice and Blossom, 1937; Kashkarov, 1938; Dice, 1947). The specificity of crepuscular vision of predators apparently determines the dominance of light and pale-yellow coloration in the majority of species of desert rodents. In moonlight such coloration makes animals unnoticeable to man, even against a relatively dark substrate in a rocky desert.

A classical example of the paramount role of protective coloration in avoiding danger, is fur color polymorphism in rodent species populating lava fields and the adjacent areas of desert in North America (Dice, 1929; 1930; Benson, 1933; Hooper, 1941). According to our observations at the volcanic Pinacate mountain in the northwest of México (Sonora State), four species of the 11 present in the area *Perognathus intermedius, Peromyscus eremicus, Neotoma albigula, Dipodomys merriami)* are distinguished by interpopulation variation in fur color. The first two species only dwell in mountainous areas of the desert, meanwhile the other two are also recorded in the valley. Undoubtedly priority should be given to the rock pocket mouse (*P. intermedius)*. Benson in 1933 registered the presence of two color forms of *P. intermedius*, however he viewed them as two different races, strictly isolated biotopically. He also discovered some differences in the skulls of representatives of these races. According to our observations both dark and light forms of *P. intermedius* live closely together beeing in direct contact at the Pinacate area. In addition, there is a wide transitional range between light and dark colored forms. At the same time, despite substantial mobility of rodents on black lava flows, running down mountain slopes, we mainly registered black or dark grey forms (four of five were dark), whereas grey and light-grey species predominate on light rocky slopes. The farther from the lava flow, the fewer dark rodents are captured.

For instance, in two plots of 1 ha, ubicated between 200-250 m from the lava borders, dark rodents made up twenty two per cent out of 18 trapped animals. Meanwhile there were no dark rodents in the plot located more than 500 m from the lava border among the 5 trapped species. There were exclusively black species in the plateau near the crater, where the terrain is covered with a vast lava field (12 individuals were trapped). Although these data are insufficient for statistical conclusions, the tendency of diminishing numbers of dark colored rodents farther from the lava seems rather clearly. Presumably such situation can be explained by the division of different forms of habitat on the basis of genetically determined preference differences in behavior, (although it is far from being clear, taking into account the fact that coloration, polymorphism and rather high mobility of animals) or by a strong selective action of predators, which simply destroy animals that stand out in color. Also, parallel occurrences in different groups of fast big species of running desert rodents exist in relation with the contrasting coloration of the tufts at the end of their tails. These convergenses also points out to the important role of predators as a selective factor (jerboas, kangaroo rats, gerbils). The black and white coloration contrast of the tail has, apparently, a distracting effect and it is related to the ability of running bipedally.

The fastest and biggest species of jerboas has a sensible developed bicolored tuft (flag); the specificity of movement of the tail during a fast run promotes a frequent flipping of the tuft in a vertical plane, making a predator switch its attention (Fokin, 1978). An increase in the contrast of the tuft by augmenting the size of the white field in large sclerophylic species of *Allactaga (A. sibirica, A. severtzovi, A. jaculus)* and *sclerophylic Dipodomys (D. spectabilis, D. nelsoni)* can be explained by low manoeuverability due to the greater inertia of large forms. In psammophylic jerboas and kangaroo rats this regularity is not so evident although it is also manifest. A weak bicoloration of the tuft in the bushy-tailed gerbil (*Sekeetamys calurus)* and in the Afganische gerbil (*Meriones zarudyi),* quadrupedal ricochet species, points to the initial possibility of other correlation than that of bipedal locomotion.

However protective role of bicolored on the tail is confirmed by the enhancement of contrast due to progressive specialization of jerboas in bipedal locomotion (Fig. 2). Jerboas are sometimes trapped with torn away ends of the tail, particularly in those close to settlements with many dogs. The morphofunctional peculiarities of sense organs, primarily of hearing organs is at least so important as protective coloration as an evidency of the role of predators as a selective factor in the evolution of desert rodents. It can be assumed that the ability for the early sound location of an approaching predator in an open area is a condition not less important for the success of the species in the struggle for survival, than its ability to run fast.

An increase in the size of the middle ear chamber is manifest in many species of desert rodents (Vinogradov, 1937; Ognev, 1948; Bartholomew and Caswell, 1951; Webster, 1962). A large variety and many parallels in the internal structure of eardrums among gerbils, jerboas, heteromyids provide grounds for assuming the presence of different adaptive peculiarities of hearing in forms of desert rodents with different danger-avoiding behavior (Pavlinov, 1983). Regrettably, no morphological parallel in the structure of the middle ear chambers have so far been confirmed by ecological data. The correlation between general dimensions of bullars and certain peculiarities of their internal structure, with the level of adaptation to life in open areas has been proved in the Heteromyidae family (Webster, 1960, 1962; Webster and Webster, 1975, 1977, 1980). The spongy structure of the middle ear chamber in *Perognathus* is apparently the ground. Such structures suppress the ability for seismic hearing and sounds coming directly to the eardrum (Simkin, 1965, 1967). The chamber type of the middle ear chamber structure of *Dipodomys,* on the contrary, allows for better perception of vibrations in the substrate, which are then transmitted to the extremities and the bones of the skull. This is also promoted by developed bone ribs that connect the walls of the ear drum to the bone case of the cochlea.

The middle ear chamber has substantially less resistance than the other elements of the middle ear. It actively participates in the regulation of sensitivity and selectivity of the system to the most biologically significant sounds. At the same time a significant role is played by the resonance that occurs in the chamber. A marked enhancement of low frequency bands within the range of 1-3 kHz (Webster, 1962; Lay, 1972) takes place in the middle ear chamber in kangaroo rats and certain species of gerbils. Webster (1962) showed that it was exactly this range that was used by rattlesnakes and produced by the wings of hunting owls.

Increased sensitivity of the hearing analyzer of kangaroo rats to low frequency sounds has been confirmed, both physiologicaly (Ruppert and Moushegian, 1970; Webster and Strother, 1972; Webster and Webster, 1972) and by observations of rodent behavior (Webster and Webster, 1972). An experimental reduction of the volume of the middle ear chamber in kangaroo rats leads to reduced sensitivity to low frequency sounds (Webster, 1961; Webster and Webster, 1972, 1980).

In addition to the middle ear chamber both, the tympanic membrane and the ossicular chain system, are involved in the perception of sounds. Of certain significance in the selective sensitivity of the ear of kangaroo rats to low frequency sounds are some peculiarities in the internal ear structure and cerebral zones connected to it (Webster and Stack, 1968; Webster *et al.*,1968).

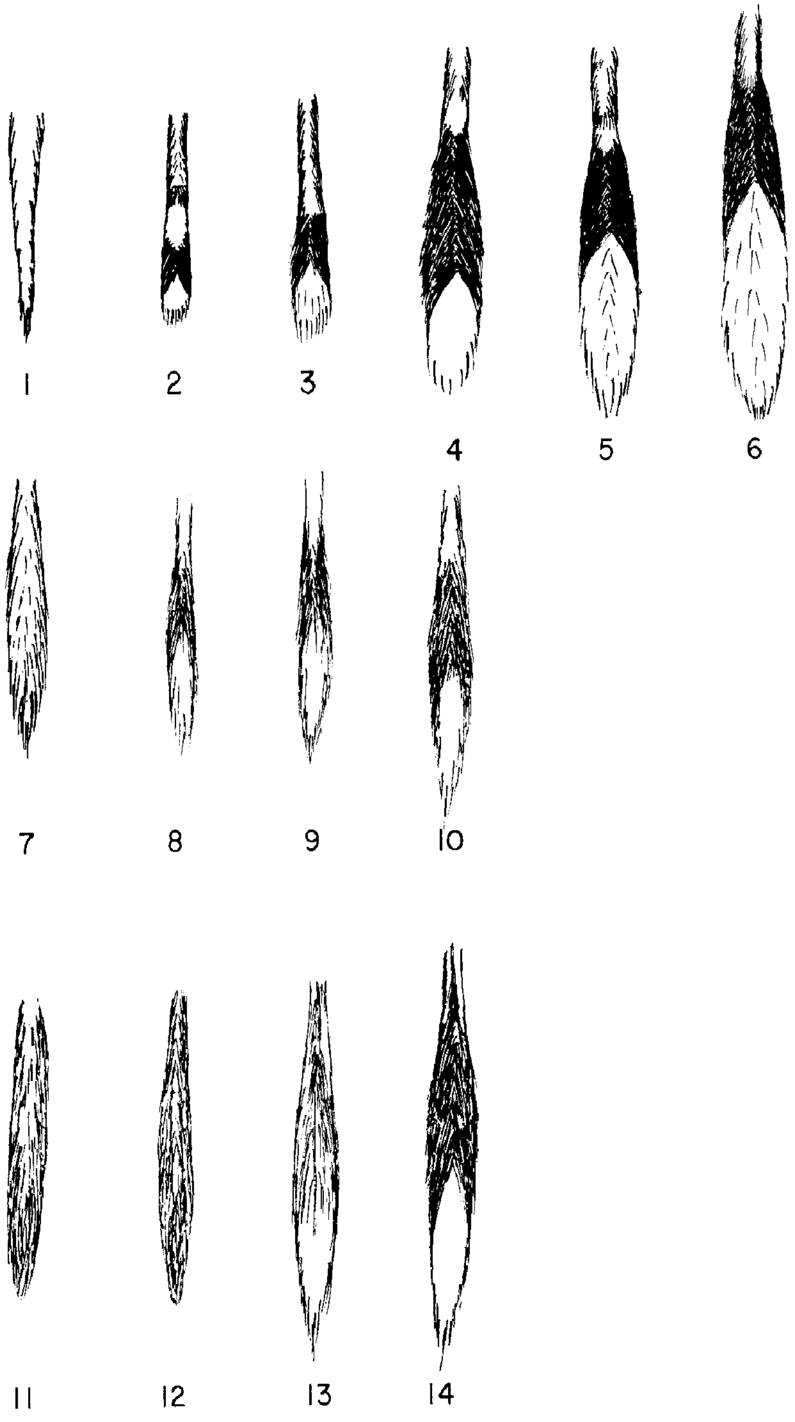


Figure 2.- Parallel series of variation of the tail flag color in different groups of bipedal rodents. A. - Allactaginae; B. - Dipodinae; C. - Dipodomyinae; Maximum speed of the run (m / sec) is given in brackets after the name of the species : 1 - Pygerethmus platiurus (5.3 *); 2 - P. zitkovi (7); 3 - P. pygmaeus (7.1); 4 - Allactaga bullata (8.5); 5 - A. sibrica (9.4); 6 - A. jaculus (13.4); 7 - Stilopidus telum (6.5); 8 - Eremodipus lichtensteini (7.3 *); 9 - Dipus sagitta (8.1 *); 10 - Jaculus turcmenicus (9.2 *); 11 - Dipodomys merriami (4.5); 12 - D. ordii; 13 - D. deserti (4.8); 14 - D. nelsoni (5.1). (* - taken from Fokin, 1978).

It is also known that the level of the development of the bullars is inversely related to the size of the auricle (Vinogradov, 1937). A marked development of the auricle in five-toed jerboas (Allactaginae) apparently compensates for a lesser development of bullars as compared to pygmy (Cardiocraniinae) and three-toed (Dipodinae) jerboas. In Allactaga the latter show a simple internal structure (Pavlinov, 1983). The development of the auricle in a five-toed jerboa is interrelated to active location and the isolation of the most important biological sounds from other sounds. It can be assumed that with such a structure of the hearing, the organ seismic signals are identified to a lesser extent. Typicaly, these forms will stand on two feet for a long time to take their bearings in a "column" fashion, like many daytime species (susliks, ground squirrels, great gerbils, etc., Fig. 3).

On the other hand, bipedal forms with markedly developed bullars (*Microdipodops, Cardiocranius, Salpingotus)* hide in case of danger. Forced to cross areas deprived of vegetation, they press themselves against the substrate in the hollows of the relief at the slightest tremors ground (Eisenberg, 1975; Rogovin, 1983).

It is quite probable that strongly developed chamber bullars in forms using protective burrows (gerbils, kangaroo rats) promote the perception of seismic oscillations within the burrow. Both gerbils and kangaroo rats are known for peculiar signals which they emit by a frequent change of the position of the hind feet. (Eisenberg, 1963, 1967; Bridelance, 1986). These sounds are emitted by the alarmed animals in the burrow right after they enter it to avoid danger. The frequencies of these tramplings in kangaroo rats lie within the range of increased sensitivity of hearing.

Elegant experiments with kangaroo rats performed by Webster (Webster, 1962; Webster and Webster, 1971), demonstrated how and with the help of which sense organs rodents manage to avoid predators (owls and rattle snakes). Animals with intact bullars succeeded in avoiding owls and rattle snakes even in complete darkness or after being blinded. Species with a reduced volume of the middle ear chamber after surgiry succeeded in avoiding predators only when the cages were well-lit. Blinded kangaroo rats with destroyed bullars inevitably fell prey to predators. Similar experiments in field conditions also revealed increased mortality among kangaroo rats with destroyed bullars, mainly on moonless nights, as compared to control animals (Webster and Webster, 1971). Thus the ability of kangaroo rats and, apparently, of other bipedal rodents to locate danger in advance can be viewed as an important factor of the adaptation of these forms to using open areas without vegetation. The fact that quadrupedal galloping gerbils have markedly developed bullars with chambers similar to those of the kangaroo rats can be viewed as a theoretically possible preadaptation to settling open desert and areas deprived of shelter. Lay (Lay, 1974) notes that gerbils (*Meriones*) with markedly developed bullars are able to avoid owls' attacks effectively by means of forestalling jumps, like those by bipedal kangaroo rats.

There is no convincing evidence of the specificity of the structure of visual and olfactory organs aimed at avoiding danger. However, it is rather difficult to expect these peculiarities to exist apart from characteristics of these organs related to the requirements of the conditions of individual activity, and to the system of intraspecific communication. From this point of view it is only the position of the eyes that can be considered as an adaptation to avoiding possible attack. In diurnal species of small mammals of opened areas, the position of the eyes on the head tallies with the need for the best view, depending on the structure of the habitat and the possible direction from which a predator may appear (Smirin and Orlov, 1975; Formozov, 1976, 1981). The position of the eyes in nocturnal desert rodents is adapted to the need for an effective control of the environment. These peculiarities can also be related to the postures of orientation-searching behavior (Table 1).

There is a positive significant correlation of the compared parameters ($r = 0.67 \pm 0.17$; $P < 0.01$). It is indicative of the fact that broadly positioned eyes and frequent rising on hind feet among nocturnal forms are mainly observed in the species that inhabit open areas (Dipodidae, Heteromyidae), and the most narrowly positioned eyes in species inhabiting thick vegetation (*Mus, Cricetulus, Neotoma, Peromyscus*). This correlation is rather strong despite natural variability in behavioral patterns of species in experimental conditions. The differences between morphologically similar species in the frequency of patterns of orientation-searching behavior can also be determined by the level of excitability of the central nervous system and by the compensatory effect of hearing organs. For instance in *Euchoreutes naso* (Dipodidae), which has big auricles, the vertical orientation posture is to a great extent related to the active location not only of predators, but also of prey insects.

The greatest field of vision is achieved by a broad positioning of the eyes in medium and large bipedal forms of rodents. Thicktailed pygmy jerboas (*Salpingotus crassicauda)* hide almost always in case of danger and have a developed system for seismic hearing and typically posses eyes pushed towards the frontal part of the skull separated by a relatively small distance for seismic hearing. This is also indicative, to a varying extent, of quadrupedal galloping species (*Meriones, Perognatgus, Peromyscus)*.

3. Bipedalism.

It is a type of locomotion in which the push is executed with the hind feet and the frontal extremeties are fully excluded from locomotion. Bipedalism has evolved independently in 8 groups of small mammals, (Berman, 1984). Five of these groups are represented by rodents. They are the Heteromyidae from north America, Pedetidae from central and southern Africa, Dipodidae from Asia and northern Africa and Muridae from the Old World and Australia. Berman also includes here the Zapodidae from north America which despite morphological requisites are not bipedal forms (Nikolai and Bramble, 1983). Some Cricetidae of the Old World can be viewed selectively as bipedal forms. Bipedal locomotion is also used by small *Antechinomys* from the Dasiuridae family as well as kangaroos (Macropodidae). Also 2 genera of the Ardiolagidae family are known as fossil bipedal marsupials from south America. Some representatives of insectivorous

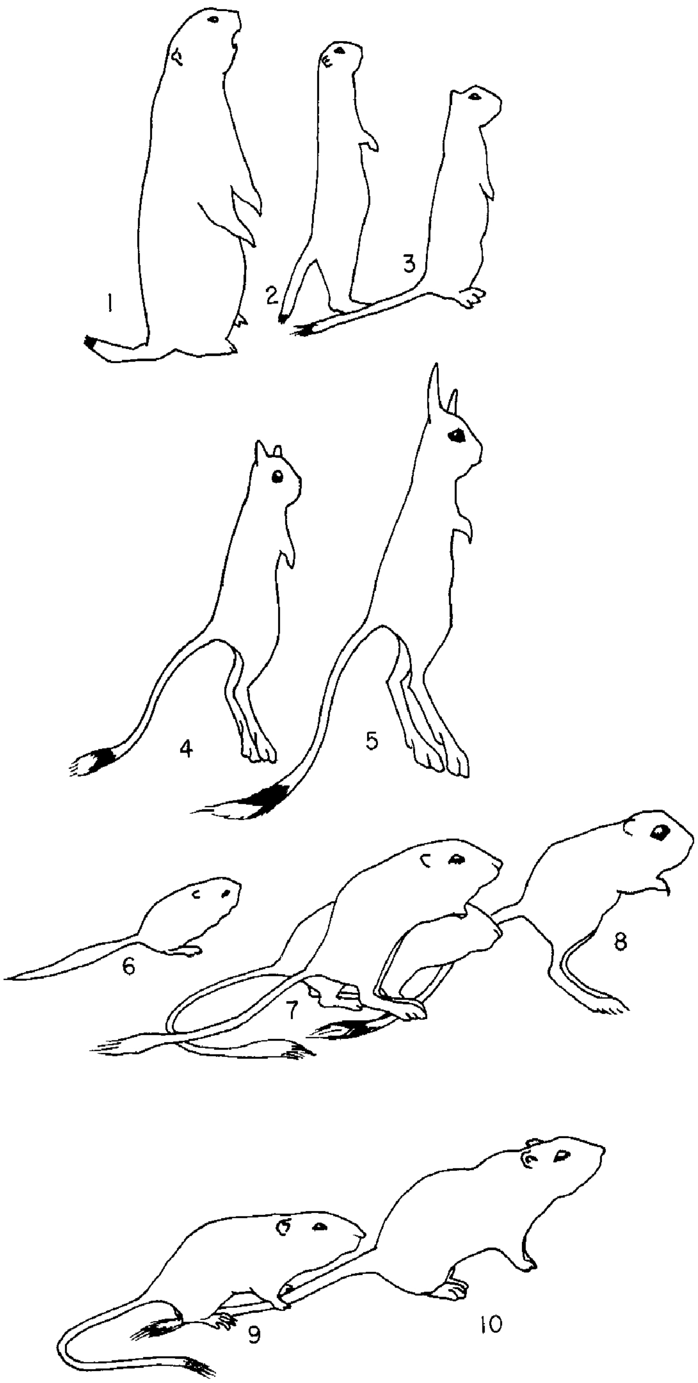


Figure 3. Orientation postures of step and desert rodents. 1-3 - diurnal quadrupedal forms: 1 - Marmota, 2 - Citellus, 3 - Rhombomys, 4-10 nocturnal forms: 4-8 bipedal rodents: 4 - Pygerethmus, 5 - Allactaga, 6 - Salpingotus, 7 - Dipodomys, 10 -Meriones.

Table 1. Relative distance between the eyes along the facial part of the head and frequency of orientation postures on hind feet in examining an unfailiar space in "open field" tests in desert rodents. (10 tests, 10 min long each with 5 and 5 OO; n - number of measured individuals; N - total number of registered elements of behavior; open-air cage: 1m x 1m).

Species	Distance between eyes/ body length (X ± m)	n	Number of vertical postures\ total number of registered elements of behavior (frecuency)	N
Euchoreutes naso	0.12 ± 0.00	10	0.16 ± 0.01	796
Salpingotus crassicauda	0.14 ± 0,00	10	0.03 ± 0.01	1220
Allactaga nataliae (balikunica)	0.17 ± 0.00	15	0.17 ± 0.01	904
A. sibirica	0.18 ± 0.00	10	0.15 ± 0.01	370
Dipus sagitta	0.19 ± 0.00	15	0.31 ± 0.02	793
Mus musculus	0.09 ± 0.00	6	0.03 ± 0.01	753
Cricetulus migratorius	0.08 ± 0.00	10	0.02 ± 0.00	662
Phodopus roborovskii	0.10 ± 0.00	10	0.02 ± 0.00	776
Rhombomys opimus	0.11 ± 0.01	10	0.10 ± 0.01	688
Meriones meridianus	0.11 ± 0.00	15	0.06 ± 0.01	833
Spermophilus spilosoma	0.14 ± 0.01	6	0.24 ± 0.02	725

Table 1 (ctn.).

Species	Distance between eyes/ body length (X ± m)	n	Number of vertical postures\ total number of registered elements of behavior (frecuency)	N
Dipodomys nelsoni	0.18 ± 0.01	10	0.22 ± 0.02	567
Perognathus flavus	0.14 ± 0.00	5	0.04 ± 0.01	235
P. penicillatus	0.15 ± 0.00	10	0.06 ± 0.01	419
P. nelsoni	0.15 ± 0.00	10	0.04 ± 0.01	394
Peromyscus eremicus	0.11 ± 0.00	10	0.06 ± 0.01	689
P. maniculatus	0.09 ± 0.00	10	0.04 ± 0.02	780
Neotoma albigula	0.09 ± 0.01	10	0.09 ± 0.02	467
Onichomys torridus	0.11 ± 0.01	4	0.12 ± 0.02	683

Some representatives of insectivorous Macroscelididae family are selectively referred to as bipedal forms.

With the exception of *Zapus* (Zapodidae) all other forms inhabit either deserts or areas with sparse vegetation. A negative correlation between the number of bipedal desert rodents in Mongolia and the development of bushes is demonstrated in Fig. 4. The scheme reflects the standardized conditional probabilities of occurrence of 8 species of central asian desert rodents depending on the distance from natural shelters (bush). It also provides information on coefficients of conjugation (Kulbak, 1967) between rodents and potential shelter. There is positive correlation between the occurrence of species far from shelter and dominance of the bipedal gate (*Euchoreutes, Allactaga, Dipus)* and the

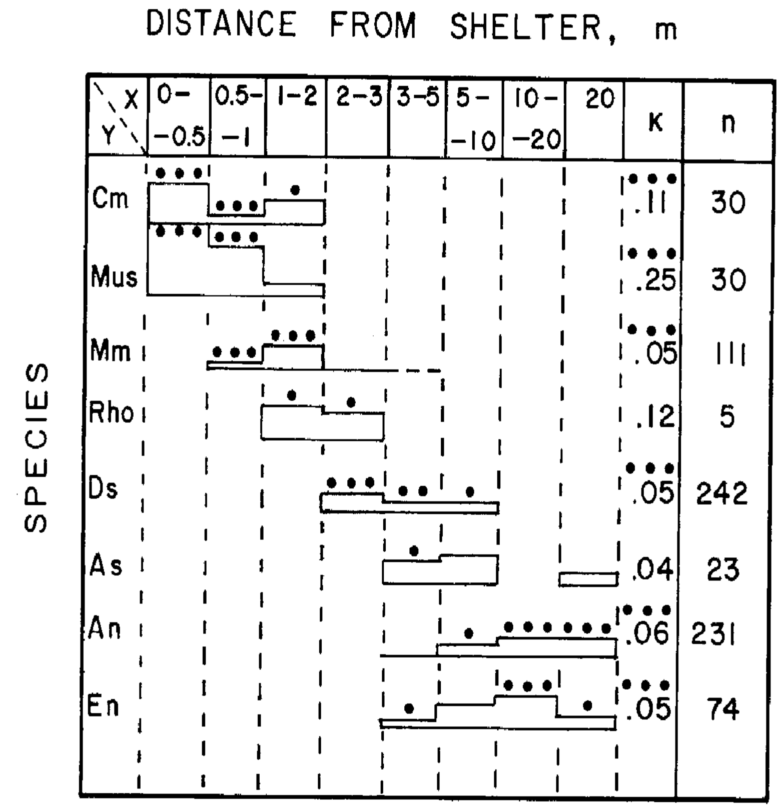


Figure 4.- Segregation of ecological optima for species of rodents of the Mongolian desert by their occurrence at different distances from bushes (shelters). The occurrence of rodents was registered by the tracks left on 475 smoked plates with a seed bait. Histograms reveal the areas of the positive logarithm transformed values of standardized conditional probabilities of species occurrence: C(Yj/Xi) = Ln (P(Yj/Xi) / P(Yj)) >0, where P(Yj/Xi) is a conditional probability equal to the proportion of the number of registers of Y-species in i-gradation of X-factor to the total number of registers of the given factor gradation; P(Yj) - probability of recording of Y-species in all factor gradations; K - information coefficient of conjugation with bushes (Kulbak, 1967; Puzachenko and Skulkin, 1981); n - number of registrations of the species. Evaluation of the significance by the X^2 criterion: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Species : Cm - Cricetulus migratorius, Mus - Mus musculus, Mm - Meriones meridianus, Rho - Rhombomys opimus, Ds - Dipus sagitta, As - Allactaga sibirica, An - A. nataliae (balikunica), En - Euchoreutes naso. (The first two species inhabit desert oases).

occurrence close to shelter - with the predominance of a symmetrical quadrupedal gate (*Cricetulus, Mus*).

Intermediate in this respect are the species that use an asymmetrical quadrupedal gate, based on a primitive ricochet jump (*Meriones, Rhombomys;* terminology by Gambaryan, 1972).

Three major hypotheses that explain origin of bipedalism in groups of desert dwelling mammals. One views bipedalism as a means to avoiding predation (Hatt, 1932; Bartholomew and Caswell, 1951; Fokin, 1978, 1981), The second one establishes the need to free the front feet for effective feeding (Bartholomew and Cary, 1954), while the third hypothesis explains the emergence of bipedalism by adaptation to harvesting food when it is patchily distributed in the desert (Dawson, 1976; Reichman and Oberstein, 1977).

The first two hypotheses do not exclude each other. Feeding in open areas increases the danger of being caught by a predator. All species of bipedal rodents prefer a nocturnal mode of life. In most cases these are unsociable forms (occasionally establishing provisional pairs) with an underdeveloped system of acoustic communication (Dixon, 1959; Reynolds, 1960; Eisenberg, 1963, 1967, 1975; Schroder, 1979; Braun, 1985; Rogovin, 1983,1985; Zeng and Brown, 1987; Ward and Randall, 1987). Warning signals emitted by nocturnal species are seismic signals, produced by footdrumming (podophonia).

Likewise, wide spread among diurnal species inhabiting open areas are social forms that prefer a family group or colonial mode of life. They are different Sciuridae (*Mormota, Spermophilus, Cynomys),* diurnal species of gerbils (*Meriones unguiculatus, Rhombomys opimus),* and voles (*Lasiopodomys, Lagurus, Eolagurus,* etc.) (Barash, 1973; Sherman, 1977; Goltsman *et al.*, 1977; Armitage, 1981; Nikolsky, 1984; Orlenev, 1987). Diurnal rodents of open areas are characterized by specific warning signals, allowing for both intra - and interspecific interactions (Nikolsky, 1984).

At night the danger of an unexpected attack by a predator in open spaces is markedly increased. Of paramount importance parallel to the development of an acoustic control system is the ability to make swift jumps and rushes in stress situations. Presumably the liberation of feet from locomotion is necessary for the effective collection of fodder in conditions of potential danger in open spaces. Bipedal forms are capable of harvesting seeds in the course of continuous locomotion (i.e., the pygmy jerboas *Salpingotus*), digging up the surface layer of soil with their forelimbs. The peculiarities of the anatomy of the forelimbs of bipedal forms are indicative of their reduced ability for manipulation. Bipedal forms have a reduced ability for rotation of the radius and ulna bones as well as a reduced mobility of the elements of the hand (Hilderbrand, 1982). By contrast. the manipulation of fodder by the front feet is characteristic of almost all quadrupedal species of rodents. It is quite possible that the effectiveness of manipulatory activity be exactly related to the involvement of forelimbs in locomotion. Active sound-absorption and partly a shoving function determine the mobility of their distal sections. All rodents use their front feet while feeding. The posture of a feeding rodent, sitting on its hind feet, has left a good imprint in our memory from childhood, be it a squirrel, mouse or hamster. As was shown by Fokin (1978,1981) that the bipedal starts from this posture, is also indicative of many species of quadrupedal ricocheting rodents. Fokin's hypothesis on the initial advantages of bipedal locomotion is based on the assumption that bipedal start is capable of providing a greater initial acceleration than a quadrupedal start. Locomotor functions of the hindlimbs prevail over those of the forelimbs (in virtually all rodents). The study of locomotion parameters in ricocheting quadrupedal gerbils revealed that at the moment of a rush start the forelimbs of rodents are entirely excluded from the locomotion cycle and the animal picks up speed only on hind feet, switching to quadrupedal ricochet only with the stabilization of the velocity of locomotion (Fokin, 1981). The occurrence of facultative bipedalism should not be obligatorily related to the transfer to life in open desert areas. American *Zapus,* a dwelleri of thick vegetation, habitats has the same correlation between the length of the front and hindlimbs as the desert bipedal forms of *Microdipodops* (Berman, 1984). The ability of these rodents to perform swift jumps in stressfull situations is well documented, and their closeness to jerboas was one of the arguments in favor of the concerted origin of obligate bipedalism due to the transfer of the ancestors of jerboas to life in a desert (Fokin, 1978).

At present the available information on the origin of bipedal kangaroo rats essentially gives grounds for relating their origin to small sections of loose sand or grass areas, devoid of thick vegetation, alternating with thick vegetation sections in savannah landscapes (Voorhies, 1975). Real deserts in the territory of North America appear only in the late Pleistocene (van Devender, 1977, van Devender and Spaulding, 1979). At the same time the existence of specialized bipedal forms, travelling great distances at high velocities is apparently related to the adaptation of animals to real desert.

The hypothesis on the role of predators in the formation of bipedalism in desert rodents tallies fully with numerous empirical data and furnishes a satisfactory explanation for a protective function of bipedal locomotion at the initial stages of its evolution. However, this hypothesis is rather weak in explaining the occurrence of specialized, bipedal gates in jerboas i.e. the fastest. The bipedal type of locomotion is not necessarily the fastest one. As revealed by observations carried out in conditions close to natural ones, small quadrupedal ricocheting rodents are capable of picking up higher speeds in short distances than bipedal species of corresponding size (Fig. 5). However with an increase in size in a series of species obligate bipedal forms gain in velocity. In jerboas, the most advanced forms with respect to running, the dependence of the ultimate velocity on the body weight can be defined as an exponential function: $Y = 0.55X^{0.60}$. In the most specialized runners (Allactaninae, Dipodinae), this dependence lineal: $Y = 5.71+2.83X$. A further increase in the velocity of locomotion in specialized bipedal forms in other groups of mammals (Pedetidae, Macropodidae) is also related to an increase in size (Nikolai and Bramble, 1983). However the biggest quadrupedal forms are not the fastest. For instance, in the galloping rodents *Perognathus, Meriones* and *Rhombomys,* the dependence of the ultimate velocity on body weight may be satisfactorily described by the following function:

$$Y = 0.25Xe^{-0.18}$$

Apparently the same form of dependence is indicative of the kangaroo rats (*Dipodomys)* that use "synchronous bipedal ricochet" (see Comment 1) - the most primitive form of bipedal locomotion and at velocity they use front foothold in the locomotion cycle. By a number of habitual symptoms kangaroo rats are closer to pygmy jerboas and even to quadrupedal gerbils, and not to genuine jerboas,

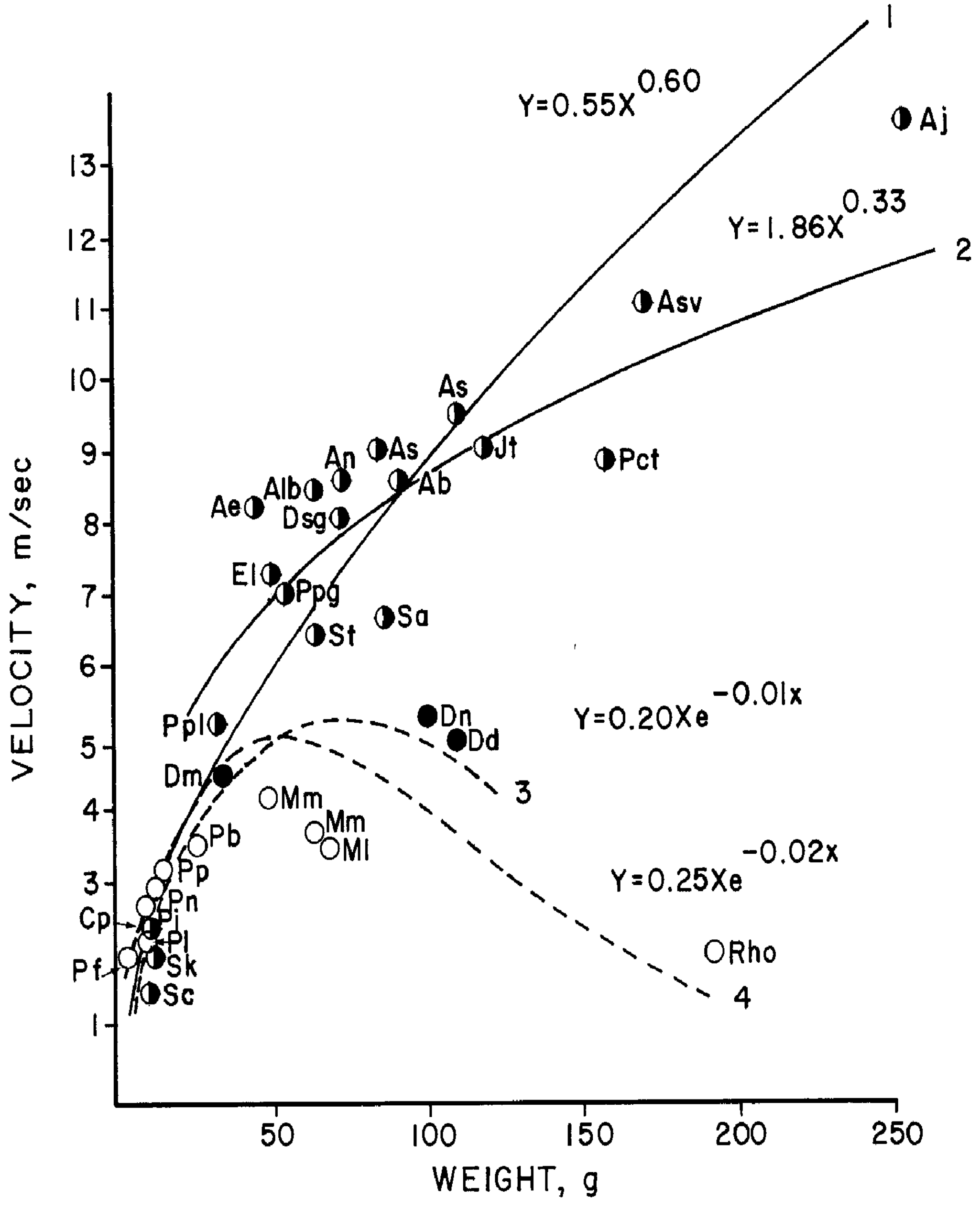


Figure 5.- Dependence of the ultimate velocity of locomotion on the body weight in different morpho-ecological groups of desert rodents: 1 - all jerboas (fam. Dipodidae); 2 - obligate bipedal jerboas, using bipedal saltation with asynchronous working of the forelimbs or trot (subfamilies Allactaginae and Dipodinae); 3 - facultatively bipedal species, using bipedal saltation with synchronous work of the extremities (subfamily Cardiocraniinae, Dipodomyinae); 4 - quadrupedal ricochetingspecies (subfamilyPerognathinae, Gerbilinae). Bodyweight (g) on the abscissa; maximum velocity of the locomotion in nature (m/sec) on the ordinate. Species on designated as in Fig. 1.

which are specialized in bipedal saltation (Mares, 1980; see also an article in this collection). In analyzing *Dipodomys* together with pygmy jerboas, using the same pace, the dependence of the velocity of bipedal saltation on weight is described by the following function:

$$Y = 0.20Xe^{-0.14}$$

No doubt the assessments of the ultimate speed of locomotion performed by us mainly in natural conditions, provides no guarantee against errors. We cannot be fully confident that the velocity of the fleeing animal at a certain section of his run is the ultimate one for the species. Nevertheless, it seems to us that the measurements taken in natural conditions are more adequate than the widely practiced measurements of the velocity of rodent locomotion in treadmills.

Obligate bipedalism in genuine jerboas is doubtlessly the fastest type of locomotion. Marked specialization of many forms of jerboas in bipedal saltation, may however be determined not by the necessity to protect them from predators, but by the dispersion of their ancestors to arid areas with poor fodder conditions. It is indicative that an increase in mobility (running speed of jerboas) is associated with an increase in the size of the home range and extensification of its use (Rogovin, 1983).

The assumption of bipedalism as a means of covering a vast open space in search for fodder contradicts the hypothesis on the protective function of bipedal locomotion. From the viewpoint of Gambaryan (1972) the emergence of bipedal saltation is related to a gradual increase in the velocity of locomotion. Bipedal saltation directly results from a primitive quadrupedal ricochet saltation, indicative of the majority of rodents. An increase in the length of the jump with the acceleration of the run is related to an increase in the swing of the hind feet forward in the phase of free flight. With a certain position of hind feet the front one stops to be an amortization foothold on the substrate. The transfer of quadrupedal ricochet into the bipedal one takes place with the maximum velocity of locomotion. This concept is confirmed by the presence of a transitional speed close to linear dependence (speed under which the transition from quadrupedal locomotion to bipedal takes place) on the size of bipedal forms (Nikolai and Bramble, 1983).

The concept of bipedalism as a high speed type of assymetrical gates of rodents, providing the possibility of movement over large distances in a short time, closely dovetails with an energy model of the origin of bipedalism. The concept of a lower energy cost of bipedal locomotion in heteromyid rodent communities in North America as compared to quadrupedal in species of similar size (Dawson, 1976), is viewed as an argument that supports the predominant role of competition in the evolution of communities (Reichman and Oberstein, 1977; Reichman, 1981). We shall analyze these issues in the next chapter.

The hypothesis on the role of predators in the evolution of bipedalism is related to the reduction of manoeuvrability of bipedal forms as compared to quadrupedal ones. A jerboa turns during a fast run by an active displacement of the center of gravity to the side of the turn with respect to the axis of the body by changing the working rhythms of the extremities. The tail, that rotates in the frontal plane during fast movemement, plays the role of an air balancing device, eliminating moments of force that would otherwise tumble the body when displacement of the center of gravity occurred (Fokin, 1978). Jerboas will out maneouver gerbils at low velocity when the tail does not function. It would be interesting to ask the question: why are there no predators that use bipedal saltation, although this gait is widely used by the prey?. The following explanation is the most logical. Since a predator is, as a rule, bigger than its prey, it is most important for it to preserve a high level of manoeuvrability. A small prey potentially wins in manoeuvre since it has less inertia. We have already noted that predatory mammals virtually never pursue rodents, providing that they fail to catch them at the beginning. The rodents' problem is to pick up the highest speed in the shortest possible time so as to leave the zone of imminent danger. There can be other explanations. There is no average size of predators that specializes in one type of prey (bipedal or quadrupedal rodents). It is quite possible that this is related to asynchronous changes in the number of different species in communities. Perhaps front feet as well as the flexibility of the predators' skeleton play a certain role in digging out their prey from burrows or in killing them.

4. Displacement of activity.

There is indirect evidence pointing to a change in the behavior of prey depending on the level of risk of being caught by a predator. Additional information in this respect is provided by observations of a change in the activity of different life forms of rodents depending on the level of illumination of the terrain. Cyclical changes in illumination, caused by the periodic change in the phases of the moon influence the correlation of different forms of activity. Our observations of individually marked *Pygerethmus pygmaeus* in the semi-desert of western Kazkhstan, show an increase in the relation of individuals to protective burrows on moonlight nights (Table 2). There the animals take their bearings and immediately flee to the burrow when alerted. It is extremely difficult to catch a jerboa in this conditions. General motor activity increases at this time and rodents move far away from their burrows. On dark, moonless nights *Pygerethmus pygmaeus* are less confident, very often they will smell the air and seem to be less frightened; they feed relatively longer, staying up to 5 minutes close to one plant. The results of counting these rodents on plants under different level of illumination are rather contradictory, despite outright differences in the nature of activity.

In some cases the number of animals registered when there is a full moon is lower as compared to the numbers observed on moonless nights. In other cases, however, an increase in the total number of animals registered occurs when there is a full moon. (Fig. 6). In all cases on dark nights, activity has a clearly pronounced two-phase nature. The periods of moonset or moonrise are accompanied by a certain increase in activity. This is apparently related to a shift

Table 2. Differences in behavior of Pygerethmus pygmaeus on moonless and full moon nights. (Results on recording of the type of activity by the light of an electric torch. Observations on individuallymarked jerboas, June - July, western Kasakhstan) N - number of registrations; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Type of activity	Full moon (frequency)	N	New moon (frequency)	N	t-criterion
Feeding	0.04 ± 0.01	17	0.19 ± 0.02	93	t = 6.7***
Escape to the burrow	0.68 ± 0.02	270	0.35 ± 0.02	173	t = 11.7***
Other locomotor activity	0.28 ± 0.02	112	0.46 ± 0.02	228	t = 6.4***

in behavior as a result of changes in the illumination of the terrain.

There is contradictory information with respect to kangaroo rats in North America. According to some authors kangaroo rats do not avoid moonlight (Kenagy, 1976; Schroder, 1979), other authors ascertain that they avoid moonlight (Lockard and Owing, 1974; Kaufman and Kaufman, 1982). Our observations of the behavior of *Dipodomys merriami* in the Bolsón de Mapimí (Durango, México) show essential differences in the mobility of species in different conditions of moonlight. (Table 3). Although differences in preference for microhabitats are manifested to a relatively small extent and are insignificant, there is a tendency among animals to use natural shelters.

Lockard (1978) assumes that *Dipodomys spectabilis* may avoid moonlit spaces, when the terrain is well provided with food, but their activity would be spread to moonlit spaces when food is not abundant. In our observations of (*Pygerethmus pygmaeus)* we found something similar, although the differences in activity in conditions of similar illumination can be explained by the phases of the reproductive cycle. In order to obtain more accurate data we had to keep the time factor constant. By changing the level of illumination of the terrain in experimental conditions, Kotler (1984 a,b) has established the reduction of feeding activity of desert rodents, at food dispensers when lighting conditions approached the intensity of illumination coming from a full moon. In addition, the author found that kangaroo rats spend more time in the shadow of bushes when lighting conditions improve.

The increase of kangaroo rats encounters on moonlit nights on dark sections of roads is well known (Kaufman and Kaufman, 1982). Illumination of the terrain inevitably affects the behavior of a predator. In 1945 Dice (1945) established that owls could hardly detect an immobilized prey under photoperiod conditions that corresponded to the conditions of a moonless cloudy night. It would be correct to assume that a predator is more successful on moonlit nights and that its prey can also easily avoid it. The quick disappearance of deafened kangaroo rats on moonless nights enabled Webster (Webster and Webster, 1971) to assume that moonlight helps both the predator and the prey.

5. Protective conditions of habitat.

The behavior of rodents can change depending on the presence of protective shelters. An artificial increase in the number of shelters will also increase the number of kangaroo rats without a shift occuring in the abundance and availability of the fodder conditions (Thompson, 1982 b). A number of experiments aimed at changing the habitat structure (manipulation of vegetation) show the correlation between the number of rodents and the habitat structure (Rosenzweig, 1973; Price, 1978 a; Thompson, 1982 b; Price and Waser, 1984). The species whose habitats are destroyed reduce their number as a rule; the species whose preferred habitat structure is recreated respond with an increase in their numbers. However, since artificial changes in natural habitats lead as a rule to changes not only in the distribution of potential shelters but also to changes in the distribution of food resources, the results of such experiments are rather contradictory and may point both to the adaptation of rodents to avoiding predators and to using different variants of seed distribution (Price, 1986). Besides, a change in the habitat structure may not only lead to a change in the behavior of the prey, but also to alterations in the habits of the predator. And, finally, a change in the number of rodents in response to a single time change in the structure of the habitat is a postponed phenomenon since the result of manipulations by an experimenter may be registered only after a substantial period of time. During that period the size of populations can be influenced by local conditions. The presence of a control plot does not fully solve this problem since the latter should be far from the experimental one to reduce the probability of rodent migration.

The observation of individual behavior of rodents in experimental, thoroughly controlled conditions is a more promising approach. Such conditions can be created in an open-air cage where food is available *ad libitum* and the habitat structure is manipulated. An approach used by us in studying the correlation between the elements of the habitat structure of three coexisting species, was changing the feeding conditions of seed feeding rodents, inhabiting sand-gravel bush desert in Trans-Altai Gobi, Mongolia (Rogovin, 1988 a) while the habitat structure remained unaltered.

The habitat structure of all three species in nature (two species of pygmy jerboas - *Salpingotus koslovi* and *S. crassicuda* - and a hamster - *Phodopus*

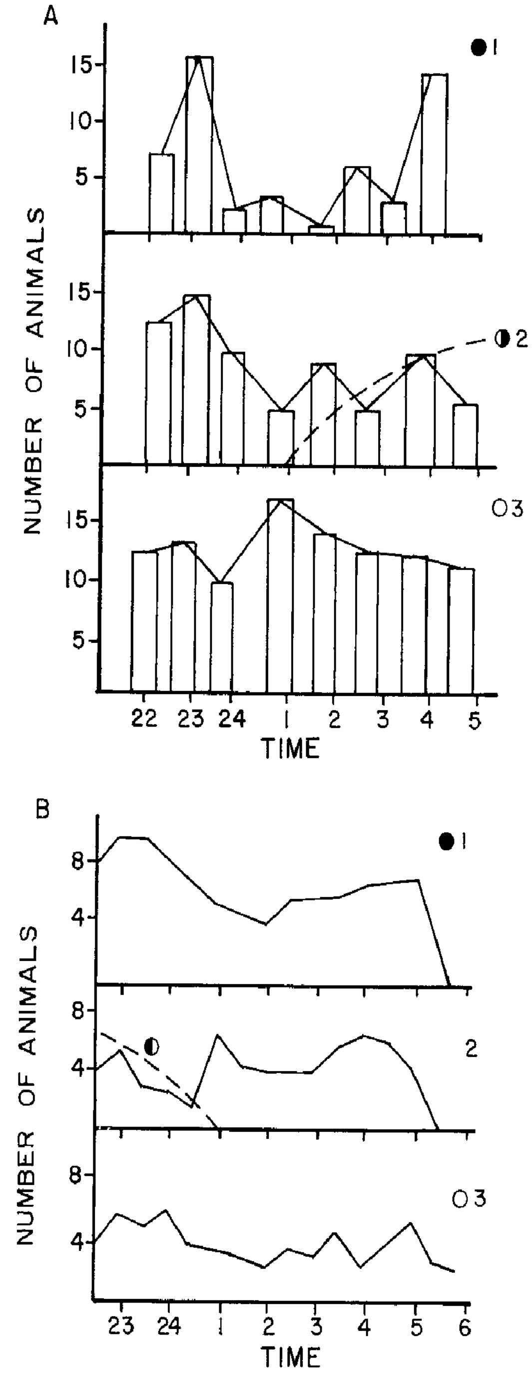


Figure 6.- Activity of Pygerethmuspygmaeus under illuminationof the terrain by the moon. Abscissa - time of the day; ordinate - number of animals recorded on a permanent route; A Recordings at the sampling plot in a clay semidesert of western Kazakhstan: 1 - moonless night (29-30. 5. 1976); 2 - the last quarter of the moon (14-15. 7. 1976); 3 - full moon (14-15. 7. 1976). Air temperature 20-25 C. B. Recordings on the permanent route in the northern subzone of the Trans Altai Gobi desert (mean data) : 1 - moonless nights, 2 - first quarter, 3. - full moon; July - August 1980, 1983, 1984, air temperature - 18-25 C.

Table 3. Differences in microhabitat adherence and mobility of Dipodomys merriami in different photoperiod conditions on the terrain. (The data were obtained by recording rodents by the light of an electric torch; the type of activity was recorded right after finding the rodents; October - November, 1987; Mapimí, Durango, México). N - number of registrations; * P<0.05; ** P<0.01; *** P<0.001.

Characteristics	Full Moon	N	New Moon	N	t-criterion
Encounters in open space, more than 1 m from the bush (frequency)	0.29 ± 0.07	43	0.43 ± 0.06	69	t = 1.5
Feeding in open space (frequency)	0.25 ± 0.13	12	0.58 ± 0.15	12	t = 1.7
Mean velocity in crossing an open space while feeding (m/sec)	2.04 ± 0.28	25	0.36 ± 0.12	11	t = 5.5***
Mean lenght of the runs over on open space (m)	3.23 ± 0.44	45	6.41 ± 1.22	36	t = 2.45*

roborovskii) is represented by virtually evenly distributed *Nitraria shpaerocarpa* and *Reamuria soongorica* shrubs with sand drifts under the shrubs. These drifts are separated by sections of packed sand with a gravel coating. The patchy structure of the habitat determines the patchy distribution of seed - the main accumulations are located close to sand drifts under shrubs. Three situations have been recreated in experimental conditions in open-air cages, divided into four equal squares; 1) four squares of homogenous sand surface, 2) two squares covered with gravel alternate with two sand squares, 3) the same, but a shrub of *N. sphaerocarpa* was implanted in the center of the sand square. *S. kozlovi* greatly preferred sand drifts under shrubs, *S. crassicauda;* however, *Ph. roborovskii* did not show its habitual preference (Table 4). When accumulations of seed were evenly distributed between all squares of the open- air cage the first two species fed mainly close to the bushes, whereas *Ph. roborovskii* examined the whole territory. These results tally fully with the observations of rodents by

Table 4. Conjugation of three syntopic species of psammophyl rodents with the structural elements of the habitat in experimental conditions. 4 m ² open cage; subdivided into 4 squares 2 m ² each. Squares represented conditions of habitat: 1 / homogenously sandy, 2/ 2 sand squares without shelter, 2 - gravel squares without shelter, 3/ 2 sand squares with a shelter (a shrub), 2 - gravel without shelter. To evaluate the conjugation we used the tetrachoric coefficient of correlation with the assessment of significance by X^2. N is the number of registers of the species at the square of the open-air cage. ** P<0.01;*** P<0.001.

Species	No of species	Habitat structural elements					
		homogenous sandy area	N	sand drifts alternating with gravel covered sections	N	same but shelter in sandy area	N
S. kozlovi	2 m 1 f	- 0.07	90	+ 0.44***	90	+ 0.58***	90
S. crassicauda	2 m 2 f	+ 0.05	120	+ 0.20**	120	+ 0.18**	120
Ph. roborovskii	2 m 1 f	- 0.09	90	+ 0.11	90	+ 0.02	90

m= male f=female

torchlight at night carried out in natural conditions. Pygmy jerboas make rectilinear runs using synchronous bipedal ricochet and hide under the bush in case of danger. *Ph. roborovskii* do not use shrubs as shelter, although they make burrows in them. The direction of their movements does not depend on peculiarities in the distribution of vegetation.

The results of these experiments suggest an important conclusion: the behavioral response of the animal is a result of assesing it under different external influences. In this case the attachment of pygmy jerboas to pre-bush sand drifts is a result of the stable behavior stereotype which could be formed either by predators or by peculiarities in the distribution of resources, or by a combination of the two. As has been noted, the distribution of protective cover allows more than one method of avoiding a predator in an heterogeneous environment. It can be theoretically assumed that behaviorally wise there are three strategies for reducing the risk of being killed by a predator. They are: 1) hiding close to natural shelters (relief, vegetation), 2) construction and active protective burrows, 3) fast escape. Desert rodents use all three strategies. At the same time different methods of avoiding danger in the desert are closely related to differences in the size and morphology of the animals. This is an important argument in favor of the possible role of the predator as a factor that structures the community. Since an increase in the velocity of locomotion in bipedal forms is dependent on the size of the body, escape from danger by bipedal saltation is characteristic of relatively large species. Jerboas are the fastest desert rodents of medium and large size, which are relatively less dependent on burrows and natural protective conditions. Species of medium and large size that are unable to quickly pick up high velocities (relatively low mobility, medium size jerboas, kangaroo rats, gerbils), actively use burrows for protection. Some of these forms use shrubs as shelter. However, unlike small species, hiding in open spaces, species of the above group do not have specific postures (flattening out on the substrate). This general regularity, registered during observations of the species of rodents is indicated in

Table 5. The use of burrows by seven species of jerboas in nature (the result of observation over individually marked animals; Rogovin,1983).

Species	**Number of burrows per 1 animal**						**Number of animals**
	1	**2**	**3**	**4-5**	**6-8**	**9-12**	
S. crassicauda	100					4	
A. severtzovi	8	31	46	15			13
A. nataliae (bali-cunica)	89	11					9
A. elater	50	25	20	5			20
P. pygmaeus			4	30	50	16	50
D. sagitta	71	29					7
S. telum			13	52	30	4	23

Table 6. Jerboas danger avoiding behavior in response to warning; P ± m -- probabilityfraction and its error; N is the total number of observations.

Species	Pattern of behavior			N
	hiding p±m	escape run P±m	escape into burrow P±m	
S. crassicauda	1			28
S. kozlovi	0.59 ± 0.12	0.41 ± 0.1		17
C. paradoxus	0.71 ± 0.10	0.29 ± 0.10		21
A. severtzovi		0.76 ± 0.07	0.24 ± 0.07	42
A. nataliae (balikunica)		0.97 ± 0.03	0.03 ± 0.03	33
A. bullata		0.49 ± 0.07	0.51 ± 0.07	45
A. elater		0.71 ± 0.03	0.29 ± 0.03	175
P. pygmaeus	0.05 ± 0.02	0.21 ± 0.03	0.74 ± 0.03	200
D. sagitta	0.11 ± 0.05	0.89 ± 0.05		35
P. ctenodactilus		1		
S. telum	0.34 ± 0.03	0.15 ± 0.02	0.51 ± 0.03	200
S. andrewsii	0.27 ± 0.11	0.23 ± 0.10	0.50 ± 0.12	18

Fig. 3, where easily it can be seen within one family of jerboas. Tables 5 and 6 show quantitative data on the results of observations of the use of burrows by jerboas in nature (Rogovin, 1983) and different danger escape variants in varios species.

The number of used burrows is not directly dependent on the locomotory velocity of species (with all likelyhood, the nature of the substrate preferred by a species is also important). A small number of burrows used simultaneously by a species is indicative of the least mobile and hiding *S. crassicauda,* and of highly mobile species (*A. nataliae, D. sagitta).* Such species as *P. pygmaeus* and *S. telum* represent settled burrowing animals among jerboas by the type of exploitation of home ranges, similar to diurnal burrowing animals of open plains, e.g. ground squirrels, susliks, marmots (Rogovin, 1983). These species feed mainly on the green mass of easily accessible plants. They inhabit deserts with a hard substrate in which they make numerous burrows. These burrows are clearly differentiated by its structure into permanent (for day time rest) and temporary (protective). The latter are characterized by large, always opened entrances (entrances into day time rest burrows of jerboas are always stoppered with earth). Protective burrows organize the area of home range, being the main centers of attraction for animals. When home ranges overlap considerably or completely coincide in dense populations, burrows are individually shaped. The majority of territorial conflicts between animals occur at these burrows (Rogovin, 1983, 1985). These and other species of jerboas, ecologically close to them, form the densest populations (Rogovin and Shenbrot, 1988).

Table 7. Danger avoiding behavior of American desert rodents in response to warning. P±m - probability and its error; N - the total number of observations. (October-November, 1987; Mapimi, Durango; México).

Species	**Pattern of behavior (P±m)**				**N**
	hiding	**escape run**	**escape under the shrub**	**escape into the burrow**	
D. nelsoni			0.10 ± 0.03	0.90 ± 0.03	97
D. merriami			0.83 ± 0.04	0.12 ± 0.04	106
P. penicillatus			0.94 ± 0.06	0.06 ± 0.06	18
P. flavus	0.37 ± 0.18			0.63 ± 0.18	8
N. albigula				1.00	22

Unlike jerboas, differentiation of species among Heteromyid rodents by means of avoiding danger is apparently less pronounced. Both bipedal and quadrupedal species, in case of danger, escape under the protection of a bush or hide in the burrow (Table 7).

Duration of stay in the burrow during active life may also be an indicator of the role of burrows as a shelter from predators. It is indicative that unlike jerboas kangaroo rats spend most of the night time in a burrow. Burrow dependence in Dipodomys has been repeatedly recorded (Eisenberg, 1963; Kenagy, 1973; Schroder, 1979; Braun, 1985). Braun showed that these rodents spend about 1.8 hr a day outside the burrow, actively harvesting seed. It is quite possible that the close burrow dependence of *Dipodomys* is, to a certain extent, determined by the phylogenetic closeness of Heteromyidae to the underground dwellers Geomyidae. It is also possible that close burrow dependence is explained by a slight specialization of kangaroo rats towards bipedal gait. Even *P. pygmaeus,* one of the most closely burrow dependent jerboa, spends from 50 to 67 per cent of the night time outside burrows (depending on the season and the state of sexual activity). *P. pygmaeus* males spend 30 ± 5 per cent of the time outside the burrow (N = 10), whereas *D. merriami* males spend 11 ± 1 per cent (N = 10) when confined in a cage subjected to a 10 hours period of darkness.

Interesting information on the level of risk of being caught by a predator is provided by comparing the harvesting and the feeding sites. These sites very often do not coincide even in non hoarding species. The most striking example is one of the fastest jerboas of Central Asian deserts - *Paradipus ctenodactilus* Sabilaev, 1969; Airapetiantz *et al.*, 1978). The comb-toed jerboa is a specialized species that inhabits beds of unfixed sand barkhans and feeds on green bush shoots scattered among sand hills (*Haloxilon, Caligonum, Salsola)* while feeding, animals run up to a bush, bite off a shoot 10 to 20 cm long (very often doing it in a jump to the height of 70 cm to 1 m) and take it away to the most open spot on a sand hill where they begin to eat it. A comb-toed jerboa is unmatched for the velocity of its bipedal locomotion along the inclined loose surface of a moving sandhill. Apparently the only place where a jerboa can be caught by a ground predator is near a bush. Thus jerboas never hide under a bush. Hairy-footed jerboa (*Dipus sagitta)* living in similar conditions (mainly inhabiting valleys between sandhills and sections of fixed sand) transport food items more rarely and for shorter distances (Table 8). In other non-sand deserts of Mongolia, *Dipus sagitta* do not usually transport fodder. This type of activity has not been recorded in other species of jerboas.

Cutting and transporting shoots of plants into a burrow by the great gerbils (*Rhomobomys opimus)* which actively stock fodder, takes place during the daytime and is conditioned by elements of mutual assistance. This mutual assistance includes: 1) visual control over the territory of the family group, performed by one of its members, 2) acoustic signaling for warning of danger, 3) elements of labor division during foraging (cutting of shoots and transport to burrows is performed by different individuals). During nocturnal loading of species

Table 8. Peculiarities of foraging activity of some psammophyl rodents of palearctic deserts. N - number of observations, X ± m - mean distance, m; max - maximaldistance, m; V - coefficient of variation.

Species	Type of fodder	Method of foraging	Distance from the site of harvesting to the site of feeding			
			N	X ± m	max	V
P. ctenodactilus (Middle Asia)	juicy bush shoots	takes to an open place aside of the bush	14	9 ± 1	15	43
D. sagitta (Middle Asia)	green parts of annual grasses, seed	feeds on seed on site, shoots - on site or takes away	17	3 ± 1	10	100
D. sagitta (Mongolia)	the same	feed on site	10	0	0	0
Rh. opimus (Mongolia)	shoots of bushes,	stocking in a burrow	14	7 ± 2	22	86
Ph. roborovskii (Mongolia)	seed, insects	feeds on insects on site, stocks seed in a burrow or provisional pantry	7	138 ± 44	360	84

with cheek pouches, the distance and duration of foraging runs may also be related to peculiarities in morphology and the type of locomotion. In the small, trotting *Phodopus roborovskii* (weight 20 - 25 g) using natural protective conditions, foraging runs can be up to 500 m long. By the same token according to Schroder (1979) the size of the home range of *Dipodomys spectabilis* (140g) averaged 0.05 ha. The animal spends less than 22 per cent of its active time outside the radius of 6m from its burrow. According to our observations of an ecologically related kangaroo rat *D. nelsoni* (weight 90 - 110 g) mean distances from the burrow during foraging were 7.6 ± 0.7 m (N = 69) in females, and 9.7 ± 1.3 m in males (N=33).Needless to say, in such comparisons it is necessary to bear in mind that the form of species behavior during foraging could be determined by the interaction of the risk of being killed by a predator and by the advantages resulting from assimilating this or other sources of fodder. The distribution of feeding resources in a heterogeneous environment is also heterogenous. The morpho-ecological differentiation of species by the types of distribution of food resources is another possibility for explaining the structure of desert rodent communities. Interspecific competition is suggested as the mechanism for such differentiation. In the next Chapter we shall discuss arguments in favor of competition as a structuring factor in the community.

THE ROLE OF INTERSPECIFIC COMPETITION IN THE FORMATION OF MORPHO - ECOLOGICAL DIFFERENCES OF SPECIES IN THE COMMUNITIES OF DESERT RODENTS.

1. The problem of community saturation.

The level of saturation of the community, as a measure of the completeness of the resources used by coexisting species (Pianka, 1972) is the most important characteristic whose registration is necessary in the search for competition for resources in nature. Since the registration of resource abundance is an extremely difficult task, it is conducted only rarely and is of a superficial nature. Guided by an unspoken agreement, mammologists studying communities of desert rodents very often view them as saturated (Shenbrot, 1986 a). Numerous data show that in the desert, provision of food is a very important factor limiting the size of rodent populations (review, Munger *et al*, 1983). However, a reduction in the intensity of reproduction is usually related not only to diminishing of food abundance, but mainly to a change in its quality, in particular, to a reduction in the water content, and also of vitamins and auxins that animals receive from plants (Chew and Butterworth, 1964; Beatley, 1969; Bradley and Mauer, 1971; Breed, 1975; Reichman and Van de Graaf, 1975). In this manner the level of precipitation in a desert, which determines the density of vegetation and fructification of plants, is a direct regulatory factor. Even in species which are able to live on a dehydrated diet, the water requirement sharply increases during reproduction and they receive it with their food. For instance the need for water during lactation in D.

merriami, which feeds mainly on seeds, increases 200 times (Soholt, 1977). We have seen in Mongolia that a five-toed pygmy jerboa *Cardiocranius paradoxus* may fully stop reproduction in dry but food abundant years, as can be seen by the beefiness of the animals (Shenbrot and Rogovin, 1988).

Experiments on additional nutrition in different species of rodents indicate the possibility for an artificial increase in the local density of populations of different species (Watts, 1970; Flowerdew, 1972; Abramsky, 1978; Taitt, 1981; Taitt and Krebs, 1981; Gilbert and Krebs, 1981). It is a well known fact that the provision of food in nature affects the reproductive success of the population and serves as a serious argument in favor of the significant role of exploitative competition in the structure of rodent communities. A whole number of indirect and direct data show that American Heteromyid rodents are capable of using virtually completely the reserves of seed in soil (Lockard and Lockard, 1971; Price and Brown, 1983). Hoarding seeds by many species is explained by an intensive usage accumulations in close proximity of the burrow. For instance we have seen in the Bolsón de Mapimí that the home ranges of kangaroo rats *D. nelsoni* average 0.08 ± 0.007 hectarea (9 males and 6 females) and are used so intensively that the zone with the radius of 5 - 7 m around the permanent burrow in the optimal habitat (density of population from 8 to 10 individuals per hectare) becomes virtually deprived of vegetation (Fig. 7). More than 70 per cent of active kangaroo rats were registered within this zone of home ranges. Regularly animals make foraging runs to the periphery of the range where they collect top shoots and Salsola kali fruits, racemes of Compositae and spikes of grasses in their cheek pouches. Being the most trophically plastic species among Heteromyid rodents in the community (Rogovin and Surov, 1986 b), *D. nelsoni* easily changes the spectrum of its diet depending on the phase of the vegetation and fructification of plants. However, some seed reserves remain in the soil even close to a burrow. The absence of grass close to the burrow can be explained by the fact that they have been trampled down. The results of our observations of *D. nelsoni* tally fully with data on the use of the home range by *D. spectabilis* (Schroder, 1979, 1987) and D. ingens (Braun, 1985).

Although limited resources as the structuring factor in the Heteromyid rodent community is used fairly frequently, the data with respect to the intensity of use of the home range and peculiarities of foraging activity in other species are rather fragmentary. There is information that the small pocket mouse *Perognathus* uses home ranges similar in size to those of bigger species (Chew and Butterworth, 1964). Schroder (1979, 1987) observed that *D. spectabilis* home ranges are smaller than those of *D. merriami,* which weighs less. According to our observations in the Bolsón de Mapimí the maximal diameters of home ranges in three coexisting Heteromyid species averaged in : *D. nelsoni* (90 - 110 g) - 40.6 ± 2.6 m (9. males and 6 females), in *D. merriami* (35 - 45 g) - 55.6 ± 5.6 m (9 males and 12 females), in *P. penicillatus* (12 - 15 g) - 58.4 ± 7.4 m (4 males and 3 females) (see Comment 2). However, the latter two species did not store seed in their burrows in Autumm. The spectrum of the diet of these species at the sites of coexistence in the period of development and fructification of annual plants virtually completely overlap. In October and November composite plants are the main food plants. Differences occur mainly at the level of use of different parts of the same plants by the feeding animals.

There is a negative relationship between the size of the home range and the size (weight) of animals of different Heteromyid species, which means an increase in the intensity of exploitation of the home range with an increase in body size. By contrast in Asian Dipodidae this relationship is positive (Rogovin, 1983). The use of vast open spaces in deserts by large species of Allactaginae and Dipodinae is associated with an extensive use of food resources, but in dense populations of varios species, there are cases of almost full overlap of the home ranges of the same and different sexes (*Allactaga elater, Pygerethmus pygmaeus, Stilopidus telum, Dipus sagitta)*.

Although it still remains obscure to what extent population densities of different species of jerboas observed in nature are determined by food resources, there is enough evidence to think that of paramount importance in determining the upper limits of population densities is not the abundance of food, but burrows and sites suitable for digging. This is also confirmed by the presence of aggressive contacts at burrows and the absence of protection of the territory of home ranges in the species of jerboa, studied by us (*A. elater, P. pygmaeus, D. sagitta*).

The extent at which the exploitation of home ranges corresponds with the peculiarities of social organization (the level of territoriality) of species on the one hand, and the abundance of food in the territory on the other, remains rather obscure and requires a detailed study. It is far from being evident for jerboas, for example, that the level of intraspecific aggression be positively related to the abundance of food. An increase in the population density of *P. pygmaeus* does not lead to an increase, but rather to a reduction in the level of intrapopulation

Figure 7. Types of home range exploitation by solitary living species of desert rodents : A - intensive, B - extensive. A1 - home range of a male specimen of Dipodomys nelsoni: 1 - boundaries of the home range; 2 - most distant points of runs from the burrow; 3 - site of fodder collection; 4 - permanent burrow; 5 - provisional burrow; 6 - Prosopis sp. bushes; 7 - boundaries of Salsola kali vegetation; 8 - clay area, deprived of vegetation. A2 - interlocation of D. nelsoni home ranges in a nonbreeding population (6- 7 animals per ha; habitat: Prosopis sp. + Salsola kali on light loams along the banks of a lake hollow: Mapimí, Durango; México; October-November, 1987): 1 - boundaries of adult female home ranges, 2 - boundaries of adult male home ranges, 3 - permanent burrows, 4 - provisional burrows. B1 - home range of an adult Dipus sagitta male : 1 - boundaries of the home range; 2 - paths of migration during feeding; 3 - points of registration of the male; 4 - permanent burrow; 5 - provisional burrow; 6 - sand mounds, covered with Nitraria roborovskii; 7 - evenly distributed vegetation of the depressed Haloxilon ammodendron, Zigophillum xantoxilon and annual grasses. B2 - interlocation of home ranges of D. sagitta in a nonbreeding population (12-18 animals per ha; habitat: suppressed bush vegetation of H. ammodendron + Z. xantoxilon on sand deposits along the banks of a lake hollow; Ulgiy, East Gobi, Mongolia, July 1986): 1 - boundaries of home ranges of adult males; 2 - boundaries of adult female home ranges. Home ranges were determined by connecting the most distant points of movement from the burrow (D. nelsoni) or the most distant points of recording of the individual (D. saggitta). We looked for marked specimens of D. sagitta by torchlight walking along the system of transects across the plot.

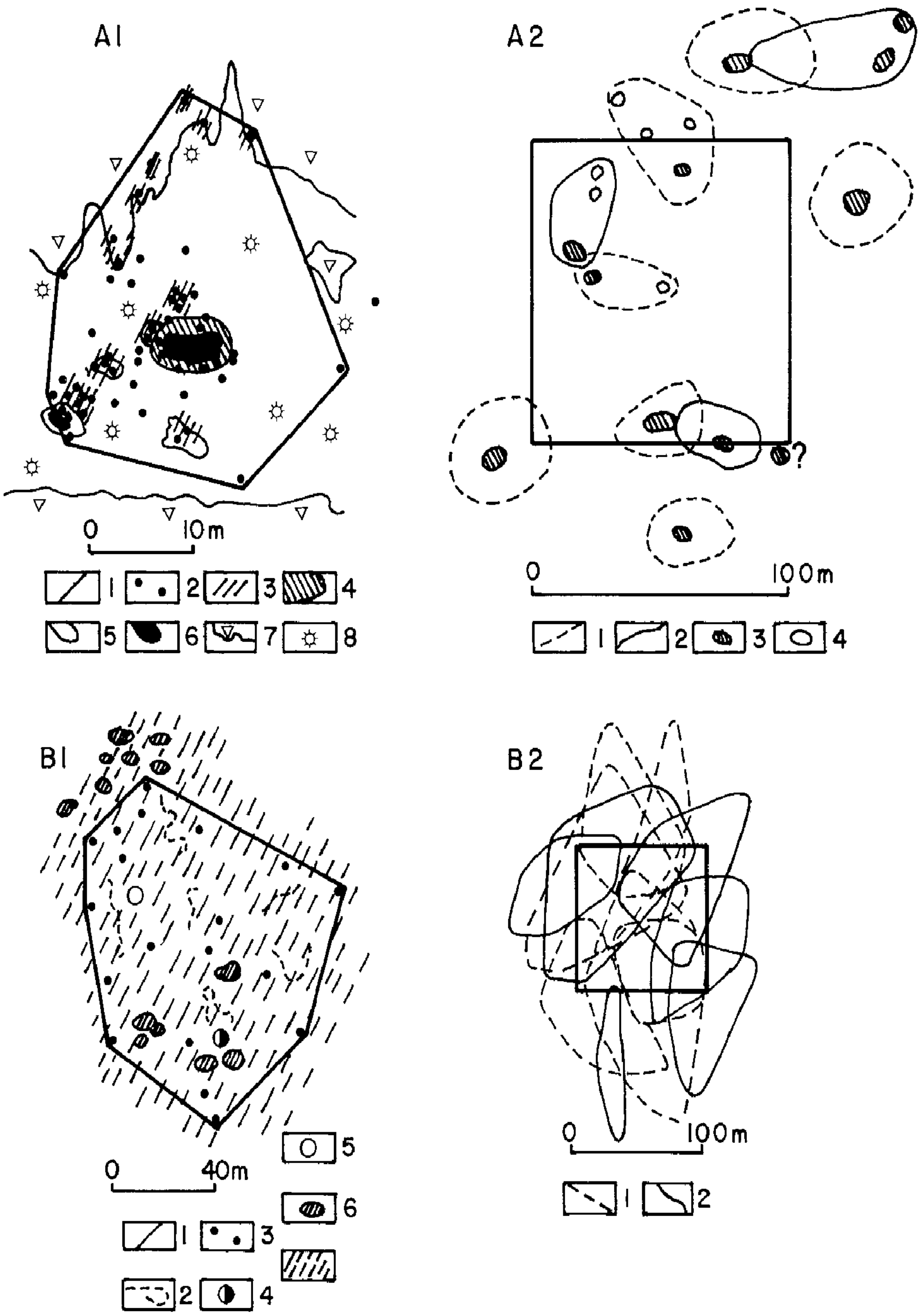


Figure 7

aggression (Rogovin, 1985). Apparently this is also typical of a number of other species of jerboa. Nevertheless, the way of checking the level of abundance of food for coexisting species is by means of direct counts of food reserves in nature. The difficulty of this calculation is evident, since it requires knowledge of all the delicate peculiarities in foraging behavior and food preferences of species. The presence of seed in the surface layer of soil does not lead to its availability to this or the other species of Heteromyidae. This should be taken into consideration when evaluating the completeness of utilization of food resources by rodents in nature.

Climate inconstancies in deserts as well as regular or irregular replacement of a relatively high level of soil moisture with drought, induces radical seasonal and perennial changes in rodents food resources. In these conditions, it would be reazonable to expect changes in the level of saturation of each independent community. The aggravation of the tension of exploitation competition in communities should occur in the most "narrow" periods in the life of sympatric populations. Such periods are most probable either in marginal or in suboptimal conditions, according to the state of foraging resources.

In marginal conditions, the competition is most realistic in case of a high overlap of both the trophic and the structural components of fundamental niches. Our observations of communities of Mongolian desert rodents in low density populations during food shortage show the highest ecological differentiation of species both by habitat and by trophic system. This shows that in the majority of cases we deal with ecologically scattered populations of species, using different resources (see also Schroder and Rosenzweig, 1975). Besides, in conditions of real food shortage a radical reduction in the number of populations can be brought about by other reasons. The low number of populations impedes the possibility of a purely experimental assessment of competition.

Interspecific relationships are rather easily recorded during the period after mass reproduction and low mortality in food abundant years. The theory of habitat selection (Rosenzweig, 1979, 1981) indicates conditions for the dynamic equilibrium of coexisting populations of rodents, and explains this situation by the mechanism of competitive displacement. However it does not take into consideration the possibility of a stable inflexible division of preferable conditions between populations (Schroder and Rosenzweig, 1975; Schroder, 1987). In the latter case the area of interaction accounts for suboptimal habitats and the recorded effects of competition in these areas represent the result of stable behavior patterns which are not directly related to competition for food resources.

Interspecific competition, as a factor that promotes the structure of communities, apparently takes effect at certain stages in the community evolution, or is otherwise manifested periodically while the existing structure is maintained Wiens, 1977). The existence of certain relationships of species composition and abundance within communities can be related to the important role of competition in the past (Schoener, 1983).

2. Trophical differentiation of species in communities.

The well known fact of size divergence of species in communities of heteromid rodents is assigned to a high level of overlap of their trophic niches. It is customary to assume that the Heteromyidae are exclusively seed-eating formswhich live in conditions of food limitation (Price and Brown, 1983). On the other hand, in species feeding mainly on unlimited resources, the differentiation in size should not have, in general, any relationship with competition for food. The opinion that heteromid rodents are exclusively seed-eating forms is not quite correct. An increase in body size in heteromid species is associated with an expansion of the diet spectrum. Among the species, studied by us in the Bolsón de Mapimí community, the level of seed consumption is decreasing and the variety of the diet, as determined by the proportion of types of food in the stomach, increases among the species : *P. flavus* (5 - 7 g), *P. nelsoni* = *P. penicillatus* (12 - 15 g), *D. merriami* (35 - 45 g), *D. nelsoni* (90 - 110 g) (Rogovin and Surov, 1986 b). According to our observations of Nelson's kangaroo rats the green parts of *Salsola kali* during vegetative growth account for 30 per cent of the food stored in a burrow. A large amount of the green mass is consumed together with the heads of composite flowers and *Salsola* fruits. *Dipodomys microps* (Kenagy, 1972 a, 1972 b; Csuti, 1979) consumes green leaves. Reichman (1975) notes that kangaroo rats eat insects. There is a definite relationship between the consumption of green food and reproduction (Van de Graaff and Balda, 1973; Reichman and Van de Graaff, 1975; Kenagy and Bartholomew, 1981). Apparently heteromid rodents feed on seed exclusively in dry periods.

The distribution of species by the types of food used in the communities of North American and Asian deserts points to a similar set of types of trophic adaptations (Fig. 8). However in Asian deserts we note a large assortment of feeding variants mainly due to the forms that combine different types of food. Among the species of the Northern Chihuahua (Bolsón de Mapimí) and Sonora (Pinacate) deserts, the averages of the diversity of diets (see Comment 3) are respectively 45.0 ± 7.8 per cent (10 species) and 39.0 ± 7.0 per cent (10 species). In Middle Asian deserts, comparable by their biological productivity (Central and North-Western Kyzylkum) and Mongolian deserts (Eastern Gobi) these indices are respectively 59.0 ± 7.1 per cent (12 species) and 68.2 ± 7.2 per cent (13 species). At the same time the coefficients of variation in the Asian deserts are lower. Only in the extremely arid desert of Trans Altai Gobi in conditions of regular shortage of food resources (especially of green food) we observe a reduction in the mean diversity of diet (41 ± 7 per cent; n = 9) and concomitantly, an increase in the coefficient of variation.

With all probability, the main condition for the trophic specialization of rodents in deserts is not only the general productivity of forage resources, but also their level of stability.

A relatively high level of ecological lability in selecting food type for a number of Asian species of jerboas suggests two possibilities: 1. Manipulation of resources under the conditions of shortage of some types. 2. The possibility of reducing the shortage of each concrete type of resource by expanding the diversity of resources used. The classification of North American and Asian terrestrial rodents in the studied communities by specialization in feeding on different types of food can be presented as follows (published data Shenbrot, 1980, 1981, 1986 b; Rogovin, 1983; Rogovin and Surov, 1986 a; Rogovin *et al.*,1987 and also unpublished data on the contents of the stomachs of rodents in the deserts of Chihuahua (Mapimí, Mexico), Sonora (Pinacate, México), deserts of Central Asia, Western Kazakhstan and Mongolia):

Deserts in the south of North America

granivores	**insectivores**	**herbivores**	**omnivores**
Perognathus flavus *P. longimembris* *P. penicillatus* *P. intermedius* *P. nelsoni* *P. baileyi* *Dipodomys merriami* *D. ordii* *Reitrodontomys megalotis*	*Onichomys torridus*	*Neotoma albigula* *N. lepida* *Sigmodon hispidus*	*Dipodomys nelsoni* *D. deserti* *Peromyscus eremicus* *P. maniculatus* *Spermophilus spilosoma* *S. mexicanus* *S. tereticaudus*

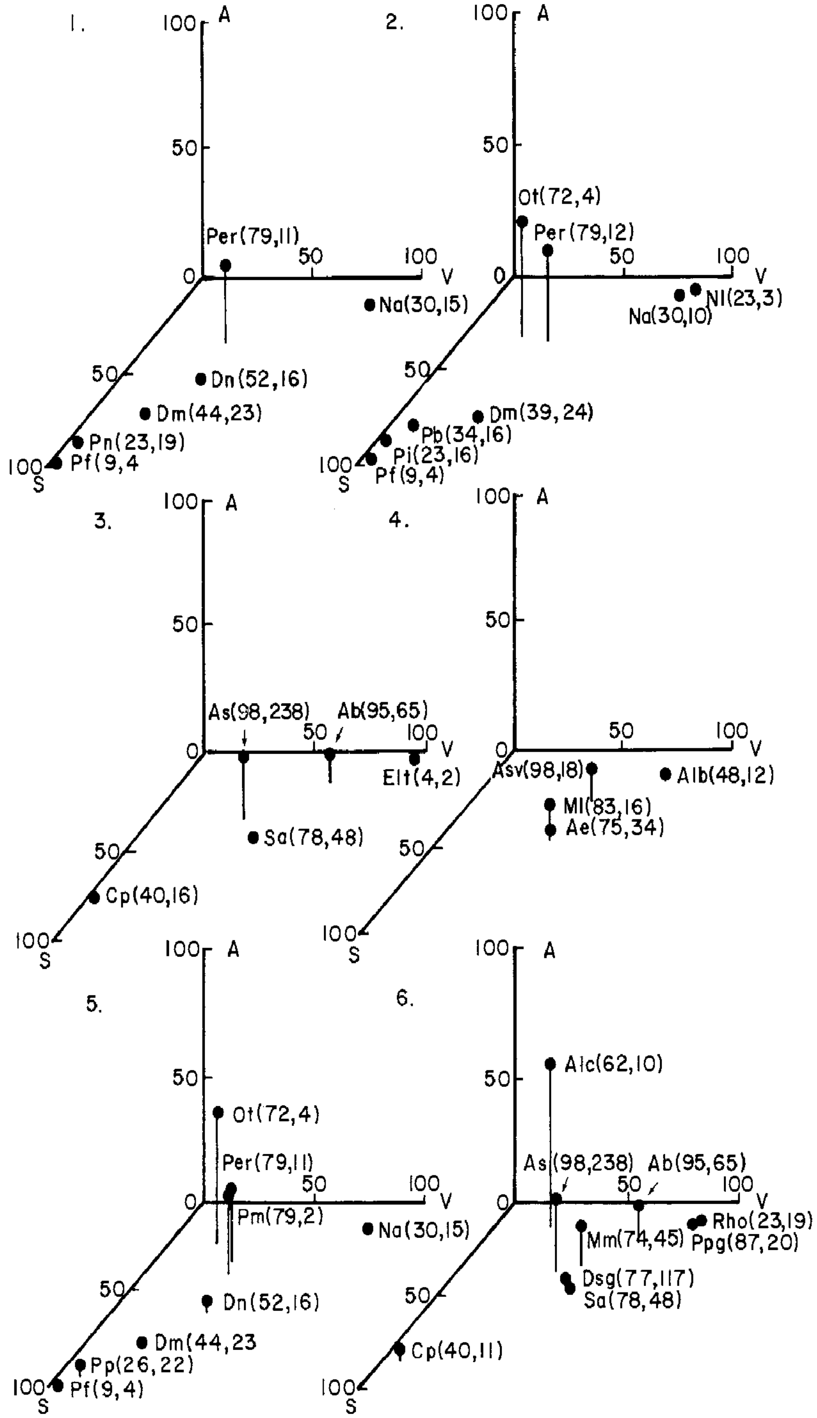
Deserts of Middle and Central Asia

granivores	insectivores	herbivores	omnivores
Cardiocranius paradoxus	*Euchoreutes naso*	*Alactodipus bobrinskii*	*Allactaga jaculus*
Salpingotus crassicauda	*Allocricetulus curtatus*	*Pygerethmus pygmaeus*	*A. severtzovi*
S. kozlovi		*P. platiurus*	*A. sibirica*
S. heptneri		*Paradipus ctenodactilus*	*A. elater*
Phodopus roborovskii		*Eremodipus lichtensteinii*	*A. bullata*
		Jaculus turcmenicus	*A. nataliae (balicunica)*
		Eolagurus luteus	*Stilodipus telum*
		Citellus fulvus	*S. andrewsi*
		C. pygmaeus	*Dipus sagitta*
		Spermophilopsis leptodactylus	*Meriones meridianus*
		Rhombomys opimus	*M. libicus*
			M. unguiculatus
			Cricetulus migratorius

Due to a different number of local communities analyzed (Fig. I), the number of species in the fauna of North American and Asian deserts do not coincide, but the prevalence of the granivorous forms in the communities of North America can be readily seen (45 per cent against 16 per cent in Asia). The prevalence of herbivores in the Asian communities (35 per cent against 15 per cent) and omnivores (42 per cent against 35 per cent) may account for disregarding the Hutchinson rule within this type of community. Among the communities given in Fig. 1, exceptions in American deserts are only pairs of species: *Dipodomys merriami - D. ordii* and *Peromyscus maniculatus* (or *P. eremicus) - Onichomys torridus.*

The possibility for coexistence of two species of kangaroo rats, (similar size), was noticeable in a number of regions of north America (Brown, 1973; Brown and Liberman, 1973; Lemen, 1978; Lemen and Rosenzweig, 1978; Hallet, 1982; O'Farrell, 1980). A possible mechanism for the partitioning of resources by closely related species has been studied (Schroder and Rosenzweig, 1975; Schroder, 1987). As Schroder (1987) views it, the possibility for coexistence of these species can be determined not by the competitive partition of microhabitats, but by the genetically determined division of optima structural niches. This possibility cannot always be considered when distinguishing communities in accordance with the type of landscape (Fig. 1). The possibility for coexistence can be provided by the essential differences jobserved both in the composition of food (*O. torridus* is mainly an insect eating species, *P. eremicus; P. maniculatus* feeds on insects, seeds and green vegetation) as well as by the different strategies adopted during foraging (*Peromyscus* climbs well, and is less mobile when foraging than *Onichomys).* Actually, in this case we mean coexistence of different morpho-ecological types of rodents (life forms). It is this peculiarity that is often observed in coexisting species of the Asian desert communities (Fig. 1). Closely related coexisting organisms (by weight), belong as a rule to different genera (20 cases out of 22) and, often, of different morpho-ecological types (gerbils-jerboas, hamsters-jerboas: 11 cases out 22).

Figure 8. Segregation of rodent species by the types of food in the stomach contents of desert rodent assemblages of North America and Asia. The diet was determined by the proportion of each type of food by volume in the stomach contents with an accuracy of ± 10 per cent : vegetative green and semiground parts of plants (axis V), seed (axis S), food of animal origin (axis A). The species are designated as in Fig. 1. The first digit after letters - diversity of diet ($H = - \sum P \log_2 P$), the second digit - number of samples. Assemblages the same as in Fig. 1: 1, 5,9 - Chihuahua desert, México (Mapimí); 2, 10 - Sonora desert, Mexico (Pinacate); 3,6,12 - deserts in the eastern and central Gobi (northern deserts of Mongolia); 7,11 - Trans-Altai Gobi (southern desert of Mongolia); 3 - central Kyzylkum, Middle Asia; 8,13 - central and north-western Kyzylkum, Middle Asia; 14 - Taisugan, western Kazakhstan. 1-4 - communities in the foothills and plateau; 5-8 communities of deluvial valleys, hollows of wind erosion and outflow; 9-14 communities of sandy habitats of different origin. The composition of food was determined during the season of high productivity of vegetation; México - Autumn, Middle Asia, Kazakhstan - spring, Mongolia - Summer. Data from : Shenbrot, 1980, 1986 b; Rogovin and Surov, 1986 a, b; Rogovin et al., 1987 and unpublished data.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Pi(23,16)
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As(98,238)
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Figure 8.

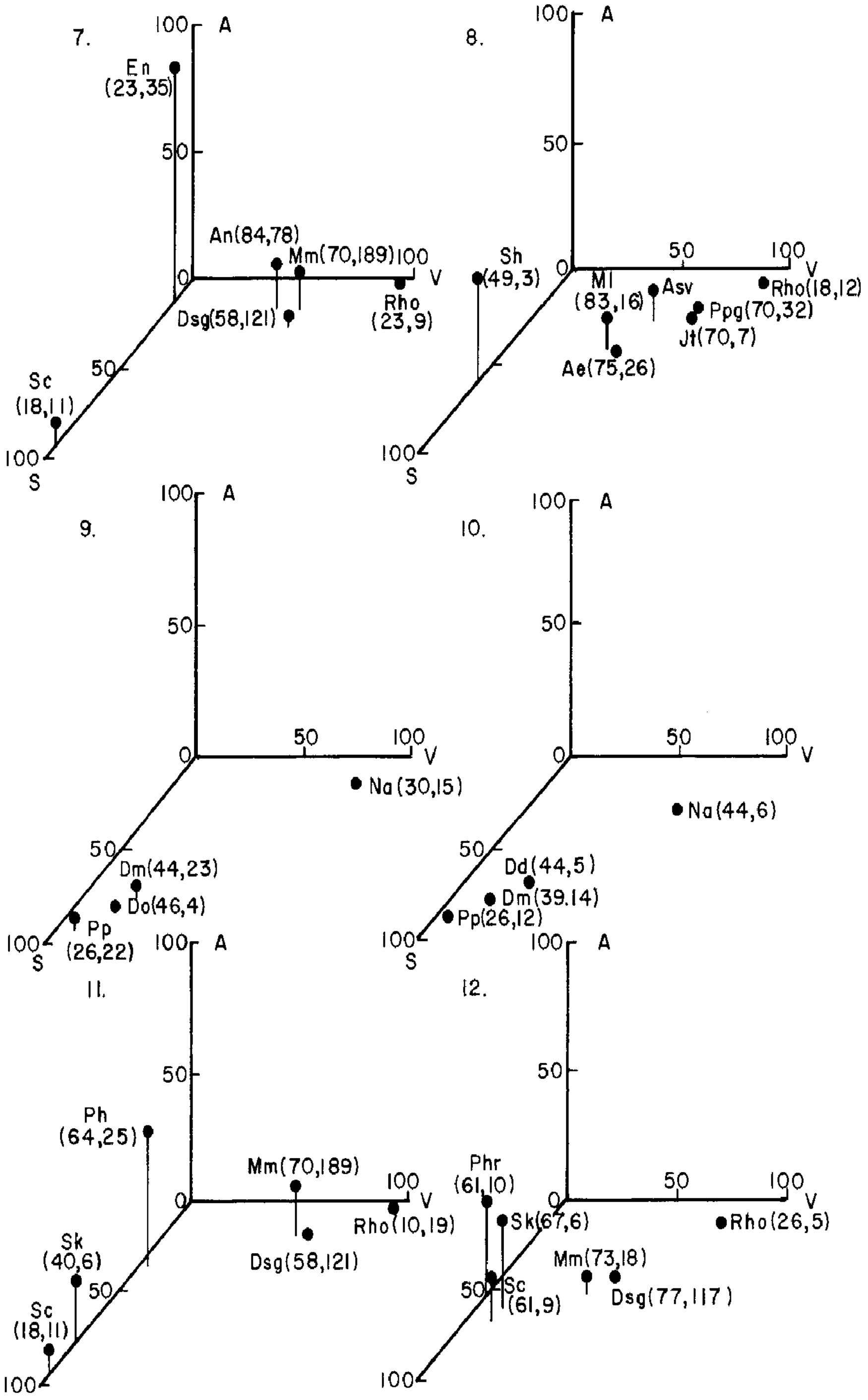
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Fig. 8 (cont.)

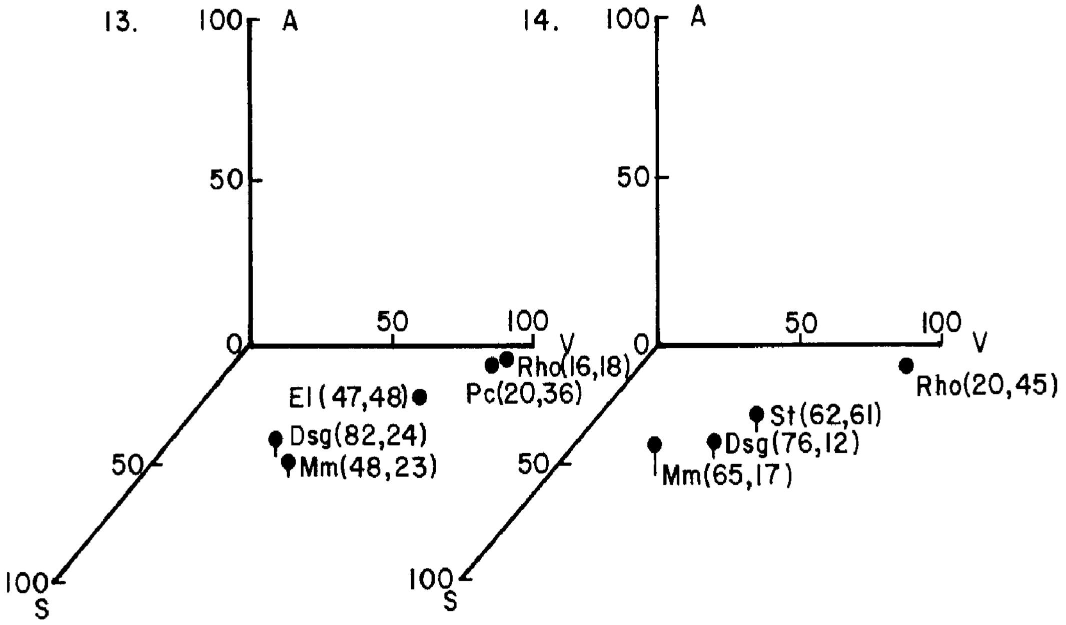

Figure 8 (cont.)

3.The problem of differentiation of coexisting heteromyid species by size and type of food items.

The weight ratio in pairs of coexisting heteromyid species was, in a number of cases, very close to the empirical ratio noted for the first time by Hutchinson (1959), and used to explain the possibility of coexistence of trophically similar forms of animals (Brown, 1973; Brown *et al.*, 1979; Price and Brown, 1983) (see Comment 4). Although this ratio is not always followed by a change in the Hutchinson index it can be determined by the local extinction of species (by the peculiarity of distribution of the size of food items along the axis of size gradations, etc.), heteromyid community members differ by weight more thancould be expected on the assumption of a random combination (Brown, 1973; Brown *et al.*, 1979; Bowers and Brown, 1982; Peterson, 1982).

The first attempts to explain the differentiation of coexisting heteromyid species in size were aimed at looking for differences in the size of fruits and seed consumed by them (Brown and Liberman, 1973; Brown, 1975; Brown *et al.*, 1979; Bowers and Brown, 1982). The initially established positive correlation between the linear dimensions of seeds and the weight of rodents (Brown and Liberman, 1973) was later rejected on the basis of the results of field data (Lemen, 1978) and laboratory experiments (Rosenzweig and Sterner, 1970; Hutto, 1978).

An absence of differentiation of large and small heteromyid species by preference for the size of food items was shown in experiments, where rodent species were presented with equal weights of four size classes of ground wheat particles (Price and Brown, 1983). For instance, the large *D. deserti* preferred to use ground wheat particles of intermediate size, but at the same time ate both the large as well as the small particles. It is only with respect to the smallest forms (*P. amplus, P. longimembris)* that a shift in preferences was noted towards small particles, although they used large ones too.

Our experiments with feeding other species of Heteromyidae in similar conditions gave similar results (Fig. 9). In the case where species were offered seeds of different plants, the significant displacement of the preference for the size of seed was noted only in *D. nelsoni* ($P < 0.01$; $t = 3.1$; $n = 14$). However, it could have been explained by the fact that the preferred food in experiments was *Prosopis* seed, which is actively stocked by this species in nature. In the case where universal food was used (peanut fragments of different size) the displacement of preference towards fragments of different sizes in different heteromyid species of Bolsón de Mapimí was not observed. However the dispersion of the size of food items somewhat increased in bigger species. Although *Perognathus* did not use whole nuts in experimental conditions, in nature we were able to see *P.penicillatus* carrying the fruit of *Opuntia leptocaulis,* whose largest diameter is close to 2 cm.

Still, the division of coexisting heteromyid species initially identified by the size of seed and fruit carried in cheek pouches is quite possible in nature. According to our observations in Mapimí, the linear dimensions of food items transported in cheek pouches, are related to a greater extent to the dimensions of the body as opposed to what is seen in the laboratory (Fig.10).

The ability of a big *D. nelsoni* to transport spikes of grass, anthodia of composite flowers and even pods of *Prosopis* and *Acacia* of 10 cm in length is probably determined by the extremely short period of foraging activity and its close relationship with the burrow, where big reserves of food are concentrated (Fig. 11). According to our observations in October-November in the Mapimí Biosphere Reserve (period of darkness is about 11 hours) the activity budget of *D. nelsoni* outside the burrow, (*i.e.* the time spent directly in foraging runs), averages about 45 min per night. An animal may spend another two hours on the surface of the burrow, not going farther than 1 m from its entrance. Thus the animal has no time to select food items and therefore takes all the items it can find in abundance. The activity budget of the smaller *D. merriami* outside its burrow averages 5 hours in Mapimí. Yet, out of this time an animal spends nearly 3 hours protected by bushes and cactuses. The time spent directly in foraging made up about 1 hour 10 minutes per night. At the same time this is distributed virtually evenly between open and protected areas (near bushes and cactuses). *D. merriani* can be more fastidious in food selection than *D. nelsoni.*

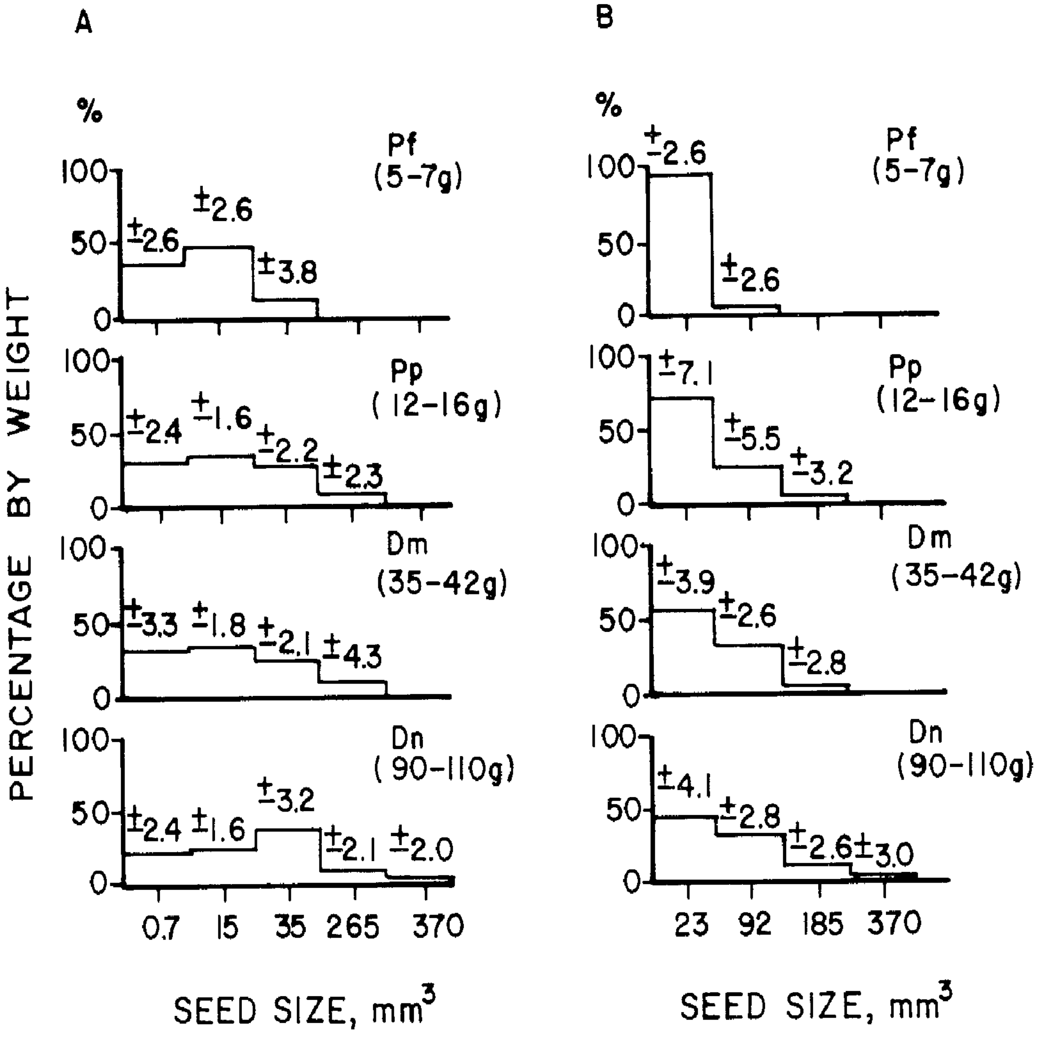

Figure 9.- Consumption of different sizes of seed from mangers by caged heteromyids from the Mapimí Biosphere Reserve. A. Percentage distribution by weight of different size classes of seed of different plant species : a - millet, b - rice, c - Prosopis seed, d - peas, e - peanut. B. Percentage distribution weight of different size classes of seed of one species (intact and fragmented peanuts were used). On the abscissa seed size (volume in mm^3); on the ordinate - mean percentage of 8 experiments with each species. Pf - Perognathus flavus Pp - P. penicillatus, Dm Dipodomys merriami, Dn - D. nelsoni.

Day rest burrows of *D. merriami* contain virtually no seed reserves (5 burrows were examined). This species carries in its cheek pouches the same composite plants seeds as *D. nelsoni*, but freed from pericarps, but rarely carries the heads of composite flowers. The fact that more than 70 per cent of *D.merriami* captured by net did not, as a rule, have seed in their cheek pouches points directly to a high probability that they are consumed not far from the site of collection. The close relationship with bushes shows the possibility for the arrangement (under their protection), of provisional pantries or otherwise the *in site* consumption of seed from the cheek pouches. The cheek pouches of *P. flavus* and *P. penicillatus* are always filled with depericarped seed. The absence of reserves in the permanent burrows of *P. penicillatus* unearthed by us, was possibly due to either the consumption of food at the foraging sites under the curtain of bushes or to

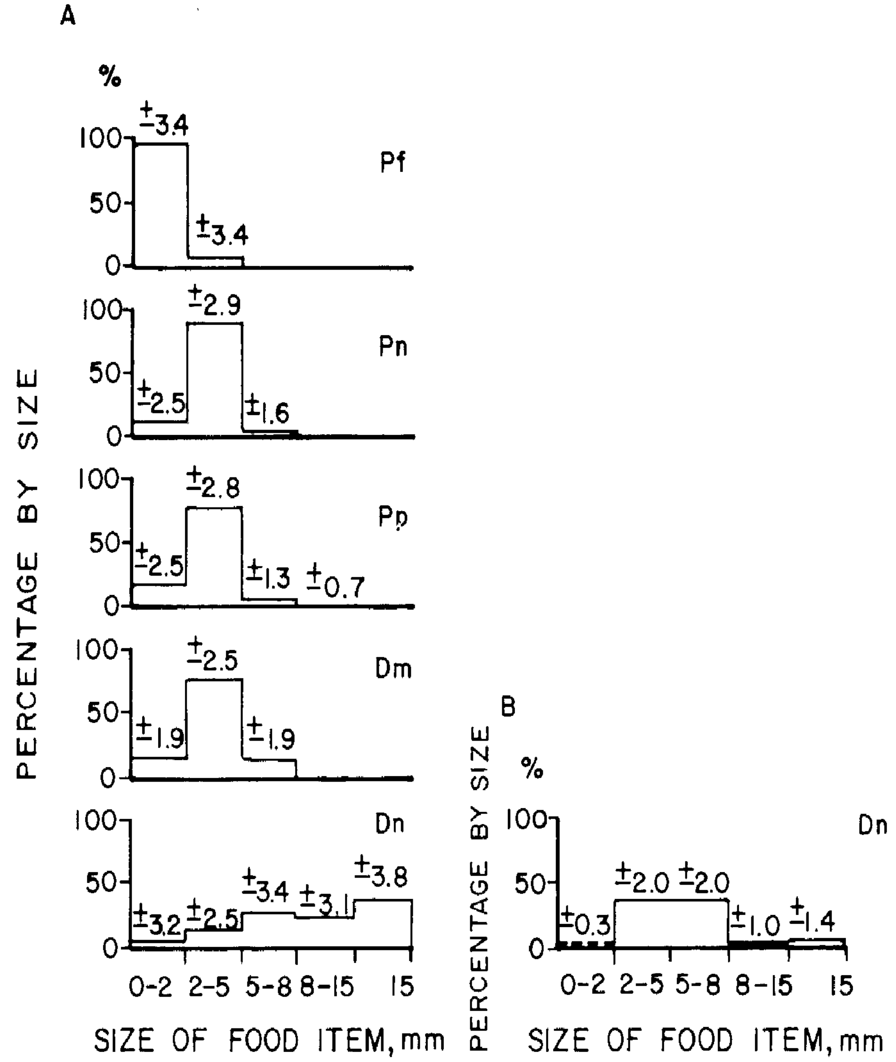

Figure 10.- Distribution of the size of food items from the cheek pouches of heteromiyds trapped in nature (Mapimí Biosphere Reserve; September - October, 1981, 1983, 1987). A. - seed and fruit; B. - seed without pericarps. Linear dimensions (the biggest length) of food items in mm on the abscissa; percentage occurrence of food items of each class on the ordinate.

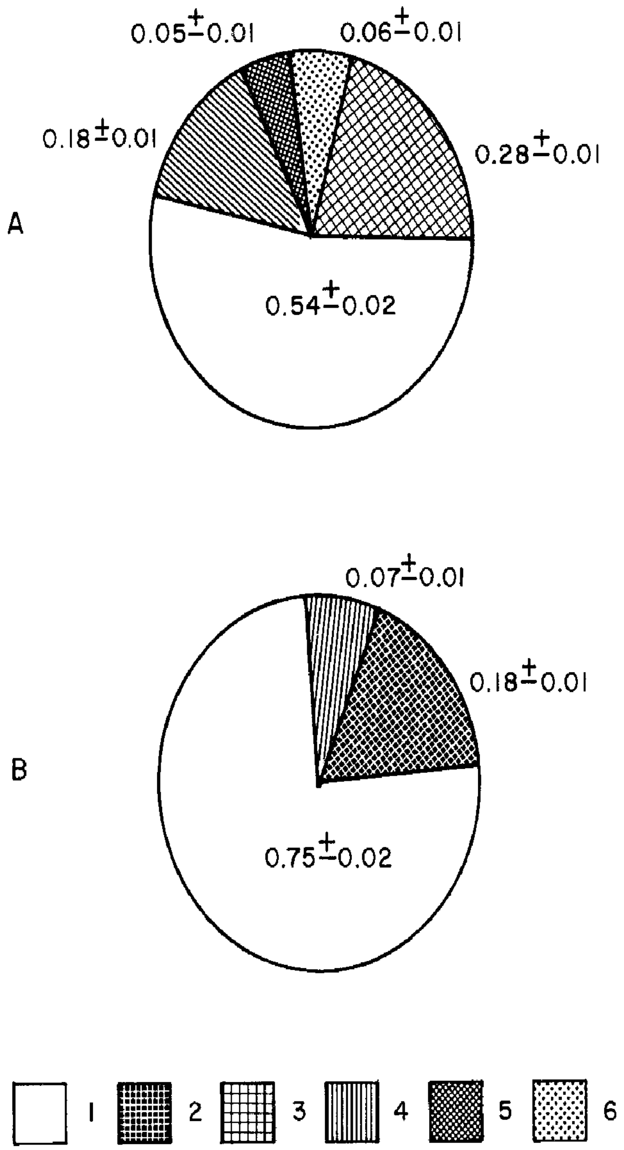

Figure 11. Proportion of different types of activity in the night time budget of two species of kangaroo rat (duration of the night about 11 hours) :

$$Pi = \frac{Mi}{\text{sum } Mi}$$

where Pi is the proportion of this type of activity in the total time budget, Mi - recording of i-type of activity during 1 min interval. Using the results of observations by torchlight. Observations were carried out at different periods of the night; then they were summarized to reproduce the general picture of activity. The conditions of illumination- the first quarter of the moon, air temperature - +18 - +22 C (Mapimí, Biosphere Reserve October, 1987). Radiotelemetry was used to find animals outside the burrows (transmitters were implanted in the abdominal cavity; a CE-12 receiver with 25 KHz channels was used). Total number of recordings ot the main types of *D. merriami* activity - 837; *D. nelsoni* - 691. Designations: 1 - presence in the burrow; 2 - on the surface of the burrow not farther than 1 m from its edge (*D. nelsoni*) 3 - under the curtain of bushes, 4 - in open area, 5 - harvesting food in an open patch, 6- -harvesting food under a bush.

its burial outside burrows. Reserves of seed in the cheek pouches of *P. nelsoni* and *P. penicillatus* caught with nets were found only in 12 per cent of animals. Although we have no data on the activity budget of *Perognathus* in nature, judging from our observations in laboratory conditions, P. nelsoni and *P.penicillatus* spend essentially more time outside a shelter than *D. merriami* and *D. nelsoni.* The differences from the results regarding the size of the seed harvested by heteromyids, as obtained by Brown and Liberman (1973) and Lemen (1978), are most probably due to differences in the methods used. The positive results of the former are due to the fact that they analyzed the linear dimensions of objects in the cheek pouches of rodents (unpeeled seed). However, dimensions of the seed could be substantially overlapped (see Fig. 10 a,b). Conversely, Lemen analyzed the weight of unhusked seed. It is interesting in this respect that the differences derived in the size of food items transported between species are directly related to the size of cheek pouches, whereas the relationship between the size of food items and of the maxillary apparatus is indirect. The interespecific variability in the volume of the cheek pouches is, apparently, substantially higher than the variability of linear dimensions of the maxillary apparatus. In two species of kangaroo rats of similar size, *D. ordii* and *D. merriami,* the cheed pouches of the former species are more developed.

The suggestion by Morton *et al.* (1980), that the transportation of husked seeds in cheek pouches by small heteromyids is accounted for by the peculiarities of their metabolic demands is rather interesting. However, we cannot but admit a certain reductionism in this approach. The large *D. nelsoni,* however, "can afford" to harvest low calorie food items, take them into the burrow, and then husk the seed. At the same time they "cannot afford" to run away too far from the burrow and stay away from it, and out of its protection for a long time due to the imperfectness of its bipedal locomotion as compared to genuine jerboas. If apredator is a constant threat to large *D. nelsoni,* then they would not have the time to select and husk food items at the site of harvesting. Differences in the content of cheek pouches of *Perognathus* and *Dipodomys* can also be explained by their differentiation in sites of harvest.

4. Differentiation of coexisting species by sites of seed harvest.

Numerous observations show that the spectra of seed harvested by coexisting heteromyids overlaps substantially (Smigel and Rosenzweig, 1974; Reichman, 1975; Stamp and Ohmart, 1978; O'Connell, 1979). Laboratory experiments also show an absence of differences between species of different size in seed preferences (Price and Brown, 1983). In nature, the largest overlapping of the food spectra in a desert takes place during mass vegetation and fructification of plants during the rainy season. The spectra of food items is broadly overlaped in the diets of species coexisting in one habitat. However, peculiarities in the distribution of seed cause these habitats to be of a heterogeneous nature (Price and Reichman, 1987). In such conditions the division of species by sites of collection of fodder resulting from different strategies of foraging behavior, is highly likely to occur (Reichman, 1975; Reichman and Oberstein, 1977; O'Connell, 1979; M'Closkey, 1980). Here we once again turn to the disputable problem of the causes of morphoecological differentiation of coexisting heteromyid species into quadrupedal and bipedal forms.

There is evidence that the Heteromyidae share the environment in accordance with differences in the choice of microhabitats. In the first Chapter we have already stated that quadrupedal *Perognathus* inhabit as a rule, areas with thick vegetation (Hall, 1946; Rosenzweig and Winakur, 1969; Brown and Liberman, 1973; Rosenzweig, 1973; Brown, 1975; Price, 1978 a, Wondolleck, 1978.), while bipedal *Dipodomys* are attracted to more open habitats with a low per cent of coverage (Hall,1946; Rosenzweig and Winakur, 1969; Brown and Liberman, 1973; Wondolleck, 1978; Price, 1978 a; Brown *et al.*, 1979.). These differences can be determined by differences in adaptive strategies for predator avoidance and by differences in foraging behavior in the heterogeneous environment. The heterogeneity of the environment caused by peculiarities in the distribution of seed occurs inevitably as a result of the patchy distribution of desert vegetation. Quantitative evidence to support this view was furnished by Nelson and Chew (1977), Thompson (1982 b), Reichman (1981), Price and Brown (1983), Price and Waser (1985), Rogovin (1988 a). It should be noted that the division of *Perognathus* and *Dipodomys* by preference for different microhabitats is not always the same. For instance, *D. merriami* ocasionally shows a distinct preference for open spaces (Brown and Liberman, 1973; Price, 1977, 1978 a; Price and Waser, 1985); in other cases a slight preference for open spaces or even complete absence of preference is noticed (Kotler, 1984 b, 1985 b); the absence of preference or a slightly higher preference for space covered with bushes is widely known (Wondolleck, 1978); and finally, full preference for areas with bushes over open space (Thompson, 1982 a) has also been recorded. These behavioral differences of *D. merriami* in different areas can be explained by differences in the structure of the habitat. Price and Waser (1985) showed that the peculiarities of the distribution of the Heteromyidae in the foraging process are substantially influenced by the soil structure, for this factor plays an important role in effectively harvesting seed.

It is also possible that an important role in the distribution of the Heteromyidae be played by the suitability of the substrate for the construction of shelters. For example, in the desert of Kazakhstan the close connection of the jerboa *Stilodipus telum* with burrows of a big gerbil (*Rhombomys opimus)* is caused by suitable conditions for the construction of its own shelters. The same is true of small gerbils (*Meriones meridianus, M. libicus*) in the deserts of Middle Asia. In all likelyhood, the functional peculiarities of the teeth (shape, angle, and the inclination of the incisors, front paws, and hind extremities together describe to an equal extent the adaptation of the jerboas to life on loose sandy or solid clay soils (Vinogradov, 1937, Zubtsova, 1980; Gambaryan *et al.*, 1980). The claws of the front paws as well as the incisors are the main instruments used in digging burrows.

In this way the structural complexity of the environment, determined by the interaction of many factors and their multiple influence may lead to different response to a certain environmental feature, particularly limited in pilot areas. Considering the independent impact of different factors (for instance: the distribution of vegetation, distribution of seed and their accessibility depending on the structure of soil) we may expect different parameters for their impact on different pilot plots. Therefore before we take up the study of the mechanism for the partition of resources by species, it is important to analyze the interrelationship of the environmental conditions and resources with the species response to them to distinguish the leading and independently acting factors (Shenbrot, 1988; Puzachenko *et al.*, 1990, in press). Regrettably, this stage is generally omitted in discussing the mechanisms of the partition of microhabitats by the Heteromyidae. Differences in the attitude of *D. merriami* may also be accounted for by the structural elements of the habitat and the peculiarity of the response of the species to the means of recording in nature. In Bolsón de Mapimí differentiation between quadrupedal and bipedal forms by their attachment to bushes is manifested even more strongly if recording is performed using Sherman's traps. When using mangers with a standard bait (the presence of species was assertained by tracks left on the smoked plates) the differentiation of species by preference is substantially weaker (Tables 9,10).

The result obtained could logically be explained as follows: traps being more complicated attracting devices than mangers, require a prolonged time for exploration until an animal enters and in this respect it describes more representatively the difference in probability for the presence of the species in open spaces as well as those protected by bushes during foraging. Besides, traps in open spaces can be interpreted as additional shelters by *D. merriami,* when harvesting seed close to them. Frequent entries of *Perognathus* to mangers located in open areas shows that *Perognathus* keeps under control, (*i.e.* examines the whole area, irrespective of the pattern of distribution of shelters). Judging by the results of direct observations of *D. merriami* in the bush desert in Mapimí, the encounters with individuals were evenly distributed between the open area and the area under the cover of creosote bush. Yet, considering that the area occupied by bushes is much smaller than the open area , the bush attachment by this species can be considered proved (Table 11). It is true that during prolonged observations of individual species under the cover of bushes, the duration of locomotion under cover in comparison to the period of rest, was substantially shorter here than in the open areas. As for *Perognathus,* almost all of the encounters of animals occurred near the bushes wether under the crown of the bush, *P. penicillatus* unlike *D. merriami* remained mobile even after they were alerted.

Table 9.- The attitude of coexisting Mapimí rodent species to shelters (frequency of registrations under the crowns of bushes) assured by the results of Sherman traps and also by the occurrence of tracks on mangers. (Traps were placed in the center of squares 20 m side (25 squares per 1 hectare) in pairs - one trap in the bush, another - in the open space. Mangers were placed one in a square; alternating squares: in one - a manger at the bush, in another - in the open space. Total number of squares (registered samples) in different habitats - 2550). ** P<0.01,N - number of registers of the species.

Species	Occurence under bushes				t/criterion
	on mangers	N	entrapped with Sherman traps	N	
P. nelsoni	0.48 ± 0.09	35	0.78 ± 0.06	55	2.77 **
P. penicillatus	0.65 ± 0.08	35	0.63 ± 0.07	45	0.19
D. merriami	0.44 ± 0.04	127	0.28 ± 0.04	137	2.82 **
D. nelsoni	0.50 ± 0.11	22	0.25 ± 0.08	32	1.84
P. eremicus	0.87 ± 0.06	31	0.80 ± 0.05	61	0.89
N. albigula	0.85 ± 0.05	48	0.93 ± 0.05	27	1.13

A number of laboratory experiments show that the Heteromyidae, in spite of differing in size as well as in peculiarities of the morphology, divide the environment in line with variations in the density of the distribution of seeds at different points in the area (Reichman and Oberstein, 1977; Price, 1978 b; Hutto, 1978; Reichman, 1981). Small quadrupedal species of the Heteromyidae harvest mainly diffusely distributed single seeds. Such a distribution of seeds is indicative of areas surrounding bush in nature. Larger bipedal species of the *Dipodomys* genus actively look for seed accumulations. Such dense accumulations in desert conditions often occur in the open space in microdepressions of the relief. These results are also confirmed by some experimental data according to which the bipedal type of locomotion (unlike quadrupedal) is energetically more beneficial at high velocity (Dawson and Taylor, 1973; Dawson, 1976). It follows that bipedal forms can rapidly cross open areas of deserts in search for sites rich with food and by finding it, utilizing quickly while remaining almost immobile. This conservative approach has its evident drawbacks. Firstly, energy efficiency of fast bipedal locomotion can be successfully used in explaining bipedality as the strategy used to avoid a predator. Secondly, field observations show in a number of cases the absence of the division of species of different sizes by preferences of the types of seed distribution (Frye and Rosenzweig, 1980; Price and Brown, 1983; Benrends, 1986).

Table 10. Parameters of the t/criterion when comparing different species of coexisting heteromyids by their attitude towards shelters. Above the diagonal - registers on mangers; below the diagonal - entrapping into Sherman traps. * P<0.05;** P<0.01;*** P<0.001.

Species	*P. Nelsoni*	*P. peniccilatus*	*D. merriami*	*D. nelsoni*
P. nelsoni		1.40	0.41	0.14
P. penicillatus	1.62	-	2.30*	1.10
D. merriami	6.93***	4.34***	-	0.51
D. nelsoni	5.30***	3.57***	0.34	-

Our observations of *D. merriami* on moonless nights show that animals are able to move slowly over open areas harvesting the fallen seeds of composite flowers, or cutting off the heads of the composite flowers moving from one plant to another for distances of the order of 1-2 meters. The rate of movement in open areas and under the cover of bushes is virtually the same. Crossing of open spaces at high speed is used only in case of danger (for instance, when started) and takes place often on moonlit nights (Table 3).

Finally, experimental data on the energy cost of bipedal and quadrupedal locomotion are rather contradictory. Using different groups of animals, including lizards, birds, bipedal and quadrupedal mammals, Paladino and King (1979) failed to reveal differences in the energy of locomotion between bipedal and quadrupedal species. Some more accurate data on bipedal rodents permit to assume that the beginning of the plateau in the initially direct dependence of the level of oxigen consumption on the speed of the run on the treadmill is related to switching on to glycolysis and therefore, is in no way related to the mechanism

Table 11.- Use of microhabitats by three species of the Heteromyidae family in the creosote desert of Mapimí grassland by the results of registered animals by the light of the torch. Three types of recording sites were determined: in the bush (1 m), in the burrow, and in the open space (1 m). Expected distributions in line with the distribution of elements of the habitat structure are indicated in brackets. The significance of the difference from expected distributions was evaluated by the criterion X^2: * P<0.05;** P<0.01;*** P<0.001.N- number of registered species.

Species	N	Elements of habitat structure (P m, %)			X -criterion
		bushes	burrows	open space	
		(21 %)	(-)	(79 %)	
		(-)	(5 %)	(95 %)	
P. penicillatus	20	70 ± 11	-	30 ± 11	31.3***
D. merriami	65	54 ± 6	-	46 ± 6	40.1***
D. nelsoni	23	26 ± 9	-	74 ± 9	0.25
D. nelsoni	96	-	47 ± 5	53 ± 5	340***

of energy saving, which is related to the energy stored in muscles (Baudinette *et* al., 1976; Thompson *et al.*, 1980). The existence of this mechanism can be confirmed by data obtained at the stage of aerobic oxidation. In addition, experimental studies on the energy cost of different gaits may provide substantial errors in measuring the ultimate possibilities for the species when using this or other gait in locomotion. The use of treadmill results in the fact that the velocity of transition from the quadrupedal to bipedal type of locomotion turns out to be too high as compared to the natural one. It is influenced by different levels of training of animals that are kept in cages, etc.

Much work is still to be done on the problem of the energy costs of different types of locomotion. According to Hoyt and Taylor (1981) the non-linear dependence of the metabolic level on the rate of locomotion with each type of the pace shows that animals have to choose the optimal regime of locomotion.

Judging by observations of low rate (foraging) movements of kangaroo rats in nature, always lean on the substrate with their front paws, *i.e.* behave as quadrupedal ricocheting forms. Leaning on the substrate in the locomotion cycles is, as a rule, absent even at low rates of locomotion in the majority of obligate bipedal jerboas of Allactaginae and Dipodinae subfamilies. The appearance of a peculiar symmetrical pace (bipedal trot) in jerboas specialized in high-speed bipedal locomotion is, possibly, correlated with the high energy cost of bipedal saltation at a low speed. It can be explained by a mechanism of bipedal saltation. At a low speed the work of the tail in the vertical plane cannot annul the torque that appears during the push and landing. On the contrary, as was showed by Fokin (1978), while hopping at high velocity the angle of inclination of the axis of the jerboa's body with respect to the substrate surface remains virtually unchanged. This is achieved by rhythmic movements of the tail in the opposite direction to that of the movement of the extremeties (Fig. 12). Our observations of *Pygerethmus pygmaeus* with partially amputated tails showed a substantial reduction in stability of the position of the body and the fall of the ultimate velocity from 7.1 m/sec to 4 - 5.2 m/sec. It is indicative that bipedal symmetrical trot pace appears independently and in parallel in the Allactaginae and Dipodinae families, yet it is more indicative of big species. Observations in nature of these forms show that during quick feeding, jerboas use either a step or a slow trot. In this way they achieve the most stable position of the body with respect to the surface of the ground and the front paws are not used for leaning.

In this way peculiarities in the locomotion of jerboas point to the reality of the energy effectiveness of the fast bipedal saltation. The first stages of this development can be seen in the Heteromyidae. A more profound insight into the problem could be provided by further studies of the energetics of locomotion performed on different species of bipedal rodents, and by direct observations in nature.

Price (1981, 1983) developed a simple model that establishes an interrelationship between body size and the choice of microhabitat by heteromyids in a desert with a patchy seed distribution. Since the rate of foraging, the speed of travel and the metabolic cost are allometric functions of body size, the latter can determine the degree to which an animal will specialize on the most profitable patches. In this connection, the concept that a certain degree of differentiation in the area used by quadrupedal and bipedal forms can be related to the expansion of the foraging area by big species does not contradict the model. In other words, it seems to us quite logical to relate the evolution of bipedal heteromyids not to the differentiation of species by the types of seed distribution in a patchy environment, but to the intensification of exploitation of the space of home ranges. This hypothesis was not given due attention until recently.

It is quite possible that differentiation by size of the ancestral forms of the recent Heteromyidae occured and served as a type of preadaptation to assimilation by large forms of small open areas which emerged as a result of the aridization of the territory. This hypothesis is supported by the above results of our observations of the behavior of *D. merriami* and *D. nelsoni* in their home ranges. It is also supported by experimental findings. On moonless nights animals were given the opportunity to chose between open squares and squares protected by bushes in an open- air cage with an even distribution of seed accumulation. In these experiments *Dipodomys* used the unprotected as well as the protected squares for foraging with the same probability whereas *Perognathus* foraged mainly close to the bushes. (Table 12). In our experiments the response of the species was greatly dependent on the size of the open-air cage (as well as on the conditions of the distribution of vegetation in nature); The distances between food sources and bushes closely resembled the least diameter of the open areas in the bushy creosote desert (Pastizal) where we studied marked *D. merriami* and *D. nelsoni*.

Table 12.- Results of foraging of coexisting heteromyid species close to a bush and in the open space in experimental conditions. (An open-air cage (4m x 4m) divided into 4 squares $4m^2$ each. A creosote bush was placed in the center of two diagonal squares). Four mangers with abundant of seeds were placed one in each square. Only adult males were used. * $P<0.05$; ** $P<0.01$; *** $P<0.001$, N - number of experiments.

Species	N	mean percentage of seed collection		t - criterion
		in the bush	in the open space	
P. penicillatus	10	46.7 ± 8.6	12.7 ± 5.1	t = 3.4 **
D. merriami	10	21.1 ± 6.9	19.7 ± 5.7	t = 0.18
D. nelsoni	10	48.5 ± 9.5	39.1 ± 6	t = 0.81

4. Experimental evidence of the role of competition in microhabitat partitioning by coexisting species.

The attempts to prove experimentally the presence of competition for food resources in communities based on the assessment of the success of reproduction in the presence and absence of a potential competitor will not be analyzed. A detailed criticism of this approach has been given by Shenbrot (1986 b). If the response of the population is assessed without preliminary fencing off sampling, the main obstacle for assessment is the impossibility of completely withdrawing one of the species without provoking the subsequent immigration from adjacent areas. If experimental plots are first fenced off there is intraspecific competition

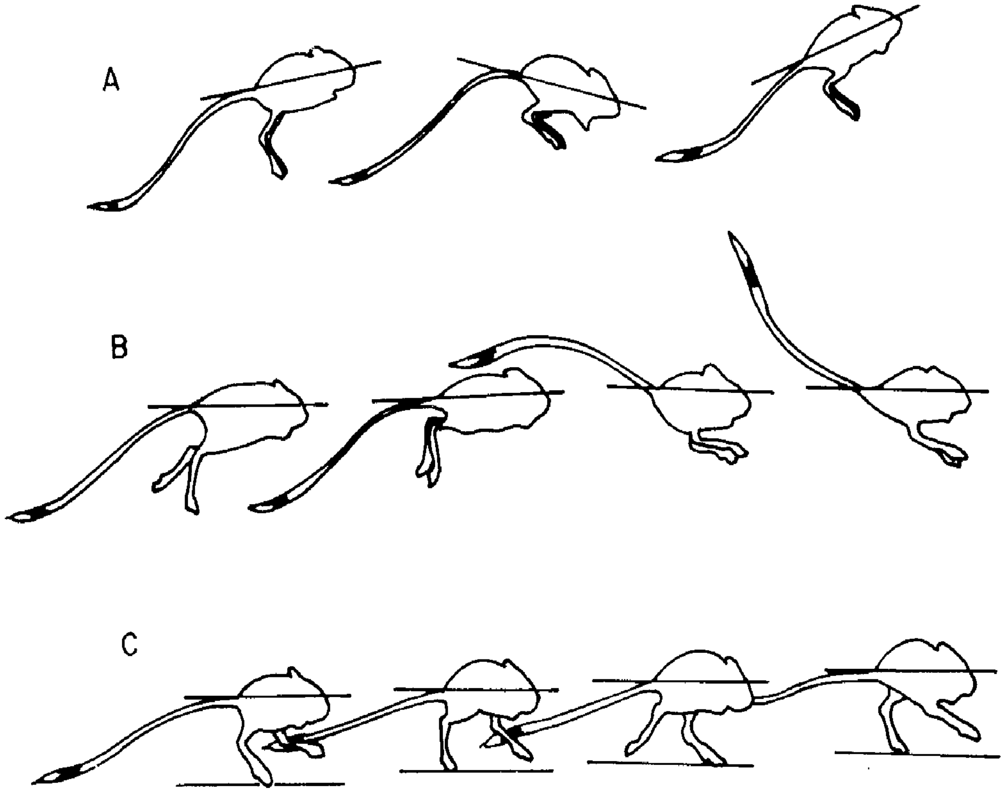

Figure 12.- Position of the jerboa body with respect to the surface of the substrate while hoping at low (A) and high (B) velocity and moving to a slow trot (C).

due to the disturbance of social structure. Needless to say in such experiments (held in field conditions), it is extremely difficult to select similar experimental and control plots. The most significant long term field experiment of this kind is the study by Munger and Brown (1981) who used a semi-permeable fence. These authors noted an increase in the density of population of *Perognathus* when the much bigger *Dipodomys* were unable to penetrate into the enclosure while *Perognathus* moved freely in both directions (see also Brown *et al.*, 1986). However, even in such an experiment, an increase in the reproductive success of *Perognathus* cannot be related only to the absence of competition with *Dipodomys*. The possibility of the impact of other factors related to the differences in conditions between experimental and control plots cannot be overruled (Mares, 1983; Munger *et al.*, 1983; Price and Brown, 1983).

More interesting for us are the experiments that allow one to register the response of another species directly after the withdrawal of animals of one species. After the stress is lifted, the species which is exposed to competition changes its microhabitat attachment. For instance, in experiments on withdrawing *Dipodomys, Perognathus* expanded the habitat area used (Wondolleck, 1978; Price, 1978 a; Lemen and Freeman, 1987). In another case the withdrawal of *Onichomys leucogaster* led to *D. merriami* to begin to feed not only in the open area, but also under the crowns where the hamster used to sit (Rebar and Conley, 1983). A small bipedal *Microdipodops megacephalus* changed the character of its foraging in the presence of large specimens of *Dipodomys*. Small *M. megacephalus* scattered seeds in the presence of big kangaroo rats and in their absence, prefer seed accumulations (Harris, 1984). These experiments are strong evidence of the reality of competition among coexisting species. However, they do not exclude the possibility for criticism. In itself, the withdrawal of animals of one species changes conditions not only for another species, but for a predator as well. The latter may increase its pressure on the population of the other prey species. In other words, the competition effect can be diminished by the influence of a predator (Price and Brown, 1983).

Experiments with the withdrawal of one of the species generally fail to reveal the causes of the registered effect of competition. These reasons could be both the competition for food resources and interference competition which is based on the peculiarities of interspecific territorial behavior. There are diverse data, pointing to the aggression of *Dipodomys* towards the smaller *Perognathus* (Hutto, 1978; Trombulak and Kenagy, 1980; Lemen and Freeman, 1987) or the aggression of big *Dipodomys* towards the smaller ones (Congdon, 1974). Although some authors note that fodder provision in the natural communities of the Heteromyidae is not so low as to justify purely economically the interspecific aggression (Brown and Liberman, 1973; Brown *et al.*, 1979; Bowers and Brown, 1982), these remarks are of a speculative nature. In the meantime there are many data on different groups of vertebrates showing that interspecific aggression is the result of intraspecific behavioral stereotypes and at least is not related to competition for food resources (Ivanitsky,1986). Our studies on the interrelationships of seed-eating pygmy jerboas of the *Salpingotus* genus in conditions of syntopy in the Trans Altai Gobi (Mongolia) show that the more aggressive species *S. crassicauda* is unable to change the microhabitat distribution of another species (*e.g. S. kozlovi*). In experimental conditions each of the species living alone used pre-bush space with sand drifts (Table 4), whereas in nature *S. kozlovi* occurs in prebush sand drifts whereas the distribution of *S. crassicauda* is independent of bushes (weak negative conjugation is not significant (Table 13). Pre bush sand drifts are the main sites for seed concentration. Negative conjugation of two species in nature and in the laboratory demonstrated the attraction of both species towards sand drifts, suggesting the presence of competition between them. However these relationships may be exploitative and interference competition. In the latter case the success of the species in the interspecific social hierarchy is enhanced proportionally to its adaptation to the type of microhabitat. *S. kozlovi* is a more morphologically specialized species which harvests seeds and insects from the surface of the loose sand layer (Rogovin, 1988 a).

On the other hand the role of interspecific aggression in the partitioning of microhabitats in heteromyid species is quite real, and is due not to the shortage of food resources, but to the shortage of shelter.

Doubtlessly, the competition for shelter does not fully reflect the essence of the phenomenon. It is difficult to imagine a shortage of bushes in nature. In practice there is ousting by certain species of other species either by direct aggression or by the subordinate species avoiding contact.

These considerations are well illustrated by our observations of the behavior of coexisting species of heteromyids in a combined group in an open-air cage limited by space. Creosote bushes were used as shelter, the structure of the natural habitat was reproduced, and the sources of fodder were evenly distributed: one in each of the four squares (Tables 14 and 15). A linear hierarchy of relationships positively related to the size of species, became evident in each group of three species males of different species). Big *D. nelsoni* dominated in terms of the number of aggressive acts initiated by him against *P. penicillatus* and *D. merriami;* whereas *D. merriami* (intermediate in size) dominated only over *P. penicillatus.* It is of importance that the number of aggressive attacks addressed by the first dominant to the phylogenetically close *D. merriami* was significantly higher ($t = 4.46$, $P < 0.01$) than that addressed to the more distant *P. penicillatus.* In these experiments, with two separate shelters, small *P. penicillatus* spent more time as compared to control, in the open squares; whereas *D. merriami* spent somewhat more time in shelter. *D. nelsoni* used the space of an open-air cage evenly and often started *D. merriami* from one shelter, making him escape into another.

Table 13.- Field registrationsof conjugation coefficientsof *S. crassicauda* and *S. kozlovi* for the same of each species with pre-bush sand driftsin the Trans-Altai Gobi desert (Mongolia), and intraspecific aggressiveness assesed by the results of experimental encounters of males of each species in a neutral territory. To determinethe conjugation we used the tetrachoric conjugation coefficientwith the assessment of the significanceby means of X^2. The field data were obtained by recording tracks of paws and tails on small grain sand plots of 0.5m x 0.5 m. The plots were located under the bushes and in the opened space with a gravel cover. The intraspecific behavior was studied in series of pair encounters of sexually active adult males of each species in a 1m x 1m open-air cage; 20 tests with each species. ** $P<0.01$;*** $P<0.001$.N - number of test plots with sunflower seed bait.

Species	**N**	**Species**		**Environmental conditions (eolian sand drift under the bush)**	**Intraspecific aggression,**
		S. kozlovi	*S.crassi-cauda*		
S. kozlovi	198	-	- 0.22**	+0.20**	0.5 ± 0.2
S. crassi-cauda	198	- 0.22**	-	- 0.09	68 ± 0.
					t = 6.8* **

5.- Segregation of spatial niches as the result of equilibium between competing populations.

Rosenzweig model (1979, 1981) of the partition of habitats by interacting populations is based on the concept of the leading role of competition for limited resources. If species "A" prefers foraging habitat "a" to "b", with the exhaustion of resources "a" and with the growth of the number of "A" specimens, then some of its individuals will resettle in habitat "b". This will take place at a time when the

Table 14. Behavior of coexisting heteromyid species in the "competition for shelter" experiment. Three males (one male of each three species) were placed in an open-air cage (see description to Table 12); the reaction of each of male to a heterospecific partner was registered. The table shows the results of 11 tests. The significance of differences was determined by the t-criterion : * P <0.05; ** P <0.01; *** P <0.001.

Reacting species	Type of reaction to a heterospecific partner	Mean number of cases of reaction to a heterospecific partner			t-criterion
		P.p.	D.m.	D.n.	
P. penicillatus	attack	-	0	-	-
	avoidance	-	2.6+0.8	3.6+0.8	0.88
D. merriami	attack	1.0+0.3	-	0.2+0.1	2.52*
	avoidance	0.5+0.4	-	8.0+1.3	5.51***
D. nelsoni	attact	1.9+0.5	7.3+1.1	-	4.46**
	avoidance	0	0.6+0.5	-	1.2

success of foraging in habitats "a" and "b" becomes even. This situation is often observed in nature when the species occupies one habitat at a low population density; when the population density is higher, them the number of occupied habitats is increased. In the case of the presence of species "B", which prefers habitat "b", there is a gradual degradation of the base of resources in "b", since species "B" is more effective in its habitat, as a result of which species "A" in habitat "b" becomes the "loser" and is once again forced out into habitat "A". The habitat division by species "A" and "B" represents a state of unstable equilibrium.

Table 15. Conjugation of coexisting heteromyid species with shelters in the absence and presence of heterospecifics. Three males (one male) of each three species was placed simultaneously in an open-air cage (see description to Table 12). The location of each of these species was registered every 10 minutes. The tetrachoric coefficient of conjugation was used. Evaluation of the significance was performed by the X^2-criterion: * $P<0.05$;** $P<0.01$;*** $P<0.001$. N - the number of registers of the species within the square with shelter in the open-air cage. Ten tests were performed with each species.

Species	In the absence of other species	N	In the presence of sintopic species	N
P. penicillatus (5 males)	+0.6***	92	-0.6***	105
D. merriami (5 males)	+0.3**	126	+0.4***	1.11
D. nelsoni (3 males, 2 females)	+0.3**	82	0.0	59

The use of this model in explaining the natural situations is rather limited in spite of all its logic, first, as already mentioned, the division of habitats by species may represent a stable state in which populations are adapted to different conditions to such an extent that there is their parapatric existence. Interactions in boundary habitats are the result of the forcing out of the part of population that do not find suitable ranges (juveniles and males) (Schroder and Rosenzweig, 1375). Secondly, this model does not consider the possibility of the effects of interspecific aggression. A skeptical attitude to the possibility of partition of habitats on the basis of interference (Ivanitsky, 1986) is based on the fact that recorded interactions between species in mixed groups do not affect the success of reproduction of any of these populations. Yet, in the majority of these cases we see equilibrium systems balanced by selection.

The question of the compatibility of social systems of rodents as the mechanism that permits the coexistence of species within one habitat has not been studied yet. Up to date there are no grounds for believing that the biotopic and the geographical separation of many species is a direct result of interspecific interactions. An alternative hypothesis is that on the evolution of populations in isolation that occurred due to these or other reasons (Mayr, 1968, 1974). The fact that potentially competing species (granivorous species of similar sizes) rarely occur within one habitat and have more separated areas than is asserted by the null hypothesis (Bowers and Brown, 1982) cannot be taken as evidence in favor of the primary role of competition. Yet the concept of the secondary role of the mechanism of interspecific competition in ordering the interrelationships of species in communities during the secondary contact of populations is quite logical. In this process interspecific territorial behavior may have even greater significance than competition for resources. A high level of variability of structures of social systems in groups of phylogenetically and ecologically related species (Ivanitsky, 1980, 1982; Goltsman *et al.*, 1981; Panov, 1983; Popov, 1986) indicates that the restructuring of social behavior may take place faster than the restructuring of the main phenomena of ecology. The mechanism of this restructuring is, as a rule, a change in the level of excitability, reactivity of the central nervous system and, respectively, thresholds of reaction to the presence of conspecifics or heterospecifics. In all likelihood such a restructuring develops in the course of evolution and does not require essential changes in physiology, such as the transition to another type of food. Since the level of reactivity of behavior is usually negatively related to body size, it would be logical to suggest that the possibility of coexistence with species of different weights be determined by the possibility of compatibility between their systems of social behavior.

Analyzing the results of Shenbrot (1982) on the Turan jerboa community (Middle Asia), it is evident that the pairs with maximally overlapping structural and tropical niches often include species differing essentially in size. Yet species of some structural guilds are either ecologically plastic in the choice of food (*Allactaga severtzovi - A. elater; A. jaculus - Pygerethmus pygmaeus, A. severtzovi - P. pygmaeus*) or feed on green plants which are not as limited as seeds (*P. pygmaeus -Jaculus turcmenicus, Alactodipus bobrinskii - J. turcmenicus*). Our observations on coexisting populations of jerboas in Kazakhstan - *A. jaculus and P. pygmaeus* - revealed that the big aggressive species *A. jaculus* does not react to the small *P. pygmaeus* (Table 16). The latter either actively avoids contacts with *A. jaculus* or does not react to it, strictly keeping a distance of 3 or more meters. The same is indicative of interactions between *A. jaculus* and *A. elater*, and also *A. evertzovi* and *A. elater*. Intraspecific relationships in natural populations of *A. elater* and *P. pygmaeus* takes place on the basis of active avoidance of encounters. The role of direct aggression in ordering relations between individuals in local intraspecific groups is insignificant (Rogovin, 1983, 1985). It is quite possible that this type of relationships in coexisting populations is specific of jerboas. Provided they are highly mobile and have large home ranges, jerboas have a tendency to reduce aggressive territorial behavior. When a conspecific stranger was placed into a cage with a jerboa, the owner of the territory did not show an aggressive reaction; but in the case of *Meriones meridianus*, the number of aggressive attacks of the owner of the territory on a stranger was significant ($P < 0.999$). Similar behavior is registered in kangaroo rats (*D. merriami*) (Table 17).

In this way the data given in this Chapter and the results of numerous studies performed in communities of rodents point to the diversity of both natural and experimental situations. The role of interspecific competition remains possible, sometimes highly probable, but not a compulsory factor in the structuring of communities of desert rodents.

Table 16.- Interspecific social relations in local assamblages of jerboas in nature. (Probability of different types of behavior per encounter. Encounters were observed by torch-light in plots with marked animals).

Pairs of co-existing species	Region	Number of registers (<5m between animals)	Reaction to other species		
			attack	no reaction	avoidance
A. jaculus	West Kazakhstan	46	0.11+0.05	0.85+0.05	0
P. pygmaeus			0	0.46+0.07	0.54+0.07
A. jaculus	West Kazakhstan	12	0.08+0.08	0.92+0.08	0
A. elater			0	0.16+0.11	0.84+0.11
A. severtzovi	Central Kyzylkum	38	0.24+0.07	0.68+0.08	0.10+0.05
A. elater			0	0.42+0.08	0.58+0.08

Table 17.- The type and direction of teritorial responce to a stranger (mean parameter) in 4 species of desert rodents with different forms of territoriality. The stranger was placed into a cage with a resident after a three day adaptation. (Dimension of cages : S. crassicauda - 0.6m x 0.6m ; other species - 1m x 1m. Duration of the test - 10 min.). * P<0.05; ** P<0.01; *** P<0.001.

Species	Number of tests	Initiator of interaction	Forms of interactions (X+m)					
			approach	t-criterion	retreat	t-criterion	aggression	t-criterion
S. crassicauda	15	stranger	2.2±0.4	0.31	4.8±0.9	2.22*	0.7±0.3	1.64
		resident	2.4±0.5		2.4±0.6		1.8±0.6	
D.sagitta	15	stranger	6.0±0.8	0.80	2.7±0.5	2.50*	0.3±0.1	1.41
		resident	5.2±0.6		1.1±0.4		0.5±0.1	
M.meridianus	10	stranger	0.5±0.1	16.99***	12.3±0.7	17.03***	0.3+0.1	1961***
		resident	14.2±0.8		0.3±0.08		6.5±0.3	
D.merriami	8	stranger	-	-	10.0±1.0	5.65***	2.0±0.6	382***
		resident	-	-	3.1±0.7	-	6.4±1.0	

DISCUSSION: PERSPECTIVES OF RESEARCH.

The debate with respect to the role of predators as well as competition in the evolution of communities of desert rodents is conditioned by two types of cause. The first of them is the insufficient attention paid by scholars to the possibility of the alternative interpretations of correlations observed in nature. A certain subjectivism in thinking has not been overcome due to a long term domination of a one factor approach to the causes of morpho-ecological diversity of species in communities. The result is, as a rule, the absence of large-scale comparative studies on the structural aspects of organization of communities.

A comparative ecological study of the breadth and overlap of niches, and the distribution of niches in multidimensional ecological spaces in a number of diverse communities is, in principle, aimed at the discovery of so-called structural explanations (Nikitin, 1970). The essence of these explanations resides in the design of generalized schemes, therefore, demonstrating the interrelationship between the main inner properties of objects. These structural explanations area necessary stage of research, which makes it possible to develop hypotheses on the causes and functions of the existing order of relations between system elements. Such hypotheses, which already relate to the categories of explanations of cause and effect (Nikitin, 1970), assume the necessity of additional, more sophisticated observations as well as experiments in strictly controlled conditions. It is in this context that we should analyze the possibilities of comparative ecological research into the structure of animal communities.

The structural approach possesses certain limitations in the synonymous interpretation of the mechanisms of forming structural regularities on the following grounds (Colwell and Winkler, 1984; Strong et al., 1984; Price, 1986:

1/ There is no single explanation of the phenomenon from the effects to observe, provided that we are unaware of the processes that determine these effects;

2/ It is extremely difficult, if not impossible, to determine in which cases different factors (directions of election) determine different effects, and in which cases these effects are similar;

3/ Structural analysis is based on the premise that correlations can be identified. Due to the multiple impact of factors and the possibility of indirect relationships, there is always the risk that a really acting factor remains unrecorded;

4/ There is no possibility to quantitatively assess the parameters of a factor that actually operates (for instance, the parameter of intensity of competition).

The second reason for different viewpoints on the structuring factors of desert rodent communities is the limitation of the experimental approaches used for testing hypotheses. These methods enable us to artificially eliminate the impact of this or other factor, but do not provide ground for expecting the same response from the animal. Quite naturally the behavioral response of the species represents an integrated inherited response to multi-factor impacts. The relative role of factors may change in the evolutionary process and the effects of differently oriented selection pressures at different stages turn out to be imprinted in behavioral stereotypes as well as in the morphological organization as a whole. From this viewpoint the absence of a positive or negative response of the species to the manipulation of resources, predators as well as other species cannot be a reason for rejecting the tested hypothesis. Generally speaking, the main limitations of the experimental approach can be presented as follows (Price, 1986). Some of them are the same as those for the structural approach.

1/ Indirect impacts which are ignored by the scholar often affect experimental findings . This is mostly applied to the initial conditions of experiments in nature;

2/ Unrealistic conditions of laboratory experiments which provoke an inadequate response from the animals. The conclusions drawn from such experiments will yield but little information on the situation in nature;

3/ Negative results show either that the factor is not effective or that the conditions of the experiment do not tally with the set objective;

4/ In an experimental approach, the scientist splits a single integrated system of animal behavioral responses, paying attention to one side of the relationship only, ignoring the other;

5/ Both laboratory and field experiments reveal only minor effects, failing to show the possible impact of a factor in the past.

Thus, positive results in tests conducted to investigate the role of predators or of competition can be expected only if factors operate so as to induce an opposite responses in the species. In the case when the behavior of an animal is such that it reduces the risk of being caught by a predator, but, at the same time increase to the same extent the success of foraging, the possibility of giving preference to this or other hypothesis is in principle absent (Price and Brown, 1983; Price, 1986). An optimistic standpoint on this issue is justified by the fact that the relationships of effective avoidance of a predator and effectiveness of foraging in concrete habitat conditions can not compensate for each other. In seems unlikely that the most profitable patches from a harvest efficiency point of view will consistently be the least risky as well. In practice, the relationships between different forms of behavior recorded in nature are not usually analyzed from the standpoint of costs (risk) and benefit (reproductive success) during foraging. The very fact that the protective behavior and the harvest mode are mutually related is no longer doubted. This can be adequately illustrated through the results of our analysis of the interdependence between reproductive strategies within the family of jerboas (20 species) and such measures as body weight, the maximum speed of the run, the number of burrows used per animal, the maximum radius of the home range, the diversity of fodder used and the level of consumption of green plants (Table 18).

The results of the Principal Component Analysis (Table 19) show that the reproductive ability of species (maximum birth-rate, duration of maturation) is, in fact, independent of the characteristics related to adaptation to high-speed bipedal runs (body weight, home range size, diversity of diet), on the one hand, and the characteristics related to the number of burrows used and feeding on nonlimited types of food on the other. This result points to the absence of a direct influence of trophic adaptation and predators on the evolution of reproductive strategies within a family. Thus, it does not seem possible to hypothesize

Table 18.- Peculiarities of demography and ecology of jerboas in Middle and Central Asia. (The Table uses the data by : 1) Mazin, 1973; 2) Fokin, 1978; 3) Shenbrot, 1980 and also the results of the observations by the author).

1* - distance from the geometrical center of the home range to the most distant point of register of an animal (mean parameters); ** - entropy measure of diversity: $H = - \quad P_i \log_2 P_i$; *** - proportion of green fodder by its volume in the stomach content.

Species	Max. anual birth-rate (pups number)	Max. age in nature (years)	Min. duration of maturation (months)	Body weight (g)	Max. velocity of locomotion (m/sec)	Number burrows per animal used simultaneously	Radius of home range (m) *	Diet diversity **	Degree of herbivoriness ***
E. naso	7	3	10	34	8	1	216	0.62	0.01
C. paradoxus	4	2	10	12	2.4	1	47	0.1	0.05
S. crassicauda	7(3	2	8	11	1.6(2	1	50	0.2	0.02
S. kozlovi	4	2	10	12	2.1	1	50	0.2	0.02
A. jaculus	10(3	4(3	8	300	13.4	3	210	0.9	0.2
A. severtzovi	10	4(3	7	170	10.9	4	180	0.9(3	0.2(3
A. elater	27(3	2(3	3	47	8.3(3	5	42	0.7(3	0.4(3
A. nataliae (balikunika)	9	4	9	73	8.7	2	151	0.9	0.5
A. bullata	7	3	10	93	8.5	4	76	0.7	0.6
P. pygmaeus	22(3	2	3	57	7.1	11	37	0.6	0.7
P. platiurus	6(2,3	2(2	10	34	5.3(2	12	31	0.1(3	0.9(3

Table 18 (ctn.)

Species	Max. anual birth-rate (pups number)	Max. age in nature (years)	Min. duration of maturation (months)	Body weight (g)	Max. velocity of locomotion (m/sec)	Number burrows per animal used simultaneously	Radius of home range (m) *	Diet diversity **	Degree of herbivoriness ***
P. zitkovi	15(1	2.5	3	57	7.0	11	37	0.5	0.7(1
A. sibirica	6	4	9	87	9.0	3	90	0.9	0.3
A. bobrinskii	20(3	2(3	3(3	68	8.5(2	3	85	0.5(3	0.8(3
D. sagitta	26(3	2	3(3	72	8.1(2	2	68	0.7	0.4(3
S. tellum	8	2	10	67	6.5	12	37	0.8(3	0.3(3
S. andrewsii	9	3	10	89	6.7	9	39	0.7	0.5
E. lichtensteini	8(2,3	2(3	9	51	7.3(2	2	37	0.5(3	0.7(3
P. ctenodactilus	5(3	4(3	8	160	8.8(2	1	500	0.2(3	0.9(3
J. turcmenicus	22(3	2(3	3(3	121	9.2(2	1	90	0.7(3	0.6(3

Table 19.- Eigenvalues and eigenvectors of principal components analysis of results of Table 18.

PC	Eigenvalue	Sum of values (%)	Eigenvectors (numbers coincide with characteristics in Table 18)								
			1	2	3	4	5	6	7	8	9
1	3.24	36.02	0.08	0.44	-0.09	0.50	0.52	-0.09	0.34	0.37	0.10
2	2.59	64.80	-0.56	0.31	0.53	0.03	-0.13	-0.27	0.29	-0.21	-0.29
3	1.19	78.04	-0.32	0.13	0.33	0.01	0.05	0.74	-0.12	0.09	0.45

about the priority of the first or the second factor in the evolution of the Dipodidae family. Both are interrelated. For instance, the number of burrows is positively related to feeding on green food; while high mobility (run speed) is positively related to the dimension of the home range and to the omnivorous condition. Similar results were obtained during the analysis of the Allactaginae subfamily (Rogovin, 1988 b). Apparently, in the Dipodidae family the reproductive potential of the species (in particular the reproductive effort) depends to a great extent on such characteristics of habitat conditions as the stability of the climate and fodder base, and not on the characteristics related to the avoidance of predators and of feeding. One of the possibilities for reducing the pressure of unpredictable changes in the food resources (shown by jerboas) resides in an increase in the hibernation period which implies a drop in the reproductive activity. Nevertheless, of paramount importance is the fact that high-speed large forms and small hiding forms possess relatively low possibilities for a rapid increase in number. This is also typical of species closely dependent on protective shelters (Fig. 13).

Thus the success of the study of the cause and effect relationship in the process of the community evolution of desert rodents can be ensured only by thecombination of different approaches and methods. The basis for adopting a hypothesis is, apparently, a similarity in the results obtained by different methods.

A large-scale biological approach to the study of community organization suggests a hierarchical scheme in the organization of the research project. Such a scheme seems to suggest the initial study of the structural aspects in the organization of communities. If we are interested in the mechanism for the formation of phenotypical diversity of species in communities, then the hierarchy of questions should be presented as follows:

1. Are there any assemblages or guilds of species at the geographical region, landscape, macrohabitat?
2. Is there any partitioning of environmental conditions and resources by species within the assemblage (guild)?
3. What are the rules for the differentiation of species? (the extent of regularity in the niches packing, the presence of permanent limits on the similarity of coexisting species, etc.).

At each of these levels there is a possibility for formulating hypotheses on possible cause and effect relations. A negative answer for questions at different levels dictates the logic of formulating hypotheses and enables us to reduce the number of possible explanations. The study of the functional aspects in the organization of communities is implemented at the second stage of a broad biological approach.

The registration of all possible reasons which may lead to a particular character of structural relationship seems to be very important. The selection of the most adequate methods for testing hypotheses depends on it. It is evident that the possibility of formulating the most correct hypotheses on the factors promoting the formation of phenetic diversity in the community depends on a detailed analysis performed at the structural level of the study. If at this level we limit ourselves by the establishment of the fact of the partition by species of conditions and resources within the macrohabitat, then possible reasons and corresponding mechanisms in the partition of niches could be as follows:

Causes	Mechanisms
1. Maladaptive response	Side effect due to species extinction, unrelated to the effect of competition, predators, or to other factors involve in the distribution of resources.
2. Predators	A. Partition of habitat conditions fixed by selection on the basis of differences in avoiding danger. B. Differential mortality of species in different conditions as a result of the direct pressure of a predator.
3. Adaptation to different environmental conditions and resources	Partition of habitat conditions and of resources on the basic of different morphofunctional adaptations to the types of substrate, relief, vegetation and food resources that were formed during the primary isolation of populations.
4. Exploitation competition	A. Partition of habitat conditions and resources on the basis of differences in the mode of foraging behavior that were formed as a result of part exploitation and competition. B. Partition of habitat conditions and resources as a result of competitivity of species in different micro habitats. Competition for resources occurring at present.
5. Interference competition	A. Partition of habitat conditions as a side effect of the need for compatibility of different social systems (systems of sexual behavior, reproductive isolation mechanisms). B. Partition of habitat conditions on the basis of direct territorial conflicts phenomena of interspecific territoriality, maintenance of interspecific individual distances).

Provided that the results point to the regularity of the packing of niches and the resource space is obtained at the structural level of the study, then the choice for the possible reasons of it remains virtually unchanged (the maladaptive answer can be excluded as the least probable in such a situation). However the number of conditions in which this structure can exist is more limited. Therefore, there is a possibility for a more stringent testing of the hypothesis. For instance, we found a regular distribution of niches along the gradient of a resource in the case of a corresponding regularity in the distribution of the resource. This case assumes that the most probable explanation of the phenomenon resides either in the mechanism of exploitation competition or in the adaptation to peculiarities in the distribution of the resource during the primary isolation of populations. The latter may not be very unlikely if we can show the absence of guilds within the territorial subdivisions of the fauna. The hypothesis on the role of predators is probable in the case of existence of different modes of predator avoidance which correspond to the resource distribution.

A more detailed study on the peculiarities of individual behavior of species that considers the energy cost of foraging behavior and benefit obtained, the risk of being killed and the success of avoiding a predator may, in all likelihood shed more light on these problems. Today, despite a large number of studies on the ecology of heteromiyd communities, there are extremely few data that result from studies on the peculiarities of the individual behavior of species in different conditions in nature. Such studies that enable us to trace the time budgets (activity) of species are absolutely necessary for evaluating the energetic costs of different behavioral patterns. No less important are the data on the diversity of the individual behavior of species in different situations (sites of seed harvest and the use of shelters in different conditions, ways of avoiding danger from air and land, etc.) The combination of these data without accurate assessments of costs and benefits in energy units, may be important for supporting this or the other hypothesis. At present, data of this type permit us to suggest a somewhat different interpretation of the problem of the origin of the bipedal type of locomotion in desert rodents and also of the problem of phenotypic differentiation of species in communities.

The present day evidence regarding bipedal forms of rodents shows that : (1) these forms are associated with sparse vegetation open areas; (2) within each taxon the most primitive of all species usually consume high-calories food which could in turn be limited by a change in conditions in nature; (3) species prefer the nocturnal and solitary mode of life. It is also known that the evolution of bipedal forms among rodents results from the aridization of climates on the territories of present deserts, that took place in the Tertiary period (Wood, 1935; Vinogradov, 1937; Lindsay, 1972; Hafner and Hafner, 1983; Shevyreva, 1983). In this way, at the initial stage of evolution, we may logically suppose the existence of a form of quadrupedal ricocheting rodent, feeding on high-calorie food (seeds, insects) the abundance of which determined the upper limit of the density of the species population. The species inhabited areas with thick vegetation. And, finally, it should be noted that this species had a certain type of social organization which determined the lower limit of population density, *i.e.* minimal allowable density, below which the existence of a population becomes impossible. This means that there is a certain minimum necessary load on the habitat resource base. Such are the bases for our model.

Desertification of the territory begins with the aridization of the climate. The main results of this process, exerting influence on the population of the hypothetical species are: a) sparse vegetation and the falling of food abundance in general; b) a change in the pattern of vegetation and food. From a relatively homogeneous environment it turns into a patchy environment.

What are the possible outcomes for the species which preserve its fitness at the former level? There are four ways out of this situation. 1) A change in social organization (system of territorial relations) in such a way that it would be possible to reduce the minimum necessary load on the habitat. 2) An increase in the range of conditions of food harvest (intensification of the use of the home range). 3) Expansion of diet (spectrum of fodder). 4) Transition to another type of food abundant in new conditions. It is evident that all these possibilities are to a certain extent interrelated. As demonstrated by the above, they all more or less describe the ecology of recent bipedal rodents. And yet, the first two conditions could be achieved almost easily, since they do not require neither substantial physiological changes nor changes in the budget of time (activity) and energy related to it. Let us see what effects could be expected if possibility 1 occurs.

1. The species will preserve its attachment to the former diet and mode of harvest. In a desert with a patchy distribution of resources and shelters this is possible only if the home ranges expand. Running across patches or in patches deprived of vegetation, in search of patch or in patches with dense vegetation, the species are exposed to the risk of being attacked by a predator. Therefore, it is necessary to spend more energy in searching for fodder andin avoiding predators. Since total energy budgest in animal of similar sizes within taxon of a

Figure 13. Direct reflections of interlocation of 20 species of jerboas in coordinates that characterize 1) average number of burrows used by an animal simultaneously; 2) maximum velocity of locomotion in nature; 3) ratio of maximum birth - yearly rate to the maximum duration of life in nature. From data on Table 18. Designations: Pz - Pygerethmus zitkovi, the rest the same as in Fig. 1. The highest ratio of birth-rate to length of life is characteristic of the populations of species that exist in conditions of unstable food supply (A. elater, A. bobrinskii, P. pygmaeus, D. sagitta, J. turcmenicus). Some species living in such conditions restructured their physiology by increasing the duration of hibernation and reducing the reproductive period (C. paradoxus, P. platiurus, S. telum, S. andrewsii). Other species live in more stable conditions of food supply on account of their ability to use different types of food and also because of specialization for regularly available food (for instance, P. ctenodactilus feeds on the green branches of bushes). Nevertheless, attention is drawn to the fact that large forms with a high velocity of locomotion as well as small hiding forms have relatively low possibilities for a rapid increase in their numbers, which is indicative of the species closely attached to protective shelters (burrows).

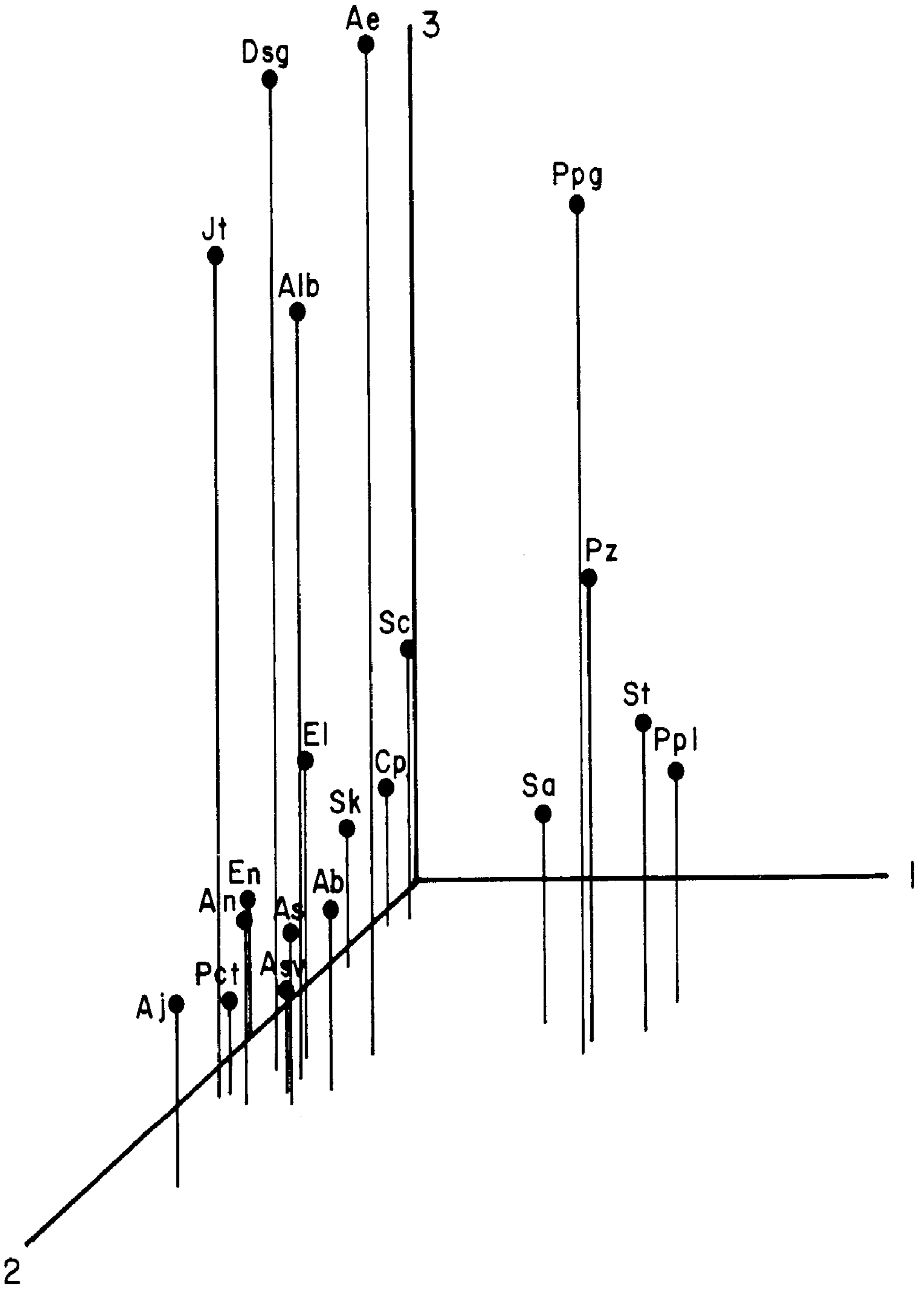

Figure 13.

low rank are as a rule, rather close (Dolnik, 1986) some part of the energy resources could be obtained by restructuring the social structure, in an effort to relax the territoriality system. But in general, energy economy is feasible only by restructuring the morphological structure, particularly increasing the effectiveness of the locomotor apparatus. As revealed by comparative avian studies a change in the morphology is usually easier in evolution than restructuring the total energy budget. The latter turns out to be limited by the general type of physiological and biochemical organization of the species within the taxon (Calder, 1974; King, 1974; Kendeigh et al., 1977).

Although the path of evolution of bipedality described is possible, this scenario is rather energy consuming. It is quite possible at the later stages of evolution of bipedal rodents and, apparently, is realized among jerboas (Rogovin, 1983). However, with respect to heteromiyds relatively unspecialized in bipedal locomotion the second possibility is the most likely to occur.

2. If foraging with the former strategy of behavior becomes ineffective (due to limitation of food resources as a result of aridization it requires too much effort and time), the use of open areas by animals is determined by the necessity to reduce the time for replenishing the energy expenditure. The expansion of conditions for harvesting food seems to be the most simple solution since it does not require an essential restructuring of the activity budget. In fact, the expansion of foraging conditions in heteromiyds with an increase in body size is not related, according to our data, with an increase in the home range. On the contrary, we see the intensification of the use of home ranges. The system of territorial relations then becomes more rigid (lowering of the level of overlap of home ranges, increase in aggression). At the same time, the risk of being killed by a predator increases and therefore, the need for additional energy to avoid danger also increases. The solution for this, as in the first case, is an increase in the effectiveness of avoiding a danger by changing the locomotion apparatus. In fact, at the initial stages of the evolution of bipedality, the most realistic standpoint is that the gain is in the initial acceleration of the pace in case of danger, but not in maximum speed or general mobility (Fokin, 1978, 1981). Either a close relationship with bushes is preserved or the relationship with the burrow is increased. Burrows and bushes are used as shelters in case of danger. The same trend of evolutionary transformation allows for a gradual extension of the range of diet (third possibility).

Both scenarios analyzed by us suggest the possibility of the formation of the bipedal type of locomotion in desert rodents without any relationship with the aggravation of interspecific competition for resources. Competition could have been significant as an additional factor limiting the food resources at the sites of coexistence of quadrupedal forms in conditions of progressive aridization of the land.

To conclude it should be stressed once again that the use of a large-scale biological approach in studying communities of desert rodents is mandatory and it remains as the only condition for the development of a vital and fruitful theory. This is a very recent theory. At present we have insufficient information regarding the peculiarities of the structural organization of different types of communities. Moreover, the results of testing the validity of hypotheses to prove the functional aspects of the organization of desert rodent communities are insufficient. It is only by considering all possible alternatives and by the use of a comparative research method that we will be able to come closer to the solution of the problem.

Comments

1. Fokin (1978) suggests to distinguish three main types of bipedal locomotion in rodents: 1) synchronous bipedal ricochet, *i.e.* an asymmetrical pace with a simultaneous push by both hind feet on the substrate; 2) asynchronous bipedal ricochet, *i.e.* a secondary asymmetrical pace during which a push is performed first by one and then by another foot which provides for an additional acceleration for the run (so-called starting run step); 3) symmetrical run (step), *i.e.* trot pace with an alternate right and left foothold, there is no phase of free flight.

2. The largest diameter of home range has been determined as the distance between the extreme points of visual registration of marked animals of *Dipodomys* species, and of entrapment of *Perognathus* species using Sherman traps (distance between traps 20 m, traps were used in an area of 1 hectare). The registration sites of individuals marked with the dye Urzol-D were determined by torchlight at night. The marking areas were located in optimal habitats : *D. nelsoni* - 8 animals/ha (peach), *D. merriami* - 17 animals/ha (Pastizal), *P. penicillatus* (20 animals/ha (greenland). Geobotanical subdivision of the territory of Bolson de Mapimi by Martinez and Morello (1977).

3. $H = - \sum_i p_i \log_2 p_i$, where p_i is the frequency by volume of each type of fodder in the stomach contents.

4. The cube of the proportion of the lengths of jaws approximately tallies with the proportion of weights: $1.28^3 = 2.10$.

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CHAPTER 3

ANALYSIS OF SPATIAL ORGANIZATION OF A DESERT RODENT COMMUNITY IN THE BOLSON DE MAPIMI, MEXICO

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Abstract

We studied the distribution of niches in resource space and niche patterns of a 12-species community of desert rodents by use of canonical- variate analysis and principal-component analysis. Fourteen characters of the environment were measured in 475 sample plots within 19 1ha grid areas (474 captures of rodents on plots), and eight morphological indicators of niches were used. The first three canonical axis of resource space accounted for 81% of the variance; each of the axis was identified by one of the characteristics of the substrate and one to two vegetation characteristics. We found a high level of dispersion in distribution of species in the resource space. The lowest values of coefficients of variation of niche overlap and of distances between niche centers characterize a group of the nearest neighbor species. There was a marked negative correlation between morphological distances between the nearest neighbors and the distances between the same species in the resource space. This evidence indicates certain limitations on the ecological similarity of coexisting species. Negative correlations between niche breadth and the position of the niche in the resource space, and between the maximum density of population and niche breadth are proved.

Of all the existing approaches to study the spatial organization of mammalian communities, the multivariate methods are perhaps the most widely used. This approach is based on gathering a large number of environmental characters from various habitats and on analyzing the specificity of the species relationships to the combinations of these characters. Further analysis of field data tries to reduce a multitude of environmental parameters to a small number of mutually independent vectors that account for most of the variation in abundance or distribution of species. The use of these vectors as ortogonal axis allows us to obtain a convenient description of the space of ecological factors (resource space), and then to use other methods to study its structure.

The task of reducing the number of characters is simply solved by methods of multivariate parametric statistics (discriminant function analysis, and principal component analysis). Although ecological data often violate the assumptions of parametric statistics (nonlinear relationships and deviation from normal distributions), these methods are widely used for the analysis of community organization (Congdon, 1974; M'Closkey, 1976; Dueser and Shugart, 1979; Morris, 1979; Van Horn, 1982; Sharples, 1983;).

Methods of multivariate parametric statistics produce stable results even in the event of substantial deviation from normal distributions (Jeffers, 1981). Such deviation, however, makes the possibility of estimating the statistical significance of the results doubtful. Furthermore, at present these methods are the only available ones, because comparable nonparametric methods have not been developed.

The construction of factorial space may be implemented by analyzing data on the structure of the environment without considering the frequency of occurrence of species by the use of principal components analysis. Numbers of individuals of each species are later projected on the resulting environmental variate corresponding to the position of microhabitats where they were recorded (Rotenberry and Wiens, 1980; Seagle and McCracken, 1986; Robey *et al*., 1987). The axis of this space describe the extent of variation of the structural environmental characters.

The construction of factorial space also may be implemented by the analysis of the environmental characters at the sites where the species were captured. As a rule, discriminant function analysis (canonical-variate analysis) is used in this case (Cody and Walter, 1976; M'Closkey, 1976; Dueser and Shugart, 1979; Morris, Regogovin, Shenbrot, and Surov 1979; Crowford *et al*., 1981; Reinert,1981). The axis of this space describe the contribution made by these variate to the division of resources by the community species (Green, 1971, 1974). Thus, the modeled factorial space is a multivariate range of variation in environmental characters used by species. The representation of the niche of the species in that space is an ellipsoid like a cloud of dots (descriptions of species occurrences). The centroid of the ellipsoid corresponds to the ecological optimum, or at least to the center of occurrence with respect to the environmental variables.

Unlike the first method of analysis, the latter approach minimizes the possibility of introducing factors in the analysis that might influence the outcome of the study.

The second method of analysis is more consistent with concepts of the ecological niche such as the combination of environmental resources used by the population of a species (Whittaker *et al*., 1973). Because the requirements of one species for an essential resource should approximate to a normal distribution, this method of analysis seems to meet the requirements of the statistical methods. We applied this method of analysis to the desert rodent community in the Bolsón de Mapimí (Durango, México) and analyzed the interrelationships among the characters of spatial (structural) niches of species as well as the interrelationship with the morphological indicators of niches that characterize the morphological organization of the community. The aim was to identify an order in the distribution of niches in the space of resources and to examine an existence of a correlation of niche positions in space of resources and in the morphological space of the community.

Material and Methods

Study area.

The field studies were conducted in September-October, 1987 in the southern region of the Chihuahua desert in the Mapimí Biosphere Reserve in northeastern México. The reserve is located in the central part of the desert basin Bolsón de Mapimí (26ß ß 29'-26ß ß 52' N, 103ß ß 58'-103ß ß 32' W). The surrounding area is a plateau divided by chains of low meridional mountains with closed valleys. The lower parts of the basin, flooded during the humid period, are grasslands of *Hilaria mutica* (<80% of the vegetation cover). *Salsola kali* accounts for <50% of the vegetation cover in grass deprived areas in the humid period. There are also scattered trees and bushes (*Prosopis glandulosa* and *Suaeda nigrescens*) in these grassland areas (called pastizal). Such clay basins (playas) are occasionally surrounded by dunes, stabilized by shrubs and little bushes (*Larrea tridentata, Jatropha dioica, Krameria grayi, Zinia acerosa*, and *Yucca* sp.) and also by annual plants. The total vegetative cover varies from 12 to 32%; however shrub vegetation composes 8-27% of it. Monospecific shrub communities (*Larrea tridentata*) with a sparse annual plant cover (mainly representatives of Compositae), called matorral, grow on sandy small stone and gravel sides of depressions adjoining dunes. The diversity of species and cover of shrub vegetation increases with elevation. *L. tridentata* dominates among shrubs as before. Cacti play an essential role (mainly *Opuntia imbricata* and *O.leptocaulis*). Plant communities of *O.rastrera, Agave asperima, Fouquieria splendens*, and *L. tridentata* grow along small alluvial deposits (bajada). The richest cactus-shrub associations (nopalera) are composed in addition to *O. rastrera* and *L. tridentata*, by representatives of *Castella, Cordia*, and *Krameria*. Cactus-shrub vegetation cover in these areas is 38-40%, and total vegetation cover, including annual grasses, is 50- 55%. Finally, the lower part of the mountain slopes with rocky substrate is occupied by vegetation communities, called magueyal, dominated by tickets of *A. asperima, Euphorbia antisyphilitica, L.tridentata*. A. asperima which compose 30-32% of the vegetation cover, and total vegetation cover rarely exceeds 50%. The middle and upper parts of the mountains are represented by numerous rock protrusions and large screen mounds (cerro). They are covered with scattered shrub communities of small cacti and yuccas (Martínez and Morello, 1977).

Climatic conditions in Bolsón de Mapimí are as follows: mean monthly temperature of January, +11 C, for July, +28 C; annual precipitation, 230 mm, (highest precipitation occurs in the Summer). The climate is dry and subtropical (Barbault and Halffter, 1981).

Twelve species composed the community of terrestrial desert rodents in the Mapimí Reserve in September-October 1987. Most of these species occur consistently in different years in the desert habitats of the reserve (Grenot and Serrano, 1981; Rogovin, *et al.*, 1985; Serrano,1987).

Number of captures in 1987 were as follows: *Spermophilus spilosoma*, 9; *Perognathus flavus*, 14; *P.penicillatus*, 72; *P.nelsoni*, 44; *Dipodomys merriami*, 148; *D.nelsoni*, 54; *D.ordii* 23; *Peromyscus eremicus*, 58; *P.maniculatus*, 3; *Neotoma albigula*,49; *Sigmodon hispidus*, 7 and *Onichomys torridus*, 2. *Spermophilus variegatus* (Grenot and Serrano, 1981), *S. mexicanus* (Rogovin *et al.*, 1985) and *Reithrodontomys megalotis* (O. J. Palaco, pers. comm.) were also registered. However, the abundance of these species in desert habitats is so low that they can be ignored for the community analysis.

We did not analyze typical mountain habitats of *S. variegatus* and *S. mexicanus*. The absence of *S.mexicanus*, which occurred in the middle and lower mountain slopes in the Autumnof 1987, can be apparently explained by early hibernation.

Data collection and analysis.

Rodents were obtained with Sherman traps of 25 X 7 X 7 cm in square 1ha grids. Each of these grids was subdivided into 25 20 X 20 m sample plots. The centers of the sample plots were marked with pegs. Two traps were set at less than 5 m from the center of each sample plot, one in the open and the other close to a shrub (shelter). Peanut butter was used as bait. Rodents were marked by toe-clipping and by marking with "Urzol-D". The traps were examined three times each night by light of a torchlight. Kangaroo rats and pocket mice not trapped in Sherman traps were caught with a net during the night time. Only points of first meeting were used in the following analysis. Each grid was checked over a period of three nights. Densities of rodent species were estimated by the number of animals caught on a grid during this time. Accuracy of estimates was verified by recapture and also by visual observation of marked animals during rechecking of the grid. Three nights were enough to mark more than 80% of the rodents on a grid. The environment was described in the center of each sample plot by 33 characters. Factors influencing the distribution of species were selected by stepwise calculation of polychoric coefficients of conjugation of species together with the environmental characters (Shenbrot, 1988). Independent environmental factors of the 1st, 2d, 3d, . . . levels of significance were selected in the course of a preliminary analysis. Later, the used factors where those that revealed a significant relation with the occurrence of at least one species of rodent (evaluation of significance by X^2).

Fifteen characters were selected for the analysis: 1) percent content of stones in a 0.5-kg soil sample 10 cm deep; 2) percent content of gravel in a 0.5-kg soil sample; 3) percent content of clay in a 0.5-kg sample; 4) percent vegetative cover of bushes and low trees (*Prosopis* sp.,*Acacia* sp.); 5) percent vegetative cover of shrubs and perennial woody vegetation of the upper layer; 6) percent vegetative cover provided by small bushes and perennial woody vegetation of the middle and lower layers; 7) percent vegetation cover of perennial grasses of middle and lower layers; 8) volume of crowns of the first vegetative layer, 0-25 cm; 9) volume of crowns of the second vegetative layer, 25-50 cm; 10) volume of crowns of the third vegetative layer, 50-100 cm; 11) percent of vegetative cover of cactus; 12) abundance of grasses (stems/1 m^2); 13) abundance of herbs (stems/1 m^2); 14) abundance of succulents (stems/1 m^2); 15) abundance of grasses, herbs and succulent species (stems/1 m^2).

Grids were distributed so as to that they cover the whole range of habitats from the middle slopes of the mountains to the clay basins and sand dunes. Data on 19 live-trapping grids, 475 descriptions of sample plots, and 474 captures of rodents on plots were analyzed.

We weighed rodents and recorded the length of the body, length of front and back extremities, length of tail, length of metatarsus, length of external ears, length of vibrissae, and the distance between the eyes at the frontal part of the head.

Distribution of niches of rodent species in the resource space was quantified by multivariate discriminant function analysis (canonical variate analysis). The initial data were sets of habitat characters in sample plots at the sites of capture of rodents. The data were log transformed. The measures of niche breadth, niche position in the space of canonical variate and distances between the niche centers of species were calculated by canonical variate analysis. The breadth of the niche was estimated as the standard deviation of capture points from the centroid of that species (Carnes and Slade, 1982). The position of the niche center was estimated by calculating the Euclidian distances of species centroids from the centroid of the whole community (mean arithmetic of the coordinates of species centroids):

$$D_E = \sqrt{} \Sigma (X_{ij} - X_j)^2$$

where X_{ij} is the position of the species in niche i on the canonical axis j; X_j is the position of the center of the community on the canonical axis j. The canonical axis were identified by correlating the projections of a sample plot data to each of the canonical variate with corresponding data for each of the resource characters. The discriminant function analysis was used to estimate niche overlap by pairwise comparison of sets of sample plots at which one species of the pair or both species were captured. The overlap of probability distributions on the discriminant axis (the probability of incorrect assignment) was used as a measure of niche overlap (Green, 1974; Cody and Walter, 1976):

$$\alpha = \frac{1 - 2x}{1 + 2x}$$

á where $\underline{x}$ is the second function of the standardized deviation for $\sqrt{D^2/2}$ (D^2 - generalized Mahalanobisdistance).

To assess the degree of regularity in the distribution of niches in resource space, we analyzed matrices of niche overlap and distances between centers by the technique of the "nearest neighbors" (Inger and Colwell, 1977).

The analysis of the distribution of species in the morphological space was accomplished by the use of principal component analysis with mean values of characters. Eight external characters related to the adaptive differentiation of the species were used: 1) head and body length; 2) weight; 3) tail:head and body length ratio; 4) hind foot:head and body length ratio; 5) ear:head and body length ratio; 6) longest vibrissae:head and body length ratio; 7) forearm from elbow joint: hind-foot length ratio; 8) frontal distance between eyes:head and body length ratio.

We estimated correlations between the main canonical variate of resource space and principal component variate of morphological space, and also the correlation of Euclidian distances between species in the space of morphological and ecological variables.

The presence of *O. torridus* was recorded only twice in essentially different habitats. To avoid distortion this species was not included in the total pool of species when estimating canonical variate. Later *O. torridus* was placed in the canonical coordinate system by multiplying the original habitat variables for the species by its corresponding discriminant function coefficients. By way of contrast, the inclusion of *P. maniculatus* in the mine analysis (despite the rarity of captures-three), was justified by the close association of this species with the maximum development of grass vegetation in clay basins.

Results

Use of macrohabitats, density, and biomass.

In comparison with the earlier estimates from 1977-1979 (Serrano, 1987), the density of most species was lower in Autumn of 1987 (Table 1). The density of *P. nelsoni* was reduced nearly 6 fold as compared to the maximum recorded

Table 1.- Maximum densities of populations of rodents in the prime types of habitats of the Mapimí reserve in September-October 1987. Habitats were distinguished according to geobotanical categories (Martínez and Morello, 1977).

	Bajada						**Playa**				**Dune**	
	Magueyal		**Nopalera**		**Matorral**		**Pastizal 1**[a]		**Pastizal 2**[b]		**bushes formation**[c]	
Species	**n/ha**	**kg/ha**	**n/ha**	**kg/ha**	**n/ha**	**kg/ha**	**n/ha**	**kg/ha**	**n/ha**	**kg/ha**	**n/ha**	**kg/ha**
S. spilosoma	1	0.12	2	0.24	2	0.24	-	-	1	0.12	-	-
N. albigula	6	1.10	2	0.37	1	0.18	-	0.73	1	0.18	-	1.46
P. eremicus	3	0.05	4	0.07	3	0.05	-	0.07	5	0.09	-	0.09
P. maniculatu	1	-	1	-	1	-	-	0.04	1	0.02	-	-
O. torridus	1	1	1	-	-	-	-	-	1	0.02	-	-
S. hispidus	1	0.12	1	-	-	-	2	0.23	2	0.23	-	-
P. nelsoni	4	0.05	8	0.10	-	0.05	1	-	1	-	-	-
P. peniciatus	1	0.01	1	0.01	4	0.06	1	0.01	4	0.06	10	0.14
P. flavus	1	0.005	1	0.005	-	-	1	0.005	3	0.015	1	0.005
D. merrimi	12	0.45	11	0.41	13	0.49	1	0.04	2	0.08	3	0.11
D. nelsni	2	0.21	3	0.31	3	0.31	2	0.21	6	0.62	-	-
D. ordi	-	-	-	-	-	-	-	-	-	-	6	0.25
Total	31	2.12	32	1.52	27	1.38	17	1.34	26	1.44	33	2.06

a= Formation *Hillaria mutica* + *Suaeda nigrescens*
b= Formation *H. mutica* + *Salsola kali* + *Prosopis* sp.
c= Formation *Larrea tridentata* + *Jatropha dioica* + *Yucca* sp.

density (1977); that of *N. albigula* was reduced 5 fold (1977), and the density of *P.penicillatus* and *D. merriami* (1979) declined 1.5-1.7 times. The high population densities estimated by Serrano may have resulted from a longer period of marking and recapture on grids in 1977-1979. There was a slight change in density interrelations (Rogovin *et al*.,1985) as compared to l98l and l983. The maximum total biomass in 1987 was recorded on rocky slopes and sandy soils; minimum densities occurred in clay depressions. As compared to 1981 and 1983, the density of *S.hispidus* had substantially increased (seven records in 1987; in 1981 and 1983 the species was not recorded).

Resource partitioning and general characteristics of the community.

Division of space resources within the community occurs mainly on the first three canonical axis, which account for about 81% of variance. The contribution of the first axis exceeds that of the second by more than 2.6 times and that of the third by more than 4.5 times (Table 2).

Each of these axis reflects a complex gradient of soil conditions and structure of the vegetation (Table 3). The first axis represents the gradient toward greater sand content in soil and the development of vegetation with a well developed middle layer; there is a parallel reduction of the content of stones and gravel in soil. The second axis reflects a gradual increase in the content of stone and cover by tall shrubs (woody vegetation of the upper layer). The third axis reflects

Table 2.- Eigenvalue and eigenvectors for the original variables of the fist three canonical axis of resource space for a communityof 11 species.

Eigen-values	Cumulative proportion of variance	Eigenvectors for the original variables									
		1	2	3	4	5	6	7	8	9	10
		11	12	13	14	15					
1.12	0.51	-0.42	-0.01	-0.34	0.40	-0.10	0.19	-0.01	-0.33	0.50	0.06
		-0.16	0.19	0.12	-0.03	-0.26					
0.42	0.70	0.31	-0.05	-0.25	0.28	-0.03	-0.09	0.22	0.15	0.29	0.39
		-0.08	0.50	-0.02	-0.29	-0.34					
0.24	0.81	-0.10	-0.01	0.13	0.27	0.43	0.26	0.53	0.07	0.11	-0.40
		0.03	-0.02	-0.12	0.11	0.39					

Table 3. - Correlation coefficients between the original resource variables and canonical variate for a community of 11-species.

Canonical	Original variables														
Variate	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	-0.73	-0.61	-0.57	0.35	0.05	0.61	-0.07	0.18	0.23	0.11	-0.28	-0.25	-0.02	-0.17	-0.30
2	0.55	0.41	-0.40	-0.03	0.49	0.14	0.38	0.42	0.61	0.42	0.41	-0.18	-0.67	-0.18	
3	-0.21	-0.11	0.37	0.41	0.22	-0.22	0.72	0.63	0.55	0.01	-0.07	0.57	0.55	0.59	0.74

a parallel increase of grasses as well as of the content of clay in the soil. The distribution of centroids of niches along the resource axis points to the absence of species guilds (Fig. 1). Although several species (*P.nelsoni, D.nelsoni, D.ordii, P.maniculatus*) occupy extreme positions, most of the species are clustered in the center of the resource space.

The canonical coordinate system, typified for a taxonomic group of species the Family Heteromyidae does not differ appreciably from the coordinate system of the whole community (Table 4 and Table 5). But among the Heteromyidae more than 87% of the variance is explained by the first two canonical axis. Relatively isolated groups of species are distinguished by the first axis (Fig. 1c). For instance, *P.penicillatus* and *D.ordii* mostly inhabit sands with low vegetation. Another group links the sclerophylls and the petrophylls. The partition of species of this group occurs mainly along the second canonical axis. The extreme positions on this axis are occupied by *P.nelsoni*, which inhabits shrub-cactus formations on mountain slopes, and by *D.nelsoni*, whose maximum density is characteristic of clay areas with sparse shrubs but with well developed annual *Salsola kali* vegetation.

Relative remoteness from each of the congeners is a typical feature of the distribution of heteromlyds along the gradients of resources represented by the first and second canonical axis. *Perognathus* species tend to be separated from each other by equal distances. Among the *Dipodomys* species, these distances

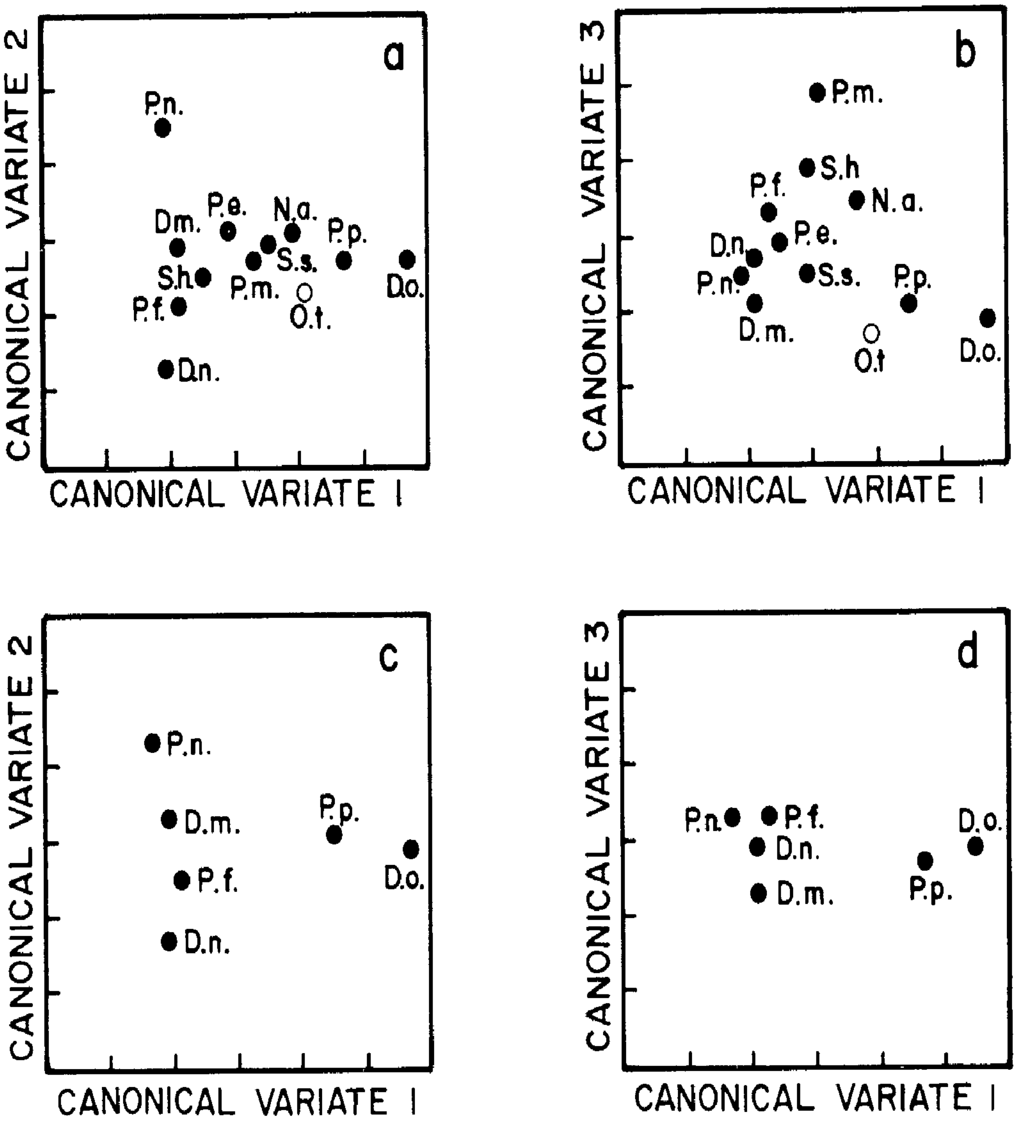

Figure 1.- Projections of niche centroids of the community in the space formed by the first three canonical variate: a and b, all species of the community; c and d, Heteromyidae species. Ss, Spermophilus spilosoma; Pf, Perognathus flavus; Pp, P.penicillatus; Pn, P.nelsoni; Dm, Dipodomys merriamy; Dn, D.nelsoni; Do, D.ordii; Pe, Peromyscus eremicus; Pm, P.maniculatus; Na, Neotoma albigula; Sh, Sigmodon hispidus; Ot, Onychomys torridus.

Table 4.- Eigenvalues and eigenvectors for each of the original variables forming the first three canonical axis of resource space for heteromiyd rodents.

Canonical Variate		Original variables									
		1	2	3	4	5	6	7	8	9	10
		11	12	13	14	15					
1.83	0.66	-0.49	0.00	-0.32	0.43	-0.05	0.21	-0.01	-0.15	0.33	-0.02
		-0.12	0.23	0.23	0.02	-0.41					
0.88	0.88	0.12	0.10	-0.24	-0.05	-0.02	0.08	0.10	0.39	-0.30	0.64
		-0.15	0.36	-0.06	-0.21	-0.20					
0.21	0.96	-0.01	0.28	-0.23	0.26	-0.06	0.39	0.34	-0.04	0.01	0.45
		-0.04	-0.22	-0.24	0.20						

Table 5.- Correlation coefficients between original resource variables and canonical variate for heteromiyd rodents.

Canonical Variate	Original variables									
	1	2	3	4	5	6	7	8	9	10
	11	12	13	14	15					
1	-0.75	-0.63	-0.58	0.37	-0.01	0.64	-0.15	0.14	0.18	
	0.08	-0.31	-0.37	-0.03	-0.17	-0.37				
2	0.53	0.41	-0.51	-0.14	0.46	0.25	0.31	0.31	0.39	
	0.66	0.42	-0.35	-0.27	-0.79	-0.33				
3	0.00	0.23	-0.14	0.16	0.05	0.18	0.52	0.56	0.53	
	0.27	0.21	0.18	0.27	0.41	0.46				

are unequal, but never the less greater than between the nearest neighbords from different genera.

Most pairs of the 11 species of the community are characterized by low values of niche overlap (Table 6). The maximum value of overlap is only 38% (between *P. eremicus* and *N. albigula*). *P. eremicus* possibly uses *Neotoma nests* as their own shelters. The overlap of spatial niches are <5% and in 30 cases they are <10% in 20 out of 55 cases.

The comparison of the data in Table 6 by the nearest neighbor analysis points to the continuous distribution of the species within the community, and to the absence of clearly defined spatial guilds (Fig.2a). This is most clearly seen from the regular increase in the coefficients of variation in niche overlap. The curve for coefficients of variation of distances between centroids also has a smooth shape, therefore reflecting varying degrees of ecological similarity. However, there is a more or less distinct discontinuity in the initial segment of the curve. This is seen to a greater extent in the analysis of the interrelationships between heteromiyd species (Table 7, Fig. 2b). Thus, the coefficients of variation of the distances in the group of nearest neighbors (species of the first class of similarity) for the whole community of 11 species is much lower than in the subsequent four classes (for

Table 6.- Euclidian distances between niche centers in resource space (above diagonal) and niches overlap (below diagonal) for a community of 11-species.

Species	Ss	Na	Pe	Pm	Sh	Pn	Pp	Pf	Dm	Dn	Do
S.spilosoma	-	0.79	0.46	1.94	0.98	1.59	1.44	1.17	1.14	1.87	2.71
N.albigula	0.20	-	0.95	1.44	0.92	1.96	1.50	1.52	1.89	2.39	2.57
P.ermicus	0.21	0.38	-	1.83	0.90	1.22	1.89	1.04	1.00	1.88	3.15
P.maniculatus	0.00	0.04	0.04	-	1.12	2.62	2.83	1.73	2.75	2.70	3.74
S.hispidus	0.00	0.10	0.13	0.05	-	1.98	2.13	0.74	1.72	1.73	3.27
P.nelsoni	0.12	0.08	0.16	0.00	0.00	-	2.80	1.99	1.26	2.70	4.01
P.penicillatus	0.02	0.26	0.18	0.03	0.08	0.03	-	2.40	2.28	2.77	1.28
P.flavus	0.09	0.20	0.18	0.00	0.00	0.06	0.11	-	1.39	1.06	3.61
D.merriami	0.19	0.19	0.35	0.00	0.11	0.24	0.13	0.21	-	1.68	3.54
D.nelsoni	0.15	0.09	0.19	0.00	0.07	0.06	0.09	0.22	0.25	-	3.89
D.ordii	0.05	0.14	0.02	0.00	0.00	0.00	0.29	0.01	0.01	0.00	-

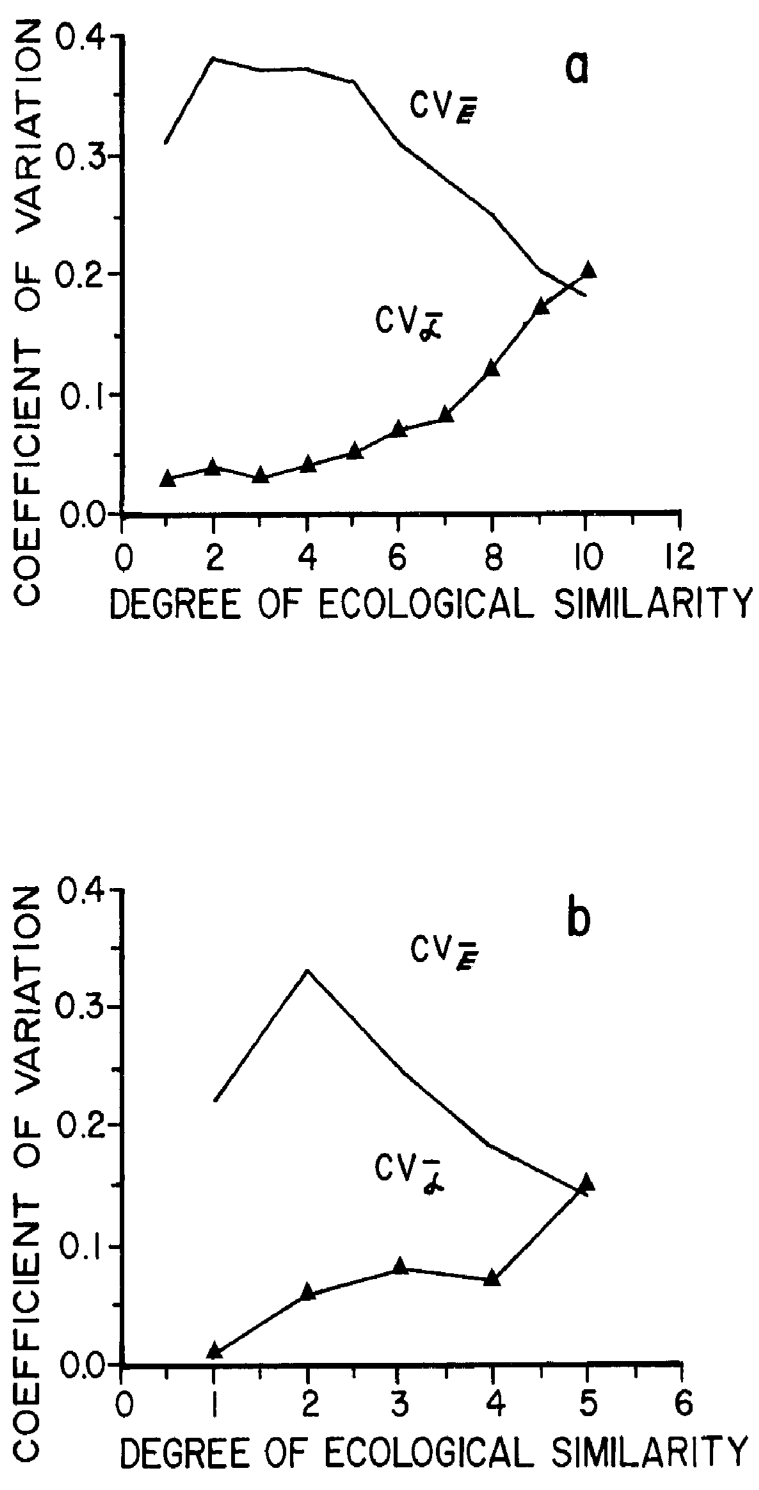

Figure 2.- The dependence of the coefficientsof variation (ordinate) on the degree of the ecological similarityof species (abscissa): a, for the 11 species of the community;b, for heteromyid species. CV - coefficients of variation of niche overlap, CV - coefficients of variation of distance between centroids.

Table 7.- Euclidian distances between niche centers in resource space (above diagonal) and niche overlap (below diagonal) for heteromiyd rodents.

species	Pn	Pp	Pf	Dm	Dn	Do
P.nelsoni	-	3.30	2.09	1.77	2.92	4.53
P.penicillatus	0.03	-	2.58	2.62	3.06	1.35
P.flavus	0.06	0.11	-	1.47	0.97	3.75
D.merriami	0.24	0.13	0.22	-	1.86	3.96
D.nelsoni	0.06	0.09	0.22	0.25	-	4.16
D.odii	0.00	0.29	0.01	0.01	0.00	-

the heteromiyd community coefficients of variation of nearest neighbors is lower than in the two subsequent classes). Also, the first classes of ecologically similar species have low coefficients of variation of overlaps, evidence of greater regularity of dispersion of these species in niche space.

The relationships between niche attributes of the community of Mapimí rodents is shown in Fig.3. There is a negative correlation between the niche breadth and its position (distance from the center of resource space; Fig.3a). An even more negative relation of these characters is observed in the analysis of the Heteromyidae (Fig.3b). Also characteristic is the negative correlation between niche breadth and abundance (maximum population density) of the species (Fig.3c). There is almost no correlation (weak positive) between abundance and distance from the center of resource space (Fig.3e) and also between biomass and distance from the center (Fig.3d) and between biomass and niche breadth (Fig.3f). The data for *P. maniculatus* were not used to estimate correlations because the assessment of the niche breadth could be strongly distorted because of the small sample size.

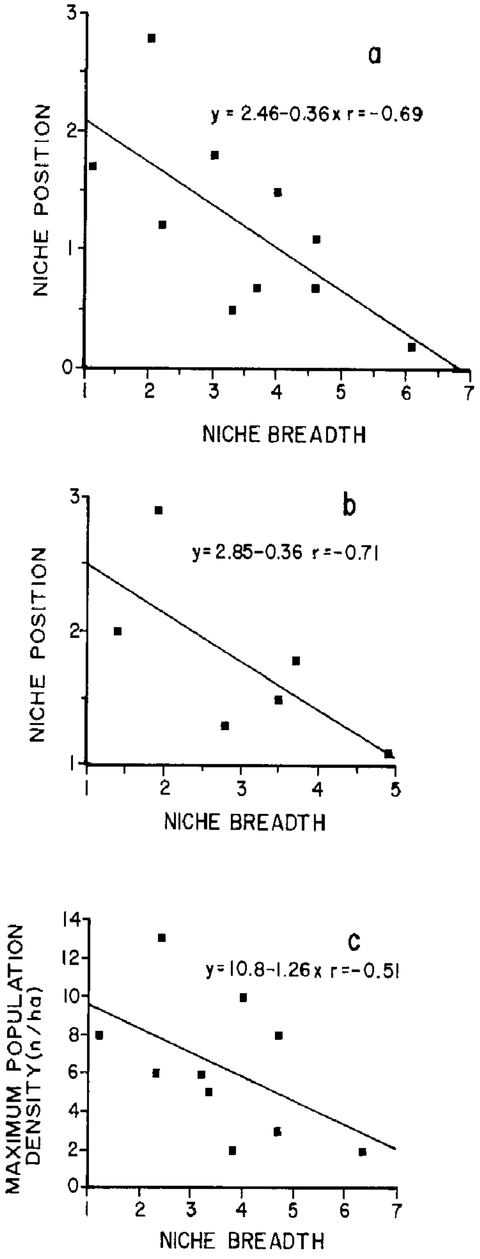

Figure 3.- Niche patterns of the community: a, dependence of position of niche centroid (ordinate) on niche breadth (abscissa) for 11 species of the community(asterisks denote that P.maniculatus was not used for regression analysis); b, the same for the heteromiyd species; c, dependence of maximum the population density (ordinate) on niche breadth (abscissa); d, dependence of maximum species biomass (ordinate) on position of the niche centroid (abscissa); e, dependence of maximum population density (ordinate) on its position on the niche centroid (abscissa); f, dependence of maximum species biomass (ordinate) on the niche breadth (abscissa).

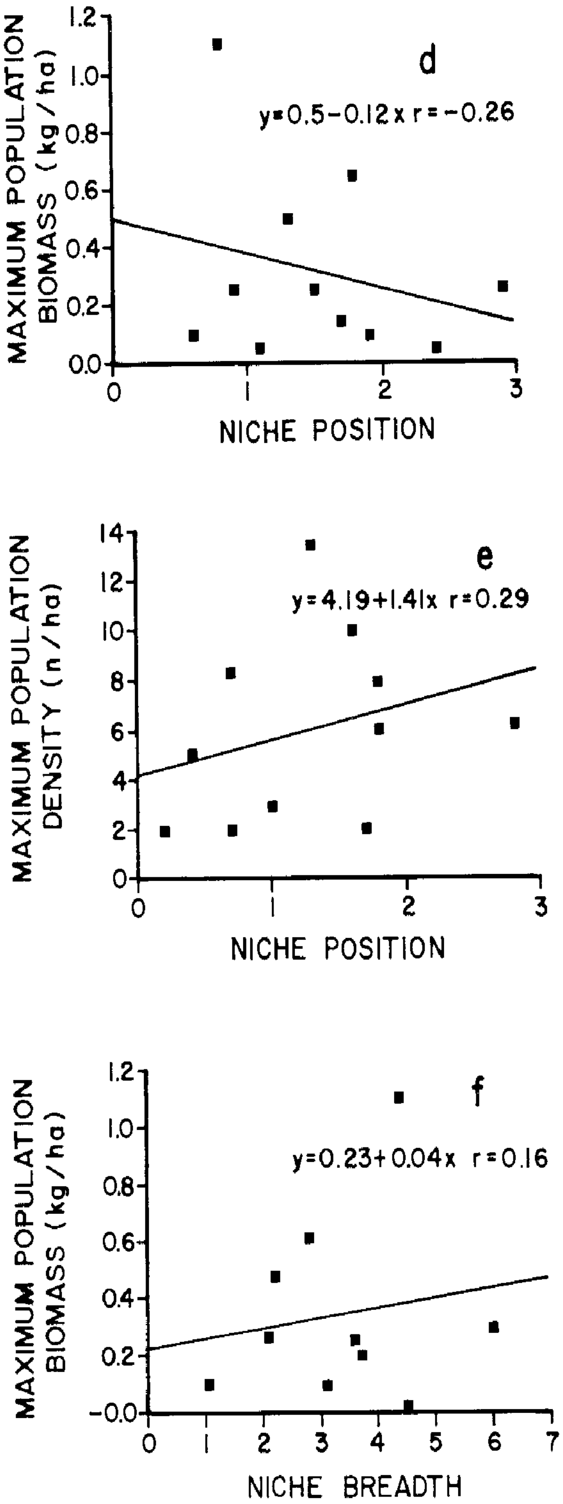
d
y=0.5-0.12x r=-0.26
MAXIMUM POPULATION BIOMASS (kg/ha)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
NICHE POSITION
e
y=4.19+1.41x r=0.29
MAXIMUM POPULATION DENSITY (n/ha)
14
12
10
8
6
4
2
0
0
1
2
3
NICHE POSITION
f
y=0.23+0.04x r=0.16
MAXIMUM POPULATION BIOMASS (kg/ha)
1.2
1.0
0.8
0.6
0.4
0.2
-0.0
0
1
2
3
4
5
6
7
NICHE BREADTH

Figure 3.- (cnt)

Correlation of distribution of species in resource space and in morphological space.

The first three principal components account for >96% of the total variance (Table 8). However, most of this is explained by the first two components (51.7% and 28.4% respectively). The first morphological component is a combination of traits characterizing the degree of adaptation to the live style in open desert landscapes with little cover (particularly the morphological specialization related to ricochetal jumping). The second principal component reflects body size and the positive correlation between linear dimensions of the body and weight. Finally, the third component is determined by a relative development of the external ear.

There is a close correlation between the first principal component of morphological space and the third canonical variate of resource space (Table 9). Thus, the degree of morphological specialization in ricochetal jumping is correlated negatively with the abundance of grass vegetation and the content of clay particles in soil ($r = -0.78$, $P < 0.001$, $Y = 2.75-0.29x$). Also, the distribution of species along the variate of body size (the second principal component) is essentially unrelated to either canonical variate.

However, more interesting is the comparison of Euclidian distances between species in morphological space (Table 10) and in resource space (Table 6). Among the Heteromyidae this correlation is substantially greater although there is an extremely weak correlation of distances for the whole community (Fig.5). Even more pronounced and significant is the correlation in distances to the nearest neighbor in morphological space with the distances between the same species in resource space ($r = -0.79$; $P < 0.001$).

Table 8.- Eigenvalues and eigenvectors forming the first three morphological components for the 11 rodent species.

Eigen-values	Cumulative proportion	Eigenvectors for original variables							
		1	2	3	4	5	6	7	8
4.17	51.6	-0.19	-0.12	0.44	0.46	-0.10	0.41	-0.47	0.37
2.20	80.2	-0.60	-0.60	0.09	-0.19	-0.24	-0.07	0.03	-0.34
1.32	96.7	0.07	0.02	-0.26	0.09	-0.77	-0.44	-0.16	0.31

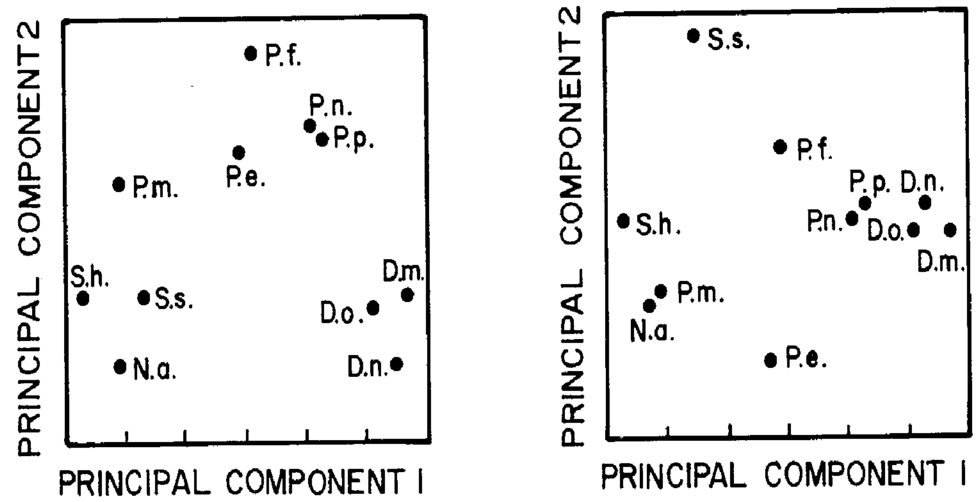

Figure 4.- Projections of 11 species of the communityin the system of coordinates formed by the first three morphological principal components. Ss, *Spermophilus spilosoma*; Pf, *Perognathus flavus*; Pp, *P.penicillatus*; Pn, *P.nelsoni*; Dm, *Dipodomys merriami*; Dn, *D.nelsoni*; Do, *D.ordii*; Pe, *Peromyscus eremicus*; Pm, *P.maniculatus*; Na, *Neotoma albigula*; Sh, *Sigmodon hispidus*; Ot, *Onychomys torridus*.

Table 9.- The results of correlation of morphological principal component variate with canonical variate of resource space.

		Canonical variate of resource space		
		1	2	3
Morphological principal components	1	0.07	-0.23	-0.78
	2	-0.06	0.26	0.12
	3	-0.16	-0.17	-0.25

Table 10.- Euclidian distances between community species in the space of the three principal morphological components.

Species	Ss	Na	Pe	Pm	Sh	Pn	Pp	Pf	Dm	Dn	Do
S.spilosoma	-	4.00	5.19	4.00	2.66	4.38	4.33	4.29	5.47	5.14	4.98
N.albigula		-	3.47	2.71	1.78	4.77	4.79	5.56	5.34	4.86	4.74
P.eremicus			-	1.97	3.74	2.59	2.71	3.55	4.25	4.54	3.89
P.maniculatus				-	2.20	3.31	3.40	3.44	5.35	5.40	4.86
S.hispidus					-	4.43	4.45	4.63	5.72	5.37	5.13
P.nelsoni						-	0.16	1.91	3.00	3.61	2.80
P.penicillatus							-	1.97	2.89	3.50	2.69
P.flavus								-	4.80	5.35	4.60
D.merriami									-	1.10	0.62
D.nelsoni										-	0.86
D.ordii											-

Discussion

Factorial variate derived through canonical analysis correspond closely to biological attributes of rodents; they represent a combination of the characters of the structure of vegetation and substrate. These characteristics have long been used by mammalogists in non-quantitative descriptions of rodent habitats. The specific features of spatial resource structure are reflected directly in the morphological features of species and corresponding forms of behavior (type of locomotion, ways of avoiding predation risk, and foraging, etc.). In fact, many characteristics of desert rodents reflect adaptations to the type of the substrate and the degree of openness of the habitat. Lower values of coefficients of variation in a group of nearest neighbors (Figs. 2a and 2b) found in subsequent groups of lesser ecological similarity indicate a regular distribution of species in a canonical variate space. This result supports the predictions of the theory of limiting similarity (May, 1973; May and MacArthur, 1972). The presence of certain limits of ecological similarity in the community is confirmed by the shapes of the curves of coefficients of variation of niche overlap and of distances between

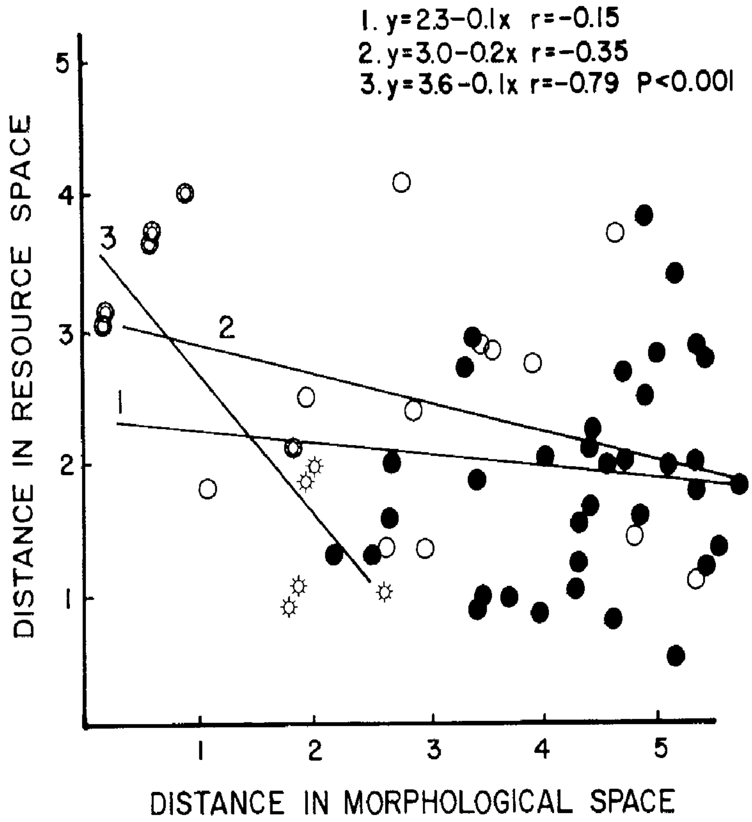

Figure 5.- Scatter diagram showing the correlation between interspecific euclidian distances in three main axis of resource space (ordinate) and three main morphological principal component axis (abscissa). Symbols: 1, all species; 2, heteromiyd species (white circles); 3, the nearest neighbors in space of morphologicalvariate (asterisks). Asterisks in circles - the nearest neighbors in morphological space for species of the Heteromyidae family.

centroids.

Fresh evidence of this regular pattern is also found in the group of nearest neighbors in morphological space of the most morphologically close species is characterized by the largest ecological distances pairs of species that belong to one genus among heteromiyds. Furthermore, a strong negative correlation of morphological distances to the nearest neighbor with the distances of the same species in resource space enables us to infer a significant role of competition in the structure of the community.

In general, communities in the Bolsón de Mapimí do not have distinct guilds of species ecologically specialized in resource space. Evidence for this is both the low values of niche overlap and the separation of niche centers of species that occupy peripheral areas in a canonical variate space. The accumulation of species in the central area of the resource space (the area of the geometrical center of the community) in the Bolsón de Mapimi is determined by the prevalence of species with broad spatial niches (Rogovin, *et al.*, 1985).

Many investigations of mechanisms of the partition of resources by heteromiyd species are based on the assumption of the existence of groups of locally syntopic species (Price and Brown, 1983). This assumption is the basis for all studies aimed at elucidating factors of the morphological differentiation of species in communities. Recent publications indicate the possibility of the partition of microhabitats by heteromiyds as a result of differences in the selection of macrohabitats within the boundaries of the area (Schroder,1987). Brown and Kurzius (1987), showed that the distribution of species is highly individual and that the possibility of co-evolution between species is rather limited. Our data on the distribution of the heteromiyd niches in resource space in the Bolsón de Mapimí support this view. Congeneric heteromiyd species are substantially separated in space even with large differences in body size: *D. merriami* (38 g), *D. ordii* (42 g), *D. nelsoni* (103 g), *P. nelsoni* (13 g), *P. penicilllatus* (15 g), *P. flavus* (6 g). The presence of a negative correlation between niche amplitude and the distance from the center of the community is directly related to the already discussed concentration of eurotopic species in the center of a resource space. Also the negative correlation between abundance (maximum population density) and niche breadth of the species is seen even with the inclusion of rare species that may not have been adequately sampled to evaluate niche breadth. There is virtually no correlation, however, when using biomass instead of population density. The maximum value of biomass in a particular type of habitat should be related to the abundance of food resources.

The absence of direct correlation between maximum density and maximum biomass may be determined by the effect of density compensation in populations of small sized species. If this is the case, then in a saturated habitat the population biomass of species of similar size and diet should be a constant. This assumption, however, was not confirmed by our data. According to our results, the population density may be determined not only by the abundance of food, but also by other factors, such as the type of social organization, which being specific species (the system of territorial relations of individuals), can influence not only the lower, but also the upper limit of the population density (Shilov, 1977).

Narrowing the spatial niche in a desert with its limited food supply is apparently possible only as a result of adaptation to relatively productive microhabitats and is accompanied by trophic specialization. For instance among asian jerboas (Dipodidae) some trophically specialized species converge in highly dense populations. The species with broad spatial niches, populating a broad spectrum of low food microhabitats are characterized by the absence of trophic specialization. In conditions of food shortage these species either use different types of food or opportunistically shift their diet to exploit available resources. These populations are usually characterized by low average density (Rogovin, 1983; Shenbrot, 1980).

Acknowledgments

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CHAPTER 4

MORPHO-ECOLOGICAL STRUCTURE OF DESERT RODENT COMMUNITIES IN CENTRAL ASIA AND SOUTHWESTERN NORTH AMERICA: A MULTIVARIATE ANALYSIS

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and Valentina Serrano

Abstract

The structural aspects of the organization of 4 rodent communities in deserts of Mongolia (Trans-Altai Gobi and Gobi-Altai) and México (Central Chihuahua and Sonora) have been studied using 20 morpho-ecological external characters of representatives of 54 populations and 41 species. Results of the principal components analysis and iterative cluster analysis show a relatively low level of convergence of species in the communities of Mongolia and México. Habitually close species in northern America and Central Asia form different dimensional groups. Rodent species of mongolian communities occupy a larger volume of the factorial space than rodent species of mexican communities, although the number of species in both types of communities is similar. The comparison of values of Euclidian distances to the nearest neighbor and their coefficients of variation in real groups of coexisting species (at the level of habitat) and in hypothetical groups formed by random combinations of species indicate the existence of regularity in species packing. The patterns of species distribution in the morphological space of mongolian and mexican communities are essentially different. Significant positive correlation between Euclidian distances in morphological space and in ecological space (distances between centers of spatial

niches) has been established for the community of mongolian rodents. However, there was no such correlation in the mexican rodent community. More than one factor must influence the community formation of each type. In the deserts of central Asia such factors could include the pressure of predators and of environmental conditions. In the deserts of North America the important role of interspecies competition is suggested.

Introduction

Interrelationships between ecological characteristics of animals and their morphological traits allow for a description ofniches on a morphological basis. These interrelationships are common knowledge. The works by Kashkarov (1938) and Lack (1947) set a first example of the use of some external structures of animals as indicators of different niche parameters.

Since niches can be identified by morphological traits, it is possible to analyze its dispersion in a multivariate space, conformed by morphological variation (Fenton, 1972; Findley, 1973, 1976; Gatz, 1979; Karr and James, 1975; Mares, 1976, 1980; Ricklefs and Travis, 1980; Ricklefs *et al.*, Cochran and Pianca,1981). Irrespective of its own limitations, the morphological approach to the study of communities possesses a number of advantages in the selection of appropriate traits as compared to the traditional ecological approach (Ricklets and Travis, 1980).

Morphological indicators may also be an important supplement for the ecological traits used in the descriptions of spatial and trophic niches. For instance, morphological factors help to reflect adequately the distribution of the centers of niches the in ecological space.

The main issues that emerge in comparing the organization of communities by morphological factors can be formulated as follows:

How similar is the structure of assemblages occupying similar habitats? How are new species incorporated into communities (with or without increase of the morphological hypervolume)?

What is the interrelationship between morphological relations of coexisting species with the trophic and the habitat relations of these species?

Is there any difference in the distribution of species in real and in random assemblages of species?

These questions suggest the possibility of characterizing the structure of communities as well as identifying certain regularities in the distribution of species. Questions on the causes for community structure can not be addressed directly, but the regular patterns may suggest mechanistic hypotheses that can be tested by a different approach of ecological research.

Considering these limitations, we used the morphological approach to compare the organization of four desert rodent communities: two from Mongolia (southern desert of Trans Altai Gobi, and the northern desert of Gobi-Altai), and the other two from the Chihuahua (Bolsón de Mapimí, Durango, México) and Sonora (Pinacate, Sonora; México).

Material and Methods

Data collection.

We have analyzed twenty morphological traits of representative of 54 populations of 41 species. Nineteen traits can be divided into two groups: those describing dimensions of structures, and those characterizing the relations between dimensions of these structures (indices). Inclusion in the analysis of both the dimensions of organs and their proportions (Mares,1976, 1980) is justified, because both are necessary to describe fully the form of a given species. Differences in indices may indicate different ways of using resources as well as divergence of species on different axis of ecological space. Differences in linear dimensions and body mass may provide evidence for the partitioning of species on some axis of ecological space. (*e.g.*, the differential use of various food items sizes of the same type by consumers of different size).

We have used the following characters: 1) head-body length, 2) tail length, 3) hind foot length (from the back of the heel to the tip of the longest toe nail),4) ear length, 5) length of the longest vibrissae, 6) distance between eyes (frontal view), 7) length of nails of front feet, 8) length of hairs on the soles of hind feet (foot bristles), 9) height of the skin cushion (support callus) on the tip of the middle toe of the hind foot, 10) length of the tuft at the end of the tail, 11) number of toes used in locomotion, 12) body weight, 13) tail/head-body length ratio, 14) foot/head-body length ratio, 15) ear/head-body length ratio, 16) forelimb (from ulnaria)/hind foot length ratio, 17) distance between eyes/head-body length ratio, 18) front foot nail/hand length ratio, 19) longest vibrissae/head-body length ratio, 20) hind foot bristle length/height of support callus on the tip of the middle toe ratio.

These characters were chosen in order to take into account peculiarities of the adaptations of species. The preference to these over other characters used in preliminary studies was based on observations of animals in nature and on published information on the comparative and functional morphology of rodents (Gambaryan,1972; Fokin,1978). The characters from 1 to 12 describe the body dimensions. Characters 2, 3, 5, and 10 are both related to dimensions of the body and to characteristic forms of locomotion.

Characters and indices 11, 13, 14, 16, and 19 reflect peculiarities of locomotion. Characters 4, 7, 15, and 18 reflect the level of adaptation for burrowing and generally, the ability to digging in the substrate (for instance in feeding). Characters 8, 9, 19, and 20 reflect adaptation to the type of substrate (loose or hard). And, finally, characters 6 and 17 reflect the relationship of the species to the cover provided by vegetation.

All measurements were taken in the field either from the carcass of animals, or from live animals (836 specimens). Their mean values of parameters were used in the analysis.

Each of the communities represent a set of populations of species potentially interacting with each other and co-occurring within a common set of habitats which included a wide range of substrates (from rocky slopes of mountains to clay and sand deserts in valleys) and of vegetation (from areas devoid of vegetation to thick covered areas of the oasis type in the deserts of Mongolia to areas of savannah interspersed in the deserts of Northern México).

Two communities of rodents representing the fauna of the deserts of Mongolia and México, were used for a more detailed analysis of their spatial organization. The data on species distribution on the environmental gradient in 1ha plots were collected in Trans-Altay Goby near Ehiin-Gol (Bayan-Hongor aimak, MPR) in June-August of 1982 and 1983, and in the central part of the Chihuahua desert in the Mapimí Biosphere Reserve near Ceballos (Durango, México) in September-November of 1981 and 1983. The physiognomic similarity of habitat conditions was also the criterion (we analyzed the distribution of species from sand dunes to gently sloping mountain foothills and of clay basins that are the result of wind erosion and water accumulation). We have not observed rare species. Their absence could be partly related to the particularities of their populations dynamics in the years of our studies.

Statistical approach

We studied the distribution of species in the morphological space using principal component analysis (PCA). The mathematics of PCA is based on parametric statistics and assumes that the variables under study are normally distributed. It is evident that the condition of normality is not met by using the mean values of the characters in interspecies comparisons. Something similar occurs if size ratios are used. As noted by Jeffers (1981), this excludes the possibility of a precise statistical evaluation of the results. Provided that the distribution of morphological factors is limited by the range of positive values of the numerical axis (the function is fully determined in that area), However, the structure of a finite model turns out to be relatively insensitive to deviations from normality. We did not include character 11 in the PCA analysis because in a series of species its change takes place with rather large increments which does not furnish the grounds to view it as a continuous parameter.

Besides the PCA technic, we have also estimated the Euclidian distances between all pairs of species by 20 morphological traits:

$$D_{ij} = [\sum_{k=1}^{20} (X_{ik} - X_{jk})^2]^{1/2}$$

where D_{ij} is the Euclidian distance between species i and j; X_{ik} and X_{jk} mean values of k character in i and j species. The mean values of each of these traits have been preliminary standardized:

$$X' = \frac{X - X''}{\text{sigma } x}$$

where X' is the standardized value of the character; X " is the mean value of the character for each species, X is the mean for all species in the community, sigma x is the standard deviation.

The distance matrix was used to classify 41 species by the entire set of characters. Classification was performed on the basis of the iterative method of cluster analysis (Puzachenco and Skulkin,1980). As a result of iteration, the initial matrix is brought to ± 1. All characteristics with coefficients of +1 in the limit are referred to as one subset; all other characteristics with maximum coefficients of -1 are referred to another one. This dichotomic procedure of classification provided a consecutive division of the whole set into pairs of subsets: from the general to the particular.

At first, approximated differences in the organization of communities were identified by comparing the regression curves of the Euclidian distances (Inger and Colwell, 1977). To plot them, the distances from each species to all others in the community were ranged from the maximum to the minimum distance by the principle of the nearest-neighbor. Then a mean value of the distance and of the coefficient of variation were derived for each rank. The latter can be viewed as characterizing the density of species packed in the factorial space of the community, which is interpreted as the evenness of the distribution of species.

We have studied morphological relationships of species in real groups that co-occur in 1ha plots in different habitats. In every group we identified distances for all species from the nearest neighbor in the group as well as the mean value and the coefficient of variation. The distance to the nearest neighbor should be the most regular characteristic, and it also should be relatively insensitive to a change in the number of species (Ricklefs and Travis, 1980). The real communities were compared with randomly organized ones (null hypothesis).

Randomly organized groups were formed whose number corresponded to the actual number of species inhabiting 1ha plots within the boundaries of the community habitat in order to formulate the null hypothesis out of the species that actually populate the area and which may potentially interact with each other (Ricklefs and Travis, formed for each case of 2,3...n species. Each of the species could be included into a random group only once. For such groups we determined mean Euclidian distances to the nearest neighbor as well as the coefficients of variation in the real groups with a different number of species from such groups were organized randomly.

The distances between centers of structural niches of coexisting species were derived by calculating the Euclidian distances between the ecological optima by each one of the independently acting and significantly influencing variables (factors) of the ecological space (amount of habitats of the region; Rogovin and Skulkin, 1986).

Results and Discussion

The PCA results reveal that the first three components account for 79% of the total variance of morphological traits (Table 1). The first PC makes for about 45% of variance; the second for about 21%, and the third for 13%, so that it is possible to consider that the space of factors, formed by the axis of the first three PC, is enough to characterize the distribution of the set of rodent species analyzed. The values of eigenvectors enabled us to determine the most informative combinations of traits.

The first PC mainly reflects the opposition of character 16 to characters 2, 3, 5, 14, and 8. The distribution of species on the axis of this PC (Fig. 1) is related to their shape, *i.e.* with the proportions of the body parts that are used in different types of locomotion and the level of adaptation to open areas of desert. The jerboas most specialized in bipedal locomotion followed by the less specialized bipedal forms (pygmy jerboas - Cardiocraniinae and kangaroo rats - *Dipodomys*), then by species using a primitive ricocheting gallop (gerbils - Gerbilinae and pocket mice - *Perognathus*), galloping ground squirrels (*Spermophilus, Ammospermophilus*) and, finally, by the species, that using mainly symmetric gaits (hamsters - Cricetinae, yellow steppe lemming - *Eolagurus*, mountain voles - *Alticola*, mouse - *Mus*). The second component reflects the linear dimensions and the body mass (characters 1 and 12). The species of rodents are distributed mainly in line with overall body size on the axis of this PC (Fig. 1a). And, finally, the third component reflects mainly positive relationship of characters 15 and 4, and also the opposition of their influence to characters 15, 10 and 18. This PC is

Table 1.- Eigenvalues and eigenvectors of components calculated by the correlation matrix of 19 morphological characteristics of species.

PC	Eigen-value	Cumulative per cent	Eigenvectors						
			1	2	3	4	5	6	7
			8	9	10	12	13	14	15
			16	17	18	19	20		
1	8.54	44.95	0.07	0.30	0.31	0.15	0.30	0.25	0.21
			0.27	0.22	0.23	0.09	0.23	0.29	0.11
			-0.29	0.18	0.24	0.23	0.08		
2	4.08	66.45	0.46	0.07	0.16	0.17	0.09	0.27	0.10
			-0.08	0.26	0.06	0.42	-0.28	-0.21	-0.06
			0.15	-0.13	-0.20	-0.31	0.08		
3	2.45	79.38	0.06	-0.05	-0.05	-0.50	-0.18	0.16	0.34
			0.04	-0.11	0.32	0.05	-0.03	-0.08	-0.56
			-0.03	0.17	0.25	-0.14	0.09		

Figure 1. Position of rodent species in the coordinate system of a) first and second, and b) first and third principal components, that describe the morphological space of communities. Species of rodents: Sc-S. crassicauda, Sk-Salpingothus kozlovi, Cp-Cardiocranius paradoxus, En-euchoreutes naso, As-Allactaga sibirica, Alb-A. balicunica, Ab-A.bullata, Ppm-Pygerethmus pumilio, Ds-Dipus sagitta, Sa-Stylodipus andrevsi Ro- Rhombomysopimus, Mm- Meriones meridianus, Cm-Cricetulus migratorius, Co C.obscurus, Ac-Alocricetulus curtatus, Pr-Phodopus roborovskii, Als-Alticola stoliczkanus, Ep-Eolagurus przewalskii, Mus-Mus musculus, Sm-Spermophilus mexicanus, Ss-S.spilosoma, St-S.tereticaudus, Ah-Ammospermophilus harrisi, Tb-Thomomys botae, Pf-Perognathus flavus, Pl-P.longimembris, Pb-P.baileyi, Pp-P.penicillatus, Pi-P.intermedius, Pn-nelsoni, Dm-Dipodomys merriami, Do-D.ordii, Dn-D.nelsoni, Dd-D.deserti, Rm-Reithrodontomys megalotis, Ot-Onychomys torridus, Sh-Sigmodon hispidus, Na-Neotoma albigula, Nl-N.lepida, Pe-Peromyscus eremicus, Pm-P.maniculatus.

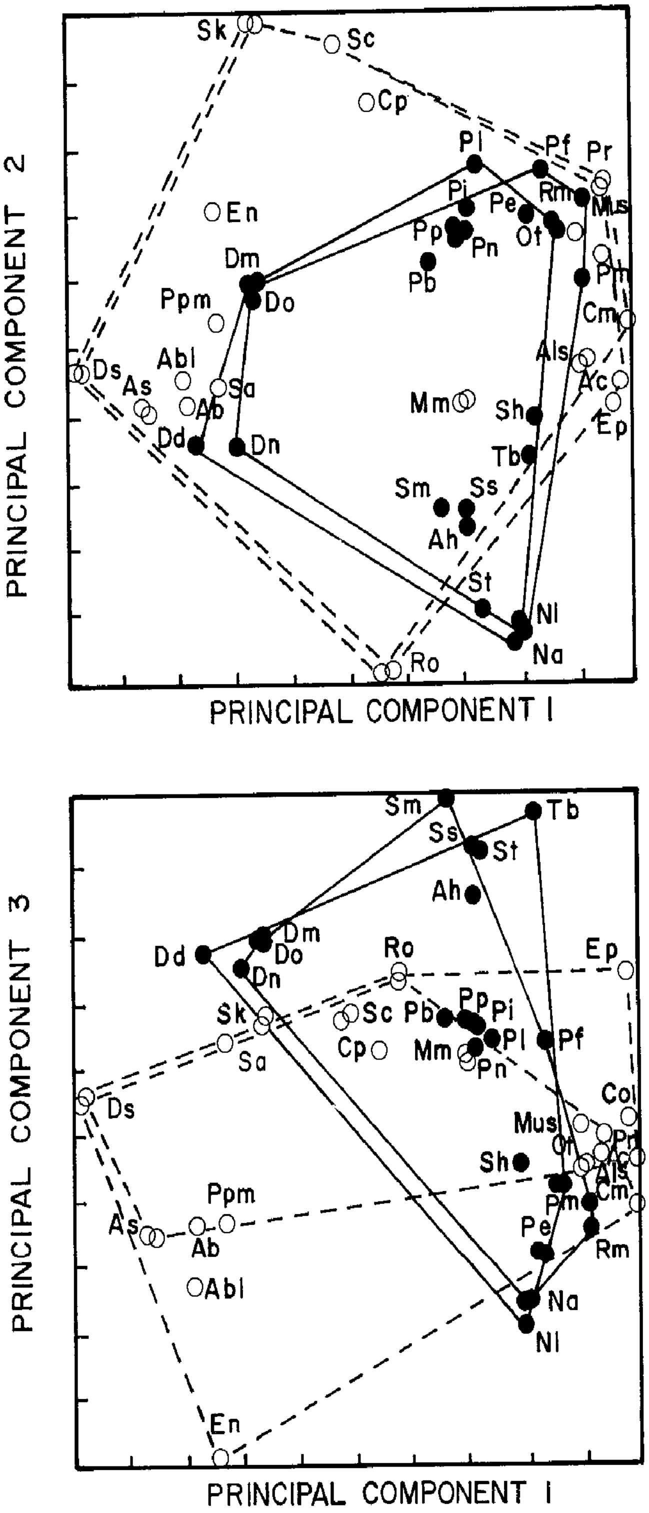
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Figure 1.

not interpreted as easily as the first two. From a certain point of view it can be characterized as the component that reveals the relationship between species of rodents to burrows or to other surface shelters: like nests, thick bushes, etc.

The analysis of the distribution of rodent species in the space of the first and second PC, and also of the first and third PC, provided the highest variance among species, to such extent that it was possible to identify the following features (Fig. 1a,b):

The rodent communities of the southern and northern deserts of Mongolia occupy a large volume of the factorial space rather than the rodent communities in the deserts of central and northwest México. This indicates a greater morphological and ecological variability in the rodents from the deserts of central Asia.

The convergent development of ecological forms of rodents in the deserts of North America and Northern Asia involves not the whole set of characters included in the analysis, but only some groups of them. For instance, the size of the body and extremities turn out to be linearly independent parameters. In North America and Central Asia, similarly shaped forms have different body sizes (*i.e.*, asian gerbils and american pocket mice).

The projection of species on the first and third axis forms groups that correspond to the traditional concept of life forms of rodents as groups of species populating one landscape-climatic zone. Pocket mice and gerbils, and to a lesser extent the kangaroo rats and some jerboas may be viewed as convergent forms in this system of coordinates.

The introduction or substitution of species in spatially separated mexican communities takes place virtually without changing the volume of the factorial space occupied by the community. However, in Mongolia, a change in the structure of communities occurs due to the infiltration of species into the already occupied area of the factorial space, and also to the expansion of the space around the periphery of the community (location of the long-eared jerboa - *Euchoreutes naso*). Nevertheless, the areas of factorial space occupied by species of communities of one continental fauna generally coincide. There is only partial coincidence of the morphological space of rodents from central Asia and north american deserts (Fig. 1a,b).

The level of external morphological similarity is limited. This furnishes fresh evidence of the absence of the stringent influence of any factor in the evolution of the desert rodents of North America and central Asia.

In line with the conclusions derived from the PCA technic, all species of rodents were also compared by the Euclidian distance taken in the space of 20 morphological traits (Table 2; Fig. 2). These results suggest a low level of convergence of rodents in mongolian and mexican deserts. The groups of species formed at the low and medium levels in a dendrogram are mainly represented by taxonomically close forms from one of the two continents with the exception of two pairs of species: one containing Andrew's three-toed jerboa 17 (*Stylodipus andrewsii*) from the Gobi desert and desert kangaroo rat (*Dipodomys deserti*) from Sonora, and the other with the house mouse from the Trans-Altai

Table 2.- Euclidian distances between species in the morphological space of the mongolian (Trans-Altai Gobi) community (above the diagonal) and of the mexican (Mapimi) community (below the diagonal).

TRANS-ALTAI GOBI (MONGOLIA)

	Sk	**Sc**	**Cp**	**En**	**As**	**Abl**	**Ds**	**Mm**	**Ro**	**Cm**	**Pr**	**Als**	**Mus**	
S.mexicanus	-	0.5	0.8	1.3	1.5	1.4	1.3	1.5	1.8	2.0	1.7	2.0	1.7	S.kozlovi
S.spilosoma	0.2	-	0.5	1.3	1.5	1.4	1.5	1.3	1.6	1.7	1.4	1.7	1.3	S.crassicauda
P.flavus	1.2	1.2	-	1.3	1.5	1.3	1.4	1.1	1.5	1.5	1.3	1.6	1.1	C.parsoxus
P.nelsoni	1.1	1.0	0..5	-	0.9	0.9	1.3	1.6	1.8	2.0	2.0	1.9	1.7	E.naso
P.penicillatus	1.0	1.0	0.5	0.1	-	0.4	0.9	1.5	1.5	2.2	2.2	2.0	1.7	A.sibirica
D.merriami	1.1	1.2	1.3	1.1	1.0	-	0.8	1.4	1.4	2.0	2.0	1.8	1.8	A.balicunica
D.nelsoni	1.1	1.1	1.6	1.3	1.2	0.5	-	0.8	1.5	2.3	2.2	2.2	2.1	D.sagitta
N.albigula	1.3	1.1	1.4	1.2	1.3	1.7	1.5	-	0.8	1.0	1.1	1.0	0.7	M.meridianus
O.torridus	1.3	1.1	0.5	0.7	0.7	1.5	1.0	1.1	-	1.5	1.6	1.4	1.5	R.opimus
P.eremicus	1.4	1.3	0.6	0.6	0.6	1.4	1.6	1.1	0.4	-	0.7	1.2	0.8	C.migratorius
P.maniculatus	1.3	1.1	0.6	0.7	0.8	1.6	1.7	1.0	0.3	0.4	-	1.3	0.9	P.roborovskii
	Mm	**Ss**	**Pf**	**Pn**	**Pp**	**Dm**	**Dn**	**Na**	**Ot**	**Pe**	**Pm**	-	1.0	A.stoliczkanus
MAPIMI (MEXICO)													-	M.musculus

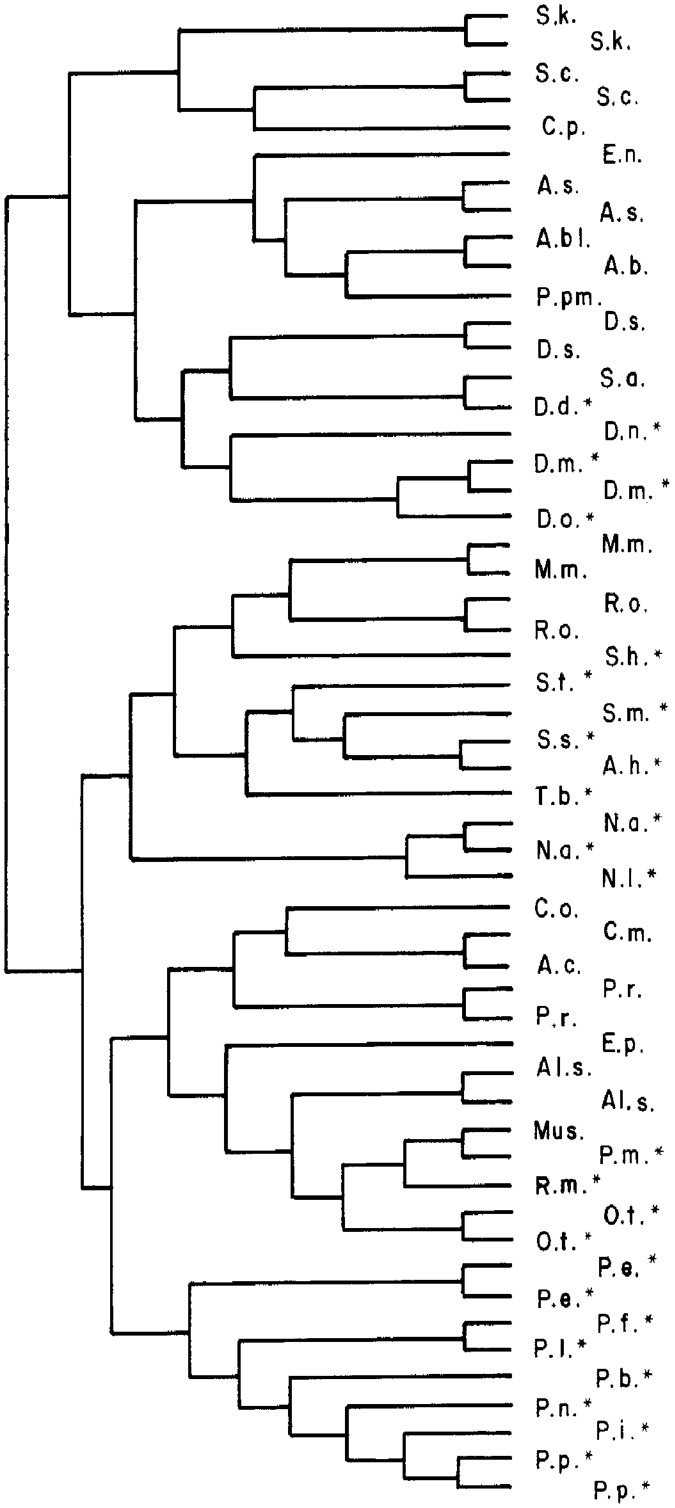

Figure 2.- Morphological classification of desert rodent. Results of the cluster analysis by Euclidian distances between species in the space of 20 morphological characters. Mexican species are designated by asterisks.

Gobi (*Mus musculus*) and a deer mouse from the Chihuahua desert (*Peromyscus maniculatus*). Among bipedal forms, the american kangaroo rats are closest to three-toed jerboas; also the level of difference remains rather high. The pygmy jerboas, similar in shape to kangaroo rats are far from them due to significant differences in size. The same disintegration of groups of similarly shaped forms can be seen during the analysis of quadrupedal species (asian jerbils and north american pocket mice, and also the north american woodrat (*Neotoma* spp.) and the deer mice (*Peromyscus* spp.).

Closest to Asian gerbils in this classification are American ground squirrels. Together with the woodrats, all these species are placed into one large group. The american pocket mice represents another isolated group of species. And, finally, another group of quadrupedal rodents is formed by asian and american small hamster-like species; these are separated by substantial distances except for the mouse (*Mus musculus*) and the deer mouse (*Peromiscus maniculatus*).

The relationships of the regression curves of mean values of Euclidian distances between species of different levels of morphological closeness and the coefficients of variation (CV) of these distances in two communities of desert rodents from Mongolia and México are shown in Fig.3. Species in the mongolian community were consistently and significantly more variable than species in the

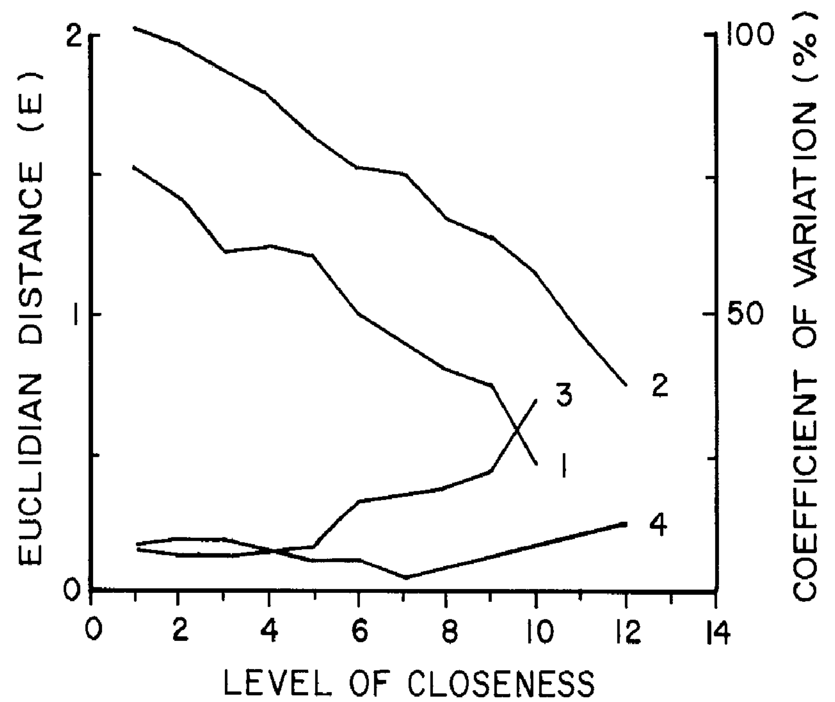

Figure 3.- Dependence of the average value of Euclidian distances between species (E) and coefficients of variation (CV,%) of these distances on the level of the morphological closeness of species (the latter increases on the abscissa from left to right). 1 - mean E values for the Mapimí community(México), 2 - mean E values for the Trans-Altai Gobi community(Mongolia), 3 - CV in the Mapimí community, 4 - CV in the Trans-Altai Gobi community.

mexican community (here and below by the criterion of exceeding one series over another, $P<0.001$; Plokhinsky, 1970). This tallies with the results of the PCA. The CV of the distances between the nearest neighbors is substantially large in the community of the mexican desert rodents. The difference in the CV values *Per se* shows the variations in the organization of the communities. A CV lower value in Mongolia in combination with a larger value of the Euclidian distances may show a more dense packing of the mongolian species in the morphological space. These features may reflect a different level of the taxonomic relationship among the species of each fauna, and may be only indirectly related to the ways that the species have partitioned the ecological space.

The communities that we have analyzed are constituted by species that use the whole spectrum of habitats in the region. At the same time the character of species packing in groups of locally coexisting species may be essentially different than the pattern for the fauna of a larger region. Species that use similar food resources (phylogenetically as a rule, and therefore, Morphologically related species) may often be divergent in their use of habitats (Schoener, 1974).

Our analysis of the morphological organization of species assemblages that populated particular habitat along similar geomorphological gradients within the mongolian and mexican deserts, supports the above considerations and enables us to represent more objectively the peculiarities of the combination of species.

Fig. 4 (a and b) depicts the average distances to the nearest neighbor and CV in groups from 2 to 8 species, that were found together in various habitats in Mongolia and México. These values are compared with similar characteristics obtained for similarly sized groups constituted by a randomly withdrawing species from their pools of the community of each type.

The average distances to the nearest neighbor in groups, constituted by a random combination of species of mongolian rodents significantly surpassed the comparable random draws from mexican communities ($P<0.001$) which, quite naturally, is related to the greater interspecies variation in the mongolian community (Fig. 4a, see also Fig. 3). However, for the groups of locally coexisting species, each of the communities has a similar distribution of values to a great extent for assemblages of 4-5 species. In the groups with a smaller number of species (2-3 species) for the average distances, the inhabited and simply structured habitats to the nearest neighbor are usually larger in México. For groups formed by 6 and more species however, the average distances to the nearest neighbor in México are less than in Mongolia. The latter may reflect the effect of the structural complexity of the environment in mexican deserts. The plots in which six or more species occurred were located in ecotonal habitats with a complex structure and, as a consequence, they contained species which are morphologically similar (representatives of the different habitat types) as well as morphologically distant species.

The CV of the distance to the nearest neighbor in randomly organized groups grew larger with an increase in the number of species in a mexican community, whereas in a mongolian community, they remained virtually unchanged (Fig. 4b).

This also tallies with Fig. 3. For real groups of species from local sites of mongolian and mexican deserts within the Mexican community, the CV are higher at the initial and final section of the axis of the number of species. The first may reflect a more regular packing of the mongolian species in small assemblages from simply structured habitats. There is also a substantial overlap of areas of the distribution of points in the graph. A substantial increase of the CV in the real groups consisted of a large number of species in México, may result from including complex structured boundary habitats with morphologically close and distant species.

Regarding the groups that were formed at random, the average distances to the nearest neighbor are smaller in mongolian real assemblages ($P<0.001$). However, in a mexican community the differences are not significant, although there is a slight tendency of the opposite action to the first case. CV of distances to the nearest neighbor in real groups, formed by a small number of species in both types of communities, are located below the lines characterizing randomly organized groups, which indicates the tendency towards regularity of the species packed in small assemblages. (The significance of differences has not been estimated due to the limited number of groups with a reduced number of species). In the mexican community the tendency towards regular combination of species is more pronounced although with an increase in the number of species in real groups the difference from the groups formed at random gradually disappears.

The approach to analysis of the morphological organization in the communities of mongolian and mexican desert rodents shows substantial differences in their organization. These differences are determined by a low level of convergence of morphological forms of rodents on both continents as well as different level of the interspecies morpho-ecological variation within each type of the community.

The taxonomic distances between species in the communities of the mongolian and mexican deserts are essentially different. The mongolian communities are usually formed by representatives of different genera and even subfamilies of rodents whereas in the mexican communities, the species of one genus often occur together. Apparently the level of morpho-ecological differences between species within communities is directly related to the peculiarities of their taxonomic organization.

In all probability, the phylogenesis of the principal taxa, which determine the composition of communities of both types, ran parallel. Findings of the earliest fossil of ricocheting rodents are referred to the Miocene. Jerboas similar to the present forms have been found in the early Miocene deposits of Central Asia. Jerbils appear in central Asia at the end of the Miocene (Shevyreva, 1983). The divergence of heteromyid rodents was well under way in North America in the Miocene-Pliocene (Lidsay, 1972; Hafner, 1978; Patton *et al.*,1981; Hafner, and Hafner, 1983). The initial isolation and differentiation of the Heteromyidae family well as that of the Dipodidae family began back in the Oligocene (Wood, 1935; Shevyreva, 1983).

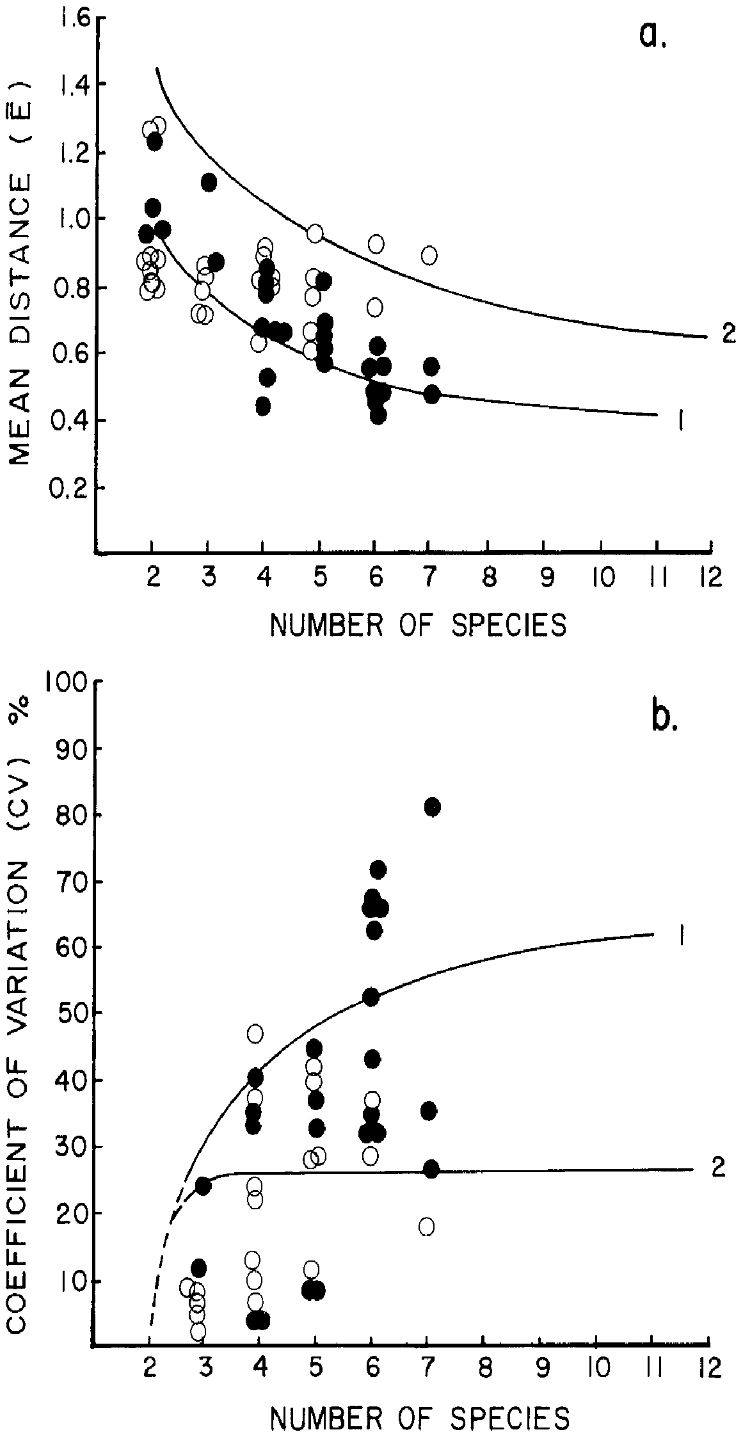

Figure 4.- Dependence of the mean distance to the nearest neighbor (a) and of coefficients of variation of distances (b) on the number of species in the biotopic group: 1) in the Mapimí community; 2) in the Trans-Altai Gobi community. Line - mean level of the process for the random groups. Black circles - real biotopic groups in the Mapimí community. White circles - the same but in the Trans-Altai Gobi community.

The formation of deserts in North America and in Asia took place almost at the same time due to the processes of mountain formation in the Miocene-Pliocene (Axelrod, 1950; Sinitzin, 1967; Petrov, 1973; Bailey *et al.*, 1977). However, the rate of development of desert landscapes on each continent remained different.

The Neogene northern american deserts did not reach the same level of development as in Asia. The formation of desert vegetation was restricted to small sections of low mountains, whereas the valleys were occupied by forests for a long time (Axelrod, 1975, 1979). In the Pleistocene glacial periods, the Sonora desert (one of the most arid regions at present in North America) was represented by mosaics of xeric refugees, intermingled with mesic habitats (Martin and Mehringer, 1965). Similar conditions existed in the post-glacial period of the Mohave, Sonora and Chihuahua deserts. Rapid desiccation of landscapes in these modern deserts began simultaneously about 8000 years ago (Van Devender, 1977; Van Devender and Spaulding, 1979; Van Devender and Burgess,1985). The mosaic nature of the distribution of arid landscapes in North America which could have promoted an increase in the rate of species formation, was not reflected in the morphological and ecological divergence of desert rodents. There is every reason to consider that the desiccation of Asia (including Central Asia), took place on a larger scale than in North America (Petrov,1973; Babaev *et al.*, 1986). The extremely low productivity of the present mongolian deserts is remarkable. The diversity of plant species, unlike mexican deserts, is extremely low, and the structure of plant communities is more simple. The deserts on both continents, although similar in topographic relief as well as in the structures of the substrate and vegetation, the history and patterns of these habitats are indisputably different.

Thus the existing differences in the morphological and ecological adaptation of the species found in mongolian and mexican communities can be explained by the history of the habitat conditions. The differences of these conditions in large regions with arid climates could influence the rate of ecological and morphological divergence of desert rodents. It should be also noted that the communities of the southern and northern deserts of Mongolia do not include such species of rodents as suslics (*Citellus*) and mole-voles (*Elobius*) which are ecologically and morphologically equivalent to american ground squirrels (*Spermophilus*) and gophers (Geomyidae). The above mentioned asian forms do not penetrate at present into the desert area due to the high aridity of the climate, but have inhabited this area in the past. The introduction of species such as *Citellus palidicauda* and *Ellobius tancrei* in the analysis would increase the volume of the morphological space of Mongolian communities even further.

Our analysis has also revealed differences between the organization of real locally coexisting sets of species and groups drawn at random and indicates the regularity in the community structures. Such a regularity can be identified only in the groups of locally coexisting species. The differences in the organization of groups (identified by morphological factors), show the variation in the ecological organization of these groups in the communities of each type. Fresh evidence for this is the difference in the correlation of distances between the centers of spatial niches of the species with distances between species in the space of morphological factors in communities of Mongolia and México (Fig. 5). The weak positive correlation (r = 0,56; P 0.01) between these characteristics in Mongolia (Fig. 5a) speaks in favor of the priority effect of the environmental conditions, since similar morphological species have a tendency to live in similar environments. This result can also be explained by the impact of predation, which could be also viewed as an external condition with respect to the community. Whereas the absence of the correlation between the above mentioned characteristics in México (r = -0.14) can be inferred as the influence on the community organization of such factors as interspecies competition (Fig. 5b). The competition in communities of american desert rodents has been confirmed experimentally (Munger, and Brown, 1981; Lemen, and Freeman, 1983,1987).

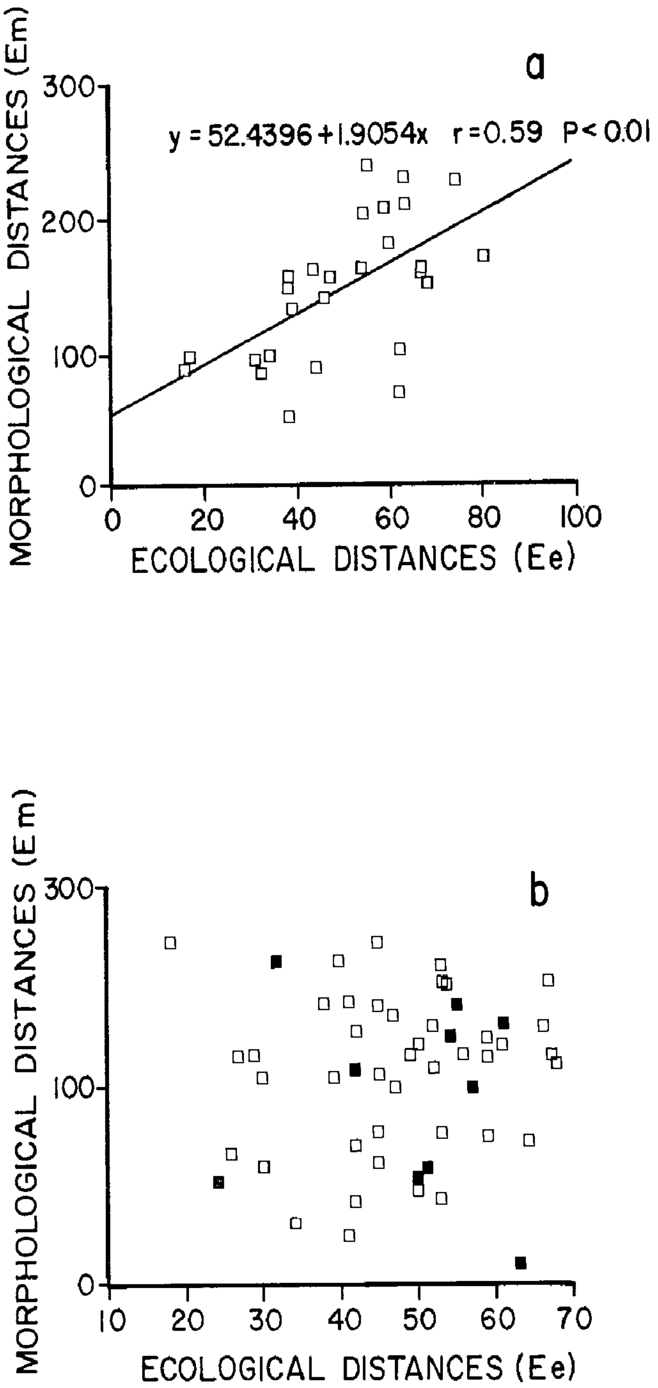

Figure 5.- Dependence of Euclidian distances between species in the space of morphological factors (Em) on the distances between centers of their spatial niches (Ee). a - community of Mapimí (México), b - community of Trans-Altai Gobi (Mongolia). Black circles - species of heteromyid rodents.

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CHAPTER 5

COMPARATIVE ANALYSIS OF THE SPATIAL ORGANIZATION OF THE DESERT LIZARD COMMUNITIES IN MIDDLE ASIA AND IN MEXICO

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and Alexey V. Surov

Abstract

The spatial organization of two lizard communities from the Turan (Bukhara) and Chihuahua (Mapimí) deserts were analyzed by the use of canonical (discriminant function) analysis. Twenty-three environmental parameters (soil structure, vegetation) were considered. The number of species in both communities is similar (13 in Bukhara and 14 in Mapimí) but the mean densities of most Mapimi populations are four times lower than those in Bukhara. Half of Mapimi's species are rare (1-4 sp/ha) and maximum densities are 18-27 sp/ha. The mean densities of most Bukhara species are at the level of 20-40 sp/ha and densities of the most abundant species are 80-120 sp/ha. In spite of these differences the lizard community biomass in both localities are similar. The ecological niches of lizards in both communities are distributed on two main ecological axis. The first axis represents the gradient of soil structure from and to clay; the second axis represents the gradient of protective conditions (percent of vegetation cover, number of rodent burrows). In the Mapimí community the distribution of niches is regular, but there are two distinct spatial guilds in Bukhara consisting of psammophilous and sclerophilous species. The niche overlap in Mapimí is lower than that in Bukhara. There is a negative correlation between the niche breadth and the distance from the center of the resource space. There are no correlations among species abundance, niche breadth and niche position in the resource space. We discuss the problem of elucidating the eco-equivalent species in the intercontinental comparison.

Introduction

Two central problems of community ecology are those concerned with the mechanisms that enable species to coexist and the analysis of community structure. In many cases the spatial displacement is an important mechanism that facilitates the coexistence of sympatric species (Schoener, 1974). The importance of spatial displacement has been demonstrated many times for desert lizards, which are a traditional subject of community studies (Pianka, 1973, 1975). A recent approach to studying the spatial displacement of co-occurring species is based on the use of discriminant function analysis methods applied to a large set of structural habitat variables at the sites where individuals were registered (Cody and Walter, 1976; Conner and Adkisson, 1976; M'Closkey, 1976; Morris, 1979; Dueser and Shugart, 1979; Crowford *et al.* 1981; Reinert, 1984). Although some applications of discriminant analysis deserve criticism (Carnes and Slade, 1982; Van Horne and Ford, 1982), this method remains theoretically suitable for the analysis of the niche structure of communities (Green, 1971, 1974). The analysis of correlations between the abundance of species and the main niche parameters, known as "niche pattern" (Shugart and Patten, 1972), is being developed within this framework. Until now niche patterns have been examined for a limited set of communities. These are insufficient in order to elaborate any definite conclusions on the generality of such relationships (Shugart and Patten, 1972; Dueser and Shugart, 1979; Seagle and McCracken, 1986; Robey *et al.* 1987).

The main objective of this paper was to study the specific features of the spatial organization and niche patterns in two genetically divergent communities of desert lizards in Middle Asia and North America. The comparison of the communities, which occur in a more or less similar environment, but possess a very different genetic structure and evolutional history, can answer general questions about their structure and niche pattern, as well as identifying specific features of each community.

Material and methods

Study sites.

The investigations in Middle Asia were conducted in the southern part of the Kyzylkum desert, in the vicinity of the Bukhara Central Asian Gaselle Ranch (referred to as Bukhara). This area is situated at 220-330 m above sea level in the Karaulbazar district of the Bukhara region of the Uzbek Republic (39 33'-39 41' N 64 35'-64 43' E). The climate is dry and extremely continental. Mean January and July temperatures average -1 C and +31 C, respectively; mean annual precipitation is 110 mm; rains occur from mid October to mid May (Balasheva *et al.* 1961). This area is an alluvial plain, formed by a blind ancient delta of the Kashkadarya river, with some low degraded uplands. Rocks on hilltops and slopes of the degraded mountains are covered with *Calligonum junceum*, *Salsola arbuscula*, *Convolvulus hammadae,* Ephedra strobilacea, *Artemisia* herba-alba. The foot of small sandy hills are covered with *Astragalus villosisimus*, *A.unifoliatus, Calligonum setosum, C.microcarpum, Convolvulus divaricatus.* The elevated parts of the alluvial plain on sandy-loam soils (tops and upper parts of the low hills) is covered with *Artemisia herba-alba, Salsola gemmascens,* and *Ammothamnus lehmannii.* The closed depressions on this plain with unsalted ("takyr") or salt ("solonchak") clay soils are inhabited by vegetation communities of *Halocnemum strobilaceum* and *Kalidium caspicum.*

In México investigations were carried out in the southern part of the Chihuahua desert at the Bolsón de Mapimí reserve (hereafter referred to as Mapimí). This area is located at 1000-1350 m above sea level at the junction of the states of Chihuahua, Coahuila and Durango (26 29' - 26 52' N and 103 58' - 103 32' W). The climate is dry and subtropical. Mean monthly temperature ranges from +11 C in January to +28 C in July; annual precipitation averages 230 mm; rains occur from June to September (Barbault and Halfter, 1981). The area is an elevated plateau split by low hills between which are closed depressions without runoff (playas). The lower part of the mountain slopes with rocky substrate (magueyal) are inhabited by vegetation communities dominated by *Agavae asperrima, Larrea divaricata* and *Euphorbia antisyphilitica*. Small gravel alluvial fans (bajadas) are covered with *Opuntia rastrera, Larrea divaricata, Agavae asperrima* and *Fouquiera splendens.* Alternating at lower elevations are playas and low hills. The playas, flooded during rains and containing clay soil, resemble the takyr and the solonchak formations. They support little vegetation except for dense thickets of sod-like grasses (*Hillaria mutica*) and shrubs (*Prosopis* spp. and *Suaeda nigrescens*). The depressions are edged by sandy hills, of smaller area, and are covered by vegetation dominated by *Larrea divaricata, Yucca elata* and *Jatropha* dioica.

Species of lizards

There are 15 species of lizards on the Bukhara study site (Shenbrot and Kulikova, 1985):

Gekkonidae:
Teratoscincus scincus (Schlegel, 1858)
Crossobamon eversmanni (Weigmann, 1834)
Gymnodactylus caspius Eichwald (1831)

Agamidae:
Agama sanguinolenta (Pallas, 1813)
Phrynocephalus helioscopus (Pallas, 1771)
Phrynocephalus reticulatus Eichwald (1831)
Phrynocephalus interscapularis Lichtenstein (1856)
Phrynocephalus mystaceus (Pallas, 1776)

Varanidae:
Varanus griseus (Daudin, 1803)

Scincidae:
Ablepharus deserti Strauch (1868)

Lacertidae:
Eremias velox (Pallas, 1771)
Eremias intermedia (Strauch, 1876)
Eremias lineolata (Nikolskiy, 1896)
Eremias grammica (Lichtenstein, 1823)

Thirteen of these species are discussed in this article. There were no *A. deserti* on the grids; *V. griseus* was present only in small numbers.

There are 17 species of lizards in Mapimí (Maury and Barbault, 1981):

Gekkonidae:
Coleonyx brevis Strejnegar (1893)

Iguanidae:
Cophosaurus texanus Troschel (1852)
Holbrookia maculata Girard (1851)
Uma exul Schmidt et Bogert (1947)
Uta stansburiana Schmidt (1921)
Sceloporus magister Hallowell (1854)
Sceloporus undulatus Girard et Girard (1854)
Sceloporus poinsetti Baird et Girard 1854)
Crotaphytus collaris Say 1842)
Crotaphytus wislizeni Baird et Girard (1852)
Phrynosoma cornutum (Harlan, 1825)
Phrynosoma modestum Girard (1852)

Xantusiidae:
Xantusia vigilis Baird (1858)

Scincidae:
Eumesces obsoletus Baird et Girard (1852)

Teiidae:
Cnemidophorus inornatus Baird et Girard (1858)
Cnemidophorus scalaris Cope, Williams et Smith (1892)
Cnemidophorus tigris Baird et Girard (1852)

Twelve of these species are discussed in this article. *S. poinsetti*, *X. vigilis* and *E. obsoletus* have not been observed on the grid, and the numbers of *S. magister* and *C. collaris* were too low to be included in the analysis.

The lizard species are divided into six foraging guilds on the basis of their foraging behavior. Four of these are common to the Bukhara and to the Mapimi communities. Table 1 gives the body weights and foraging guild affinities of the species included in the analysis.

Table 1.- Composition of foraging guilds in the desert lizard communities of Bukhara and Mapimi (mean weight of lizards in brackets).

Type of foraging behavior	Lizard species			
	Bukhara		**Mapimí**	
1. Nocturnal active Foragers	*C. versmanni*	(1.91)	*C. brevis*	(2.00)
	G. caspius	(4.90)		
2. Nocturnal sit-and-wait	*T. scincus*	(11.14)		
3. Diurnal sit-and-wait under shrubs	*A. sanguinolenta*	(14.63)	*U.stansburiana*	(3.85)
			S. undulatus	(11.78)
			C.wislizeni	(13.32)
4. Diurnal sit-and-wait on open sites	*P. helioscopus*	(5.03)	*C. texanus*	(8.55)
	P. reticulatus	(2.54)	*H. maculata*	(5.76)
	P. mystaceus	(30.19)	*U. exul*	(9.57)
	P. interscapularis	(1.15)		
5. Diurnal active foragers	*E. velox*	(6.53)	*C. scalaris*	(9.05)
	E. intermedia	(4.77)	*C. tigris*	(9.50)
	E. grammica	(13.13)	*C. innornatus*	(3.56)
	E. lineolata	(1.84)		
	E. scripta	(1.21)		
6. Specialized mirmecophagous			*P. cornutum*	(49.70)
			P. modestum	(5.13)

Data collection.

Data were collected in Bukhara in April-May, 1980-1982 and in Mapimí in October-November 1987.

The system of data collection was as follows. Squares 1ha grids were selected at random in the study sites. Each of these grids was divided into 25 smaller sample plots, 20 x 20 m, whose centers were marked with 50 cm aluminum stakes. The location of each lizard encountered in these plots was recorded during one to two days (and at night, by the light of a torchlight). A 0.5 kg soil sample was taken from the center of each plot for laboratory analysis of its mechanical composition. The number of shrubs (by species) in each plot was counted in a circle 5m in diameter; to determine the vegetation cover and volume by height layers within each plot, we measured the height and diameter of the crowns of shrubs (for 30 shrubs of each species in the plot). Additionally we counted the number of rodent burrow openings in these 5m circles. The abundance of grasses was evaluated by clipping all grass in 0.25 m^2 sample plots (4 sample plots in each plot).

Twelve parameters have been used for the subsequent analysis (Table 2). We have sampled and characterized a total of 24 1-ha plots in Bukhara and 16 plots in Mapimí.

Statistical treatment of data.

Discriminant (canonical) analysis was used to describe the dispersion of species niches in resource space for these two communities. All species of one community were simultaneously introduced in the analysis. Some groups of species in certain foraging guilds were analyzed separately. Before the analysis, the initial data were log-transformed to normalize them. Indices of the niche breadth and position (distance from the centroid of a particular species to the centroid of the community) were calculated for each species by the results of the analysis of the canonical variates. Unlike Dueser and Shugart (1979), we measured the niche breadth as the standard deviation of observation points for a given species from the centroid of that species in the space of the canonical axis (Carnes and Slade, 1982). To avoid the effect of differences in the abundance of species on the calculation of the niche position, these were calculated not as the distances of species centroids from the initial coordinates of canonical space, but as the distances of species centroids from the centroid of the whole community whose coordinates were calculated as the arithmetic mean coordinates of the species centroids.

Niche overlap was evaluated by paired comparisons of the observation points of two species using discriminant analysis. As a measure of niche overlap we used the overlap in the probability of displacement on the discriminant axis, *i.e.* the probability of erroneous assignments (Green, 1974; Cody and Walter, 1976).

To evaluate the degree of unevenness in niche displacement in resource space, we analyzed a niche overlap matrix, employing the method of the "nearest neighbor analysis" (Inger and Colwell, 1977). As a measure of species abundance less (influenced by possible artifacts of estimation) the directly observed maximal population density (or biomass) of the species estimated for each of the 1ha plots, was used as an index of species abundance instead of the commonly used estimation indices (Dueser and Shugart, 1979; Robey *et al.* 1987).

Table 2.- Designation and description of the 12 habitat-structure variables included in the observation vectors for multiple discriminant function analysis.

Mnemonic	Variable	Unit
DRB	Density of rodent burrow openings	no/sq.m.
RCK	Contents of rocks in the soil	%%
GRW	Contents of gravel in the soil	%%
CLY	Contents of clay in the soil	%%
AGR	Abundance of annual grasses	no/sq.m.
FRB	Abundance of annual forbs	no/sq.m.
SAL	Abundance of annual succulents	no/sq.m.
AGF	Overall abundance of annual plants	no/sq.m.
PPG	Perennial grass cover	%%
PSH	Shrub cover	%%
SHV1	Perennial plant crown volume at the level 0-25 cm	%%
SHV2	Perennial plant crown volume at the level 25-50 cm	%%

Results

Patterns of species abundance and habitat use.

On the 24 1ha grids in Bukhara we recorded 146 *Crossbamon eversmanni*, 112 *Teratoscincus scincus*, 62 *Gymnodactylus caspius*, 120 Agama *sanguinolenta*, 160 *Phrynocephalus helioscopus*, 178 *Ph.reticulatus*, 21 *Ph.mystaceus*, 455 *Ph.interscapularis*, 92 *Eremias velox*, 146 *E.intermedia*, 82 *E.grammica*, 151 *E.lineolata* and 34 E.scripta.

At Mapimí on 16 1ha grids we recorded 5 *Coleonyx brevis*, 6 *Crotaphytus wislizeni*, 2 *C.collaris*, 18 *Sceloporus undulatus*, 2 *S.magister*, 45 *Cophosaurus texanus*, 20 *Holbrookia maculata*, 48 *Uma exul*, 7 *Phrynosoma cornutum*, 7 *Ph.modestum*, 45 *Uta stansburiana*, 61 *Cnemidiphorus tigris*, 23 *C. scalaris* and *C. inornatus*.

The distribution of lizards by habitats in Bukhara and Mapimí is presented in Tables 3 and 4. Three species out of 13 at Bukhara and 5 out of 14 at Mapimí occurred in only one biotope. Narrowly specialized species at Bukhara, such as *Ph.interscapularis, Ph.mystaceus* and *E.scripta*, occurred on sands; whereas in Mapimí one stenotopic species occurred on sand dunes (*U.exul*), one (*Ph.modestum*) on bajadas and 3 (*S.magister, H.maculata* and *S.innornatus*) on playas. The majority of species in both faunas occurred in 2-3 habitats; only 2 species at Bukhara (*A. sanguinolenta* and *E. lineolata*) and 1 at Mapimí (*C. tigris*) occurred in all biotopes. Mean values for each species of the 12 environmental parameters are given in Tables 5 and 6.

Table 3.- Density (no/hectare) of lizard species and overall lizard biomass (g/hectare) in the Bukhara desert.

Lizard species	Habitats				
	Rock hills	Gravel plains	Clay plains	Sand plains	Sand dunes
Teratoscincus scincus	-	1.6	-	0.2	14.1
Crossobamon eversmanni	-	2.6	-	1.0	17.2
Gymnodactylus caspius	-	1.2	1.8	8.3	-
Agama sanguinolenta	1.0	3.8	5.0	10.5	2.8
Phrynocephalus helioscopus	1.0	7.6	15.4	-	-
Phrynocephalus reticulatus	-	22.0	1.0	-	-
Phrynocephalus interscapularis	-	-	-	-	68.3
Phrynocephalus mystaceus	-	-	-	-	2.8
Eremias velox	-	3.6	9.2	4.0	-
Eremias intermedia	5.0	8.4	1.2	16.5	-
Eremias lineolata	1.0	12.1	0.4	10.5	1.1
Eremias scripta	-	-	-	-	4.2
Eremias grammica	-	0.6	-	0.2	11.4
Overall density	8.0	63.5	34.0	51.2	121.9
Overall biomass	35	375	317	469	691

Table 4-. Density (no/hectare) of lizard species and overall lizard biomass (g/hectare) in the Mapimi desert.

Lizard species	Habitats			
	Magueyal	**Bajada**	**Playa**	**Sand dunes**
Coleonyx brevis	-	0.8	-	0.5
Crotaphytus wislizeni	-	0.8	0.1	0.5
Crotaphytus collaris	.	0.2	0.1	-
Sceloporus undulatus	1.5	1.6	1.0	-
Sceloporus magister	-	-	0.3	-
Cophosaurus texanus	6.0	5.4	-	-
Holbrookia maculata	-	-	2.9	-
Uma exul	-	-	-	24.0
Phrynosoma cornutum	-	0.4	0.7	-
Phrynosoma modestum	-	1.0	-	-
Uta stansburiana	-	1.6	0.4	16.5
Cnemidophorus tigris	1.5	4.6	0.4	16.0
Cnemidophorus scalaris	1.5	0.8	2.3	-
Cnemidophorus innornatus	-	-	1.3	-
Overall density	10.5	17.2	9.5	57.5
Overall biomass	97	160	99	453

The density of populations of both the separate species ad of all species of lizards combined at Bukhara were generally higher that at Mapimí. However, the biomass of lizards in both faunas were characterized by similar values ad showed similar trends with respect to habitat: it was maximum on sands and minimum on rocky foothill grids (Table 3,4).

Table 5.- Sample estimates of mean and standard deviation (x±s) for each lizard species in Bukhara on the 12 log-transformed habitat variables included in the observation vector for the multiple discriminant analysis. Mnemonics for variables are from Table 2.

Variable	**C. eversmanni** (n=146)	**T. scincus** (n=112)	**G. caspius** (n=62)	**A. sanguinolenta** (n=120)	**P. helioscopus** (n=160)
DRB	0.026±0.065	0.020±0.051	0.740±0.232	0.309±0.271	0.107±0.237
RCK	0.072±0.362	0.057±0.344	0.739±0.578	0.347±0.552	0.513±0.445
GRW	0.310±0.812	0.204±0.657	1.626±0.489	0.985±0.949	1.571±0.868
CLY	1.402±0.674	1.354±0.677	2.529±0.580	2.186±0.638	3.079±0.611
AGR	2.673±2.309	2.371±2.434	4.110±1.073	4.051±1.402	2.098±1.694
FRB	2.394±1.541	2.284±1.469	3.782±1.272	4.181±1.116	3.365±1.868
SAL	0.398±0.631	0.494±0.710	1.116±1.033	1.009±1.313	2.000±1.316
AGF	3.463±1.996	3.196±2.071	4.972±0.989	5.167±1.021	3.962±1.732
PPG	0.447±0.493	0.512±0.533	0.051±0.401	0.130±0.488	0.000±0.000
PSH	2.531±0.792	2.287±0.669	1.804±0.873	2.327±0.954	1.671±0.925
SHV1	1.958±0.571	1.797±0.559	1.448±0.743	1.922±0.770	1.335±0.833
SHV2	2.169±0.730	1.969±0.687	1.018±0.946	1.562±1.101	0.632±0.775

Variable	**P. reticulatus** (n=178)	**P. mystaceus** (n=21)	**P. interscapularis** (n=455)	**E. velox** (n=92)	**E. intermedia** (n=146)
DRB	0.012±0.077	0.013±0.044	0.036±0.063	0.166±0.245	0.216±0.245
RCK	0.677±0.937	0.000±0.000	0.007±0.086	0.499±0.545	0.414±0.762
GRW	1.776±1.055	0.000±0.000	0.010±0.120	1.346±0.845	1.165±1.053
CLY	2.997±0.386	1.029±0.091	1.219±0.126	2.940±0.761	2.404±0.616
AGR	0.535±0.939	1.955±1.862	3.886±1.770	2.678±1.876	2.418±1.827
FRB	1.203±1.727	2.375±1.586	3.211±1.125	3.641±1.820	3.256±1.766
SAL	0.891±1.087	0.184±0.347	0.625±0.663	1.680±1.383	0.813±1.115
AGF	1.572±1.777	2.967±1.837	4.574±1.330	4.221±1.916	3.904±1.729
PPG	0.000±0.000	0.824±0.425	0.447±0.574	0.065±0.441	0.000±0.000
PSH	1.457±0.768	2.158±1.010	2.763±0.499	2.028±0.931	2.485±0.785
SHV1	1.156±0.665	1.643±0.607	2.182±0.410	1.707±0.812	2.076±0.711
SHV2	0.643±0.579	2.000±0.804	2.489±0.424	1.001±0.852	1.722±1.063

Variable	**Eremias grammica** (n=82)	**Eremias lineolata** (n=151)	**Eremias scripta** (n=34)
DRB	0.029±0.063	0.196±0.268	0.011±0.031
RCK	0.065±0.350	0.531±0.808	0.000±0.000
GRW	0.145±0.576	1.299±1.024	0.000±0.000
CLY	1.301±0.433	2.439±0.553	1.013±0.093
AGR	3.389±2.138	2.355±2.053	1.865±2.049
FRB	2.914±1.371	2.731±1.812	2.439±1.433
SAL	0.595±0.624	0.738±0.974	0.175±0.369
AGF	4.121±1.735	3.526±1.962	2.992±1.700
PPG	0.392±0.535	0.000±0.000	0.815±0.532
PSH	2.692±0.696	2.612±0.686	2.278±0.903
SHV1	2.115±0.511	2.200±0.625	1.698±0.593
SHV2	2.369±0.648	1.685±0.871	2.103±0.729

Table 6. Sample estimates of mean and standard deviation (x±s) for each lizard species in Mapimi on the 12 log-transformed habitat variables included in the observation vector for the multiple discriminant analysis. Mnemonics for variables are from Table 2.

Variable	**C. brevis** (n=5)	**C. wislizeni** (n=6)	**S. undulatus** (n=18)	**C. texanus** (n=45)	**H. maculata** (n=20)
DRB	0.019±0.042	0.062±0.075	0.026±0.061	0.025±0.057	0.040±0.091
RCK	2.115±1.184	2.552±1.328	2.051±1.182	3.322±0.557	1.415±0.783
GRW	2.842±1.184	2.517±1.008	2.091±1.037	2.878±0.594	0.999±0.655
CLY	2.429±0.364	2.439±0.302	2.924±0.779	2.337±0.603	3.346±0.407
AGR	1.255±1.435	1.116±1.288	2.070±1.624	1.760±0.877	1.141±1.060
FRB	1.067±1.280	2.030±1.088	1.930±1.581	1.494±0.929	1.347±1.225
SAL	0.358±0.801	0.183±0.449	0.938±1.627	0.064±0.431	1.423±1.725
AGF	1.710±1.591	2.332±1.258	3.012±1.542	2.345±0.861	2.648±1.317
PPG	0.019±0.042	0.536±0.831	1.467±1.198	0.507±0.794	0.090±0.225
PSH	2.262±0.690	2.363±0.545	2.163±0.627	2.282±0.637	0.900±0.703
SHV1	1.075±0.576	1.192±0.519	1.482±0.629	1.123±0.587	0.630±0.617
SHV2	1.243±0.604	1.334±0.396	1.622±0.599	1.291±0.512	0.653±0.643

Variable	**U. exul** (=n48)	**P. cornutum** (n=7)	**P. modestum** (n=7)	**U. stansburiana** (n=45)	**C. tigris** (n=61)
DRB	0.041±0.060	0.014±0.036	0.052±0.089	0.044±0.061	0.024±0.053
RCK	0.084±0.407	1.162±1.045	3.213±0.638	1.051±1.278	1.490±1.501
GRW	0.683±0.662	1.805±1.163	3.172±0.148	1.390±1.028	1.696±1.216
CLY	1.637±0.374	3.069±0.679	2.262±0.803	2.071±0.617	2.119±0.643
AGR	0.480±0.639	1.784±1.278	1.869±0.491	1.087±0.937	1.219±1.207
FRB	1.248±0.673	2.679±1.352	2.430±0.625	1.434±1.021	1.490±0.994
SAL	0.000±0.000	2.200±1.811	0.198±0.338	0.205±0.724	0.188±0.727
AGF	1.472±0.660	3.608±1.374	2.891±0.511	2.008±1.030	2.058±1.136
PPG	0.054±0.175	0.394±0.556	0.099±0.262	0.636±1.013	0.444±0.884
PSH	2.168±0.503	1.275±1.044	2.352±0.284	2.143±0.579	2.268±0.580
SHV1	1.186±0.356	1.198±0.695	1.026±0.319	1.311±0.368	1.231±0.422
SHV2	1.307±0.399	1.319±0.686	1.308±0.390	1.471±0.326	1.389±0.401

Variable	**C. scalaris** (n=23)	**C. innornatus** (n=9)
DRB	0.028±0.058	0.032±0.047
RCK	1.430±1.184	0.788±0.155
GRW	1.728±0.805	1.308±0.433
CLY	3.072±0.593	3.800±0.200
AGR	2.676±1.808	1.534±0.863
FRB	2.259±1.784	2.706±1.118
SAL	2.921±1.972	2.574±1.931
AGF	4.400±1.208	4.056±0.756
PPG	0.963±1.420	2.372±1.259
PSH	1.317±1.186	1.572±0.383
SHV1	1.360±0.906	2.368±0.313
SHV2	1.445±0.917	2.388±0.351

The distribution of lizards with respect to maximum population density and biomass differed between Bukhara and Mapimí (Figs. 1 and 2). Species with average density (20-40 id/ha) and high biomass (100-400 g/ha) predominated at Bukhara, whereas at Mapimí relatively rare species with low indices of maximum population density (1-5 ind/ha) and moderate maximum biomass (25-100 g/ha) were most frequent.

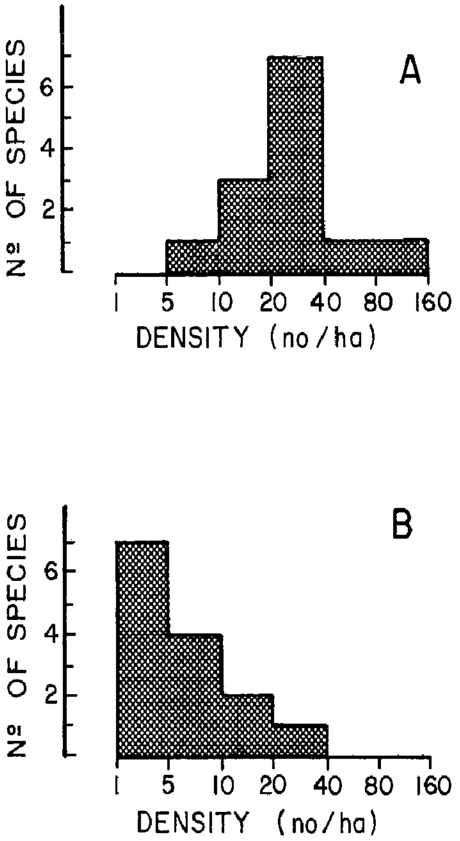

Figure 1.- Frequency distributions of species with respect to maximum density in lizard communities A - Bukhara, B - Mapimí.

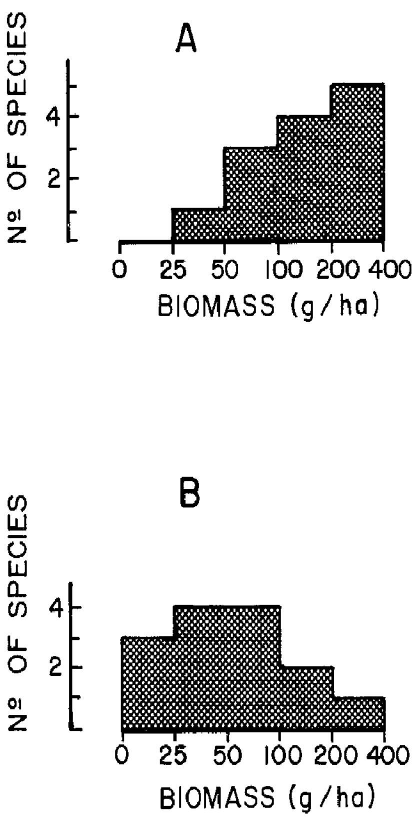

Figure 2.- Frequency distributions of species with respect to biomass in lizard communities A - Bukhara, B - Mapimí.

Partitioning of resources within foraging guilds.

Partitioning of resource space between four species of the "sit-and-wait-on-open--sites" guild of lizards at Bukhara occurs mainly on the first discriminant axis and, to a lesser extent, on the second (Table 7). The first axis characterizes the soil gradient by its mechanical composition, ranging from sandy to clay and also by clay-gravel soils, and it is associated to a reduction in the abundance of large shrubs and annual grasses. The second variable reflects the gradient of an increase of the abundance of annual grasses (Table 8). The species of this guild were distinctly divided into two groups: sclerophylic (*Ph. helioscopus* and *Ph reticulatus*) and psammophylic (*Ph. mystaceus* and *Ph. interscapularis*). The spatial niches of species in these two groups do not overlap at all, however, the species overlap broadly within the groups (Fig. 3). Niche overlapping of species averages 24.6 percent, and 35.9 percent in the first and second groups respectively (Table 17).

Table 7.- Summary of multiple discriminant analysis of the inches of 4 species from "diurnal open sit-and-wait" guild in Bukhara. *** P<.001, ** P<.005. DF1 and DF2 are the first 2 possible discriminant functions. Mnemonics are from Table 2.

Information		DF1	DF2
Eigenvalue		29.271	0.430
Chi-square test for significance of the discriminant function		3071***	41**
Degrees of freedom		36	22
Percentage of discriminant information		98	1
Normalized eigenvectors (w)	DRB	0.456	0.934
	RCK	0.092	0.001
	GRW	0.256	-0.127
	CLY	0.766	0.164
	AGR	0.001	-0.026
	FRB	0.015	0.011
	SAL	0.028	0.111
	AGF	-0.061	0.132
	PPG	0.011	0.118
	PSH	0.175	0.144
	SHV1	-0.010	-0.127
	SHV2	-0.308	-0.050

Table 8.- Linear correlation (r) between each discriminant function (DF1, DF2) and each habitat variable in the observation vector for "diurnal open sit-and- wait" guild in Bukhara. Mnemonics are from Table 2.

Variable	DF1	DF2	Variable	DF1	DF2
DRB	0.089	0.448	SAL	0.381	0.623
RCK	0.524	-0.165	AGF	-0.464	0.752
GRW	0.806	-0.112	PPG	-0.472	0.042
CLY	0.951	0.061	PSH	-0.656	0.173
AGR	-0.600	0.476	SHV1	-0.620	0.178
FRB	-0.283	0.769	SHV2	-0.864	0.018

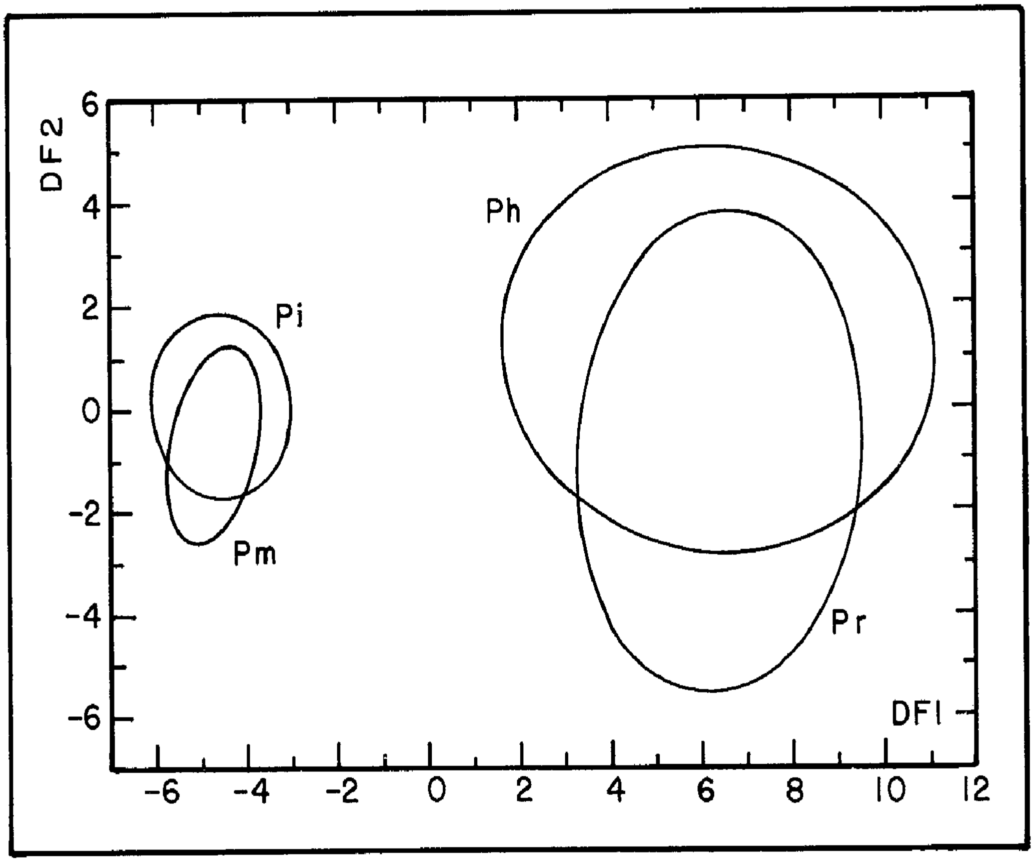

Figure 3.- Ninety five percent confidence ellipses for the species observations on the first pair of discriminant axis (DF1, DF2) for the "diurnal, open, sit-and-wait" guild in Bukhara. *Ph* -*Phrynocephalus whenlioscopus*, *Pi* - *Ph. interscapularis*, *Pm* - *Ph. mystaceus*, *Pr* - *Ph. reticulatus*.

Partitioning of resource space among three species of the similar guild at Mapimí also occurs along two axis, although the contribution of the second axis is relatively greater than at Bukhara (Table 9). The first variable reflects the gradient of soils, with a decreasing proportion of stones and gravel (from rough fragmentary soil of foothill areas to sand dunes). The second axis also correlates the mechanical properties of the soil, but reflects an increase in the proportion of clay particles from dunes and talus slopes to playas; this gradient is also related to the reduction of shrubs cover and to the increment of the annual *S. kali* (Table 10). The spatial niches of species in this guild do not overlap and do not even come into contact (Fig. 4, Table 18).

Table 9.- Summary of multiple discriminant analysis of the niches of 4 species from "diurnal open sit-and-wait" guild in Mapimí. *** P<.001. DF1 and DF2 are the first 2 possible discriminant functions. Mnemonics are from Table 2.

Information		DF1	DF2
Eigenvalue		13.72	2.62
Chi-square test for significance of the discriminant function		416***	73**
Degrees of freedom		24	11
Percentage of discriminant information		84	16
Normalized eigenvectors (w)	DRB	0.322	-0.636
	RCK	-0.719	-0.039
	GRW	-0.202	-0.241
	CLY	-0.377	0.539
	AGR	0.085	0.062
	FRB	0.038	-0.173
	SAL	-0.175	0.225
	AGF	-0.135	0.174
	PPG	-0.101	-0.201
	PSH	-0.186	-0.294
	SHV1	0.003	0.058
	SHV2	0.307	-0.032

Table 10.- Linear correlation (r) between each discriminantfunction (DF1, DF2) and each habitat variable in the observation vector for "diurnal open sit-and-wait" guild in Mapimí. Mnemonics are from Table 2.

Variable	DF1	DF2	Variable	DF1	DF2
DRB	0.112	0.063	SAL	-0.107	0.665
RCK	-0.955	-0.206	AGF	-0.444	0.276
GRW	-0.815	-0.396	PPG	-0.360	-0.200
CLY	-0.508	-0.725	PSH	0.017	-0.767
AGR	-0.600	0.067	SHV1	0.101	-0.424
FRB	-0.128	-0.033	SHV2	0.072	-0.524

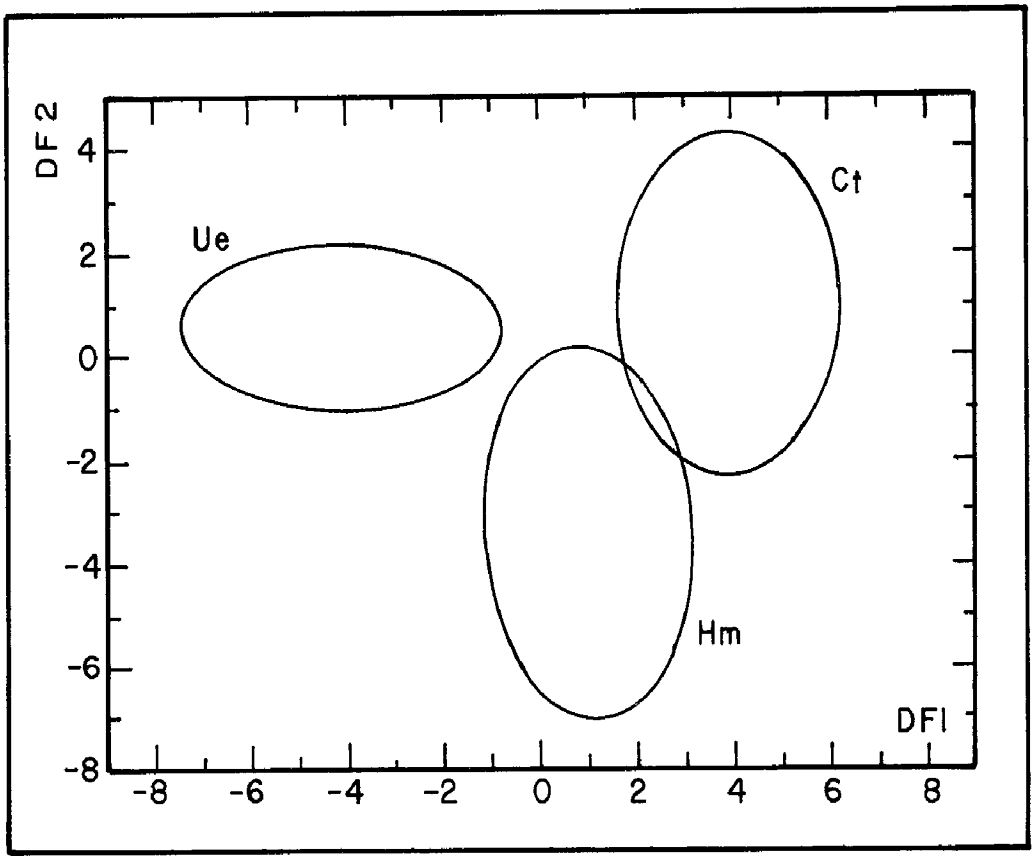

Figure 4.- Ninety five percent confidence ellipses for the species observations on the first pair of discriminantaxis (DF1, DF2) for the "diurnal, open, sit-and-wait" guild in Mapimí. Ct - Cophosaurus texanus, Hm - Holbrookia maculata, Ue - Uma exul.

The five species of the guild of actively foraging lizards in Bukhara become separated mainly along the first discriminant axis and to a lesser extent along the second (Table 11). The first axis is correlated to the soil gradient from sands to clays; the second axis reflects the gradient of increment of the total abundance of shrubs (Table 12). The spatial niches of the majority of species in this guild overlap broadly, with the exception of the pairs *E. velox* - *E. grammica* and *E. lineolata* - *E. scripta* (Fig. 5). The maximum overlap of niches (67.0 percent) occurs between *E. intermedia* and *E. lineolata*. As a average, however, overlap is only 19.9 percent for all pairs of species of this guild (Table 17).

Table 11.- Summary of multiple discriminant analysis of the niches of 5 species from the diurnal active forager guild in Bukhara. *** P<.001. DF1 and DF2 are the first 2 possible discriminant functions. Mnemonics are from Table 2.

Information		**DF1**	**DF2**
Eigenvalue		3.168	0.289
Chi-square test for significance of the discriminant function		909***	76**
Degrees of freedom		48	33
Percentage of discriminant information		88	8
Normalized eigenvectors (w)	DRB	-0.350	0.154
	RCK	-0.029	-0.069
	GRW	-0.060	0.178
	CLY	-0.280	-0.292
	AGR	-0.013	-0.048
	FRB	-0.071	-0.118
	SAL	0.016	-0.093
	AGF	0.043	0.054
	PPG	0.439	-0.535
	PSH	0.455	-0.389
	SHV1	-0.621	0.616
	SHV2	0.041	0.094

Table 12.- Linear correlation (r) between each discriminant function (DF1, DF2) and each habitat variable in the observation vector for the diurnal active foragers guild in Bukhara. Mnemonics are from Table 2.

Variable	DF1	DF2	Variable	DF1	DF2
DRB	-0.338	0.171	SAL	-0.279	-0.557
RCK	-0.305	0.044	AGF	-0.054	-0.170
GRW	-0.542	0.020	PPG	0.645	-0.317
CLY	-0.800	-0.329	PSH	0.090	0.548
AGR	-0.069	-0.051	SHV1	-0.029	0.560
FRB	-0.130	-0.282	SHV2	0.385	0.516

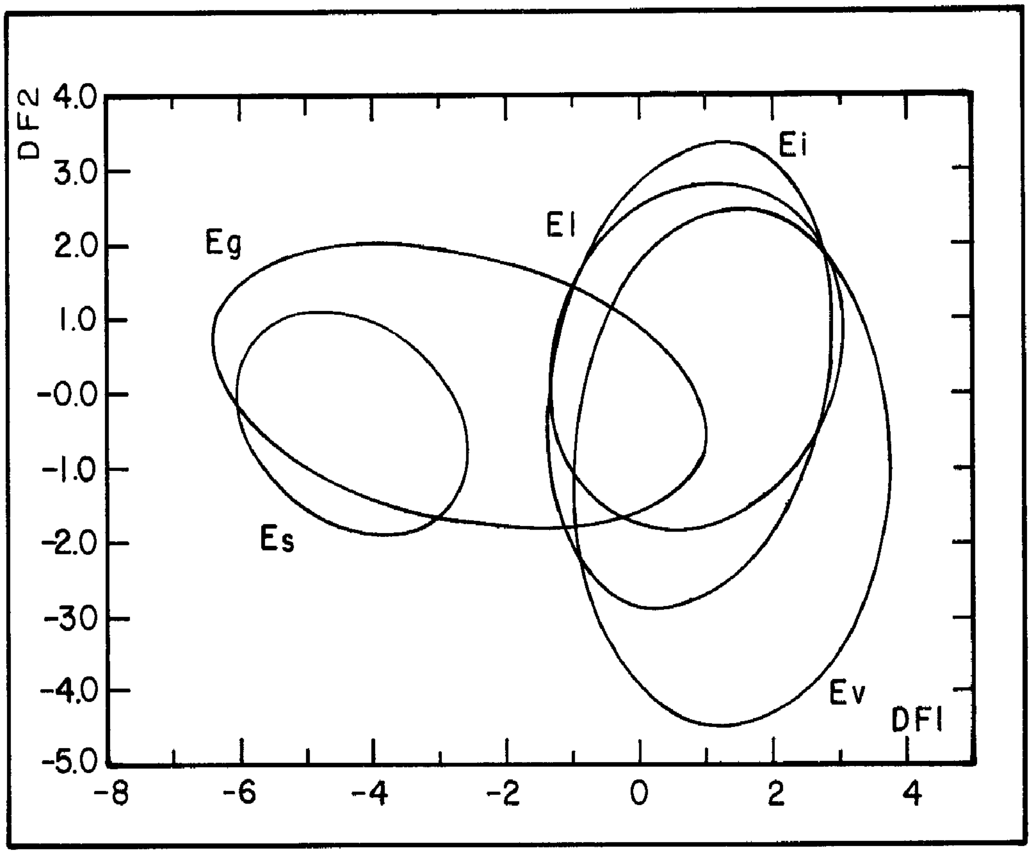

Figure 5.- Ninety five percent confidence ellipses for the species observations on the first pair of discriminant axis (DF1, DF2) for the "diurnal active foraging" guild in Bukhara. Eg - *Eremias grammica*, Ei - *E. intermedia*, El - *E. lineolata*, Es - *E. scripta*, Ev - *E. velox*.

The spatial niches of three species of lizards in the analogous guild at Mapimí are also partitioned along two axis. However, as in the case with the previous guild, the role of the second variable at Mapimí is greater than at Bukhara (Table 13). The first axis is a complex gradient of the increasing content of clay particles in the soil from sand dunes to playa, with a parallel increase of the abundance of annual grasses, especially *S. kali*. The second axis reflects the increasing abundance of shrubs with a parallel reduction in the abundance of annual plants (Table 14). The overlap of species niches in this guild is rather low (Fig. 6). Maximum overlap is only 4.6 percent and mean overlap is 1.8 percent (Table 18).

Table 13.- Summary of multiple discriminant analysis of the niches of 3 species from the diurnal active foragers guild in Mapimí. *** P<.001. DF1 and DF2 are the first 2 possible discriminant functions. Mnemonics are from Table 2.

Information		DF1	DF2
Eigenvalue		2.223	0.933
Chi-square test for significance of the discriminant function		154***	59**
Degrees of freedom		24	11
Percentage of discriminant information		70	30
Normalized eigenvectors (w)	DRB	0.678	-0.910
	RCK	0.051	0.028
	GRW	-0.079	0.020
	CLY	0.257	0.133
	AGR	-0.209	-0.138
	FRB	-0.156	0.102
	SAL	0.069	-0.018
	AGF	0.319	-0.107
	PPG	0.143	0.058
	PSH	0.000	0.077
	SHV1	-0.300	0.313
	SHV2	0.425	-0.067

Table 14.- Linear correlation (r) between each discriminant function (DF1, DF2) and each habitat variable in the observation vector for the diurnal active foragers guild in Mapimí. Mnemonics are from Table 2.

Variable	DF1	DF2	Variable	DF1	DF2
DRB	0.055	0.006	SAL	0.794	-0.124
RCK	-0.141	-0.137	AGF	0.778	-0.370
GRW	-0.081	-0.128	PPG	0.525	0.275
CLY	0.845	0.042	PSH	-0.532	0.310
AGR	0.352	-0.436	SHV1	0.438	0.436
FRB	0.412	-0.012	SHV2	0.416	0.442

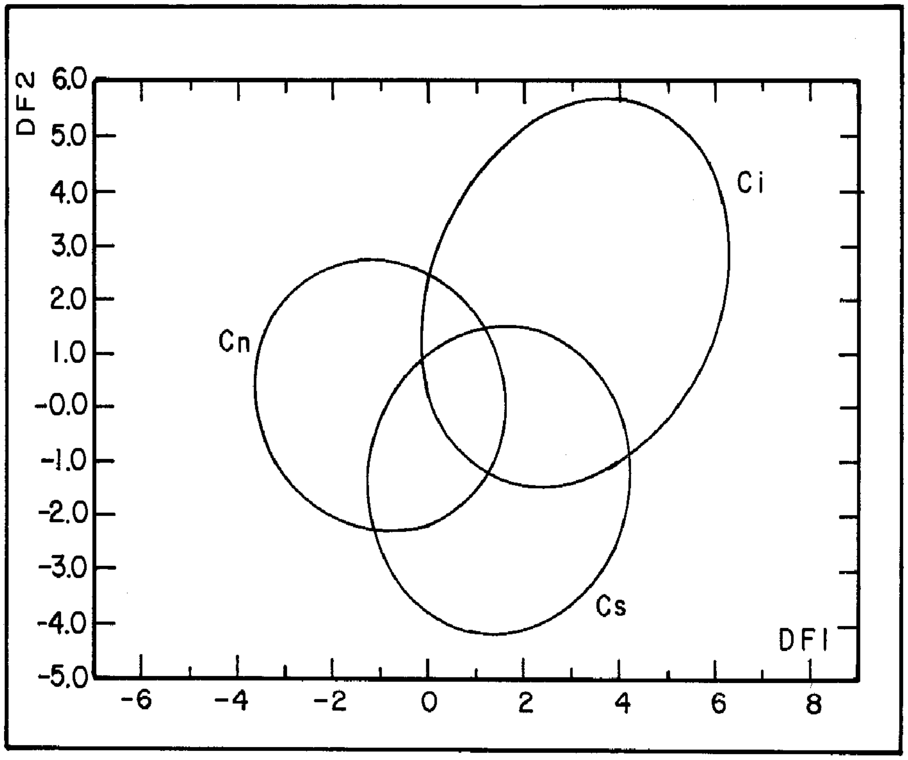

Figure 6.- Ninety five percent confidence ellipses for the species observations on the first pair of discriminant axis (DF1, DF2) for the "diurnal active foraging" guild in Mapimí. *Ci* - *Cnemidophorus innornatus*, *C* - *C. tigris*, *Cs* - *C. scalaris*.

The sit-and-wait-under-shrubs guild of diurnal lizards is represented by several species only at Mapimí. The partitioning of habitat in this guild takes place along two variables (Table 15). The first is a soil gradient on which the abundance of rocks and clay particles increases. The second is the complex gradient of decreasing abundance of shrubs, sod grasses and annual plants (Table 16). A more or less significant overlap of niches which averages 17.3 percent (Table 18) is characteristic of this guild (Fig. 7).

Table 15.- Summary of multiple discriminant analysis of the niches of 3 species from the "diurnal sit-and-wait under shrub" guild in Mapimí. ** P<.01; S - not significant. DF1 and DF2 are the first 2 possible discriminant functions. Mnemonics are from Table 2.

Information		DF1	DF2
Eigenvalue		0.843	0.230
Chi-square test for significance of the discriminant function		49**	12 NS
Degrees of freedom		24	11
Percentage of discriminant information		79	21
Normalized eigenvectors (w)	DRB	0.278	0.927
	RCK	0.147	0.005
	GRW	-0.024	0.049
	CLY	0.525	0.063
	AGR	0.009	0.039
	FRB	0.305	0.210
	SAL	0.231	-0.005
	AGF	-0.269	-0.205
	PPG	0.051	-0.095
	PSH	0.584	0.090
	SHV1	-0.229	0.124
	SHV2	-0.075	-0.121

Table 16.- Linear correlation (r) between each discriminant function (DF1, DF2) and each habitat variable in the observation vector for the "diurnal sit-and-wait under shrub" guild in Mapimí. Mnemonics are from Table 2.

Variable	DF1	DF2	Variable	DF1	DF2
DRB	-0.101	0.350	SAL	0.363	-0.427
RCK	0.589	0.214	AGF	0.468	-0.325
GRW	0.527	0.228	PPG	0.383	-0.506
CLY	0.702	-0.398	PSH	0.086	0.204
AGR	0.424	-0.461	SHV1	0.150	-0.375
FRB	0.086	-0.204	SHV2	0.131	-0.408

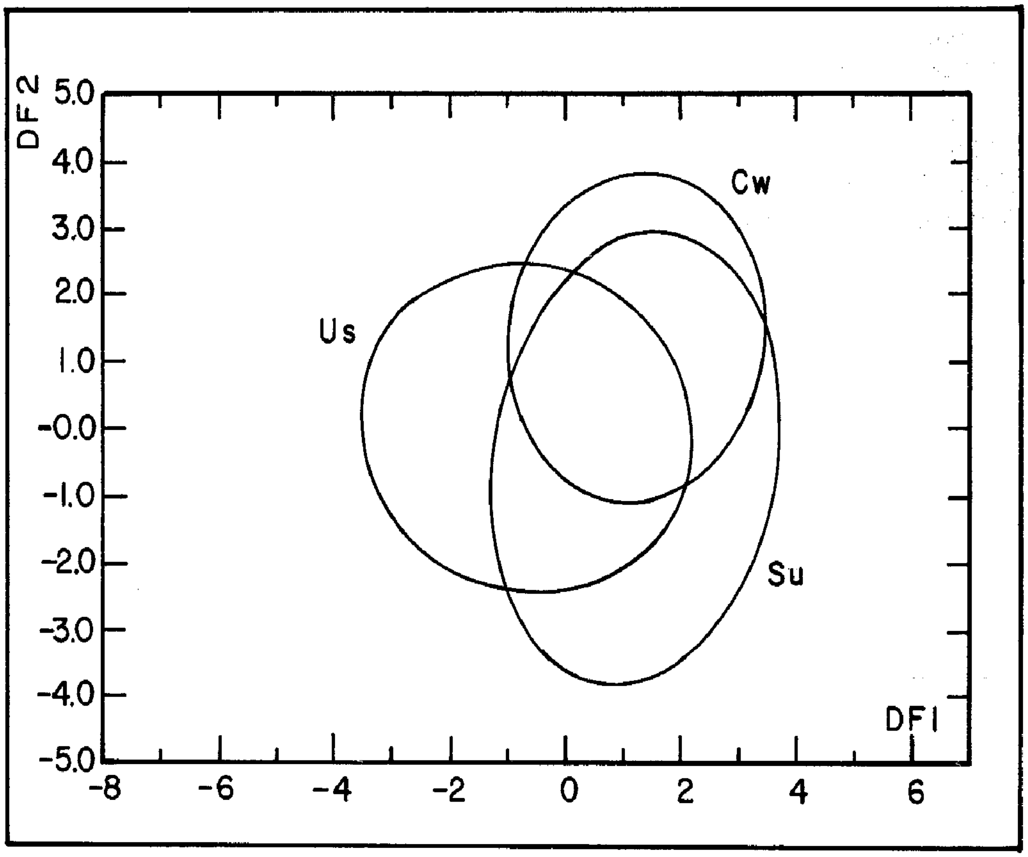

Figure 7.- Ninety five percent confidence ellipses for the species observations on the first pair of discriminant axis (DF1, DF2) for the "diurnal sit-and-wait under shrub" guild in Mapimí. Cw - Crotaphytus wislizeni, Su - Sceloporus undulatus, Us - Uta stansburiana.

Table 17.- Niche overlap in the Bukhara lizard community. CE - *Crossobamon eversmani*, TS - *Teratoscincus scincus*, GC - *Gymnodactilus caspicus*, AS - *Agama sanguinolenta*, PH - *Phrynocephalus helioscopus*, PR - *Ph. reticulatus*, PM - *Ph. mystaceus*, PI - *Ph. interscapularis*, EV - *Eremias velox*, EI - *E. intermedia*, EG - *E. gramica*, EL - *E. lineolata*, ES - *E. scripta*.

	TS	GC	AS	PH	PR	PM	PI	EV	EI	EG	EL	ES
CE	0.713	0.001	0.182	0.026	0.050	0.475	0.525	0.033	0.120	0.700	0.140	0.475
TS		0.001	0.166	0.024	0.054	0.465	0.430	0.028	0.098	0.625	0.120	0.442
GC			0.251	0.151	0.006	0.000	0.000	0.170	0.130	0.000	0.123	0.000
AS				0.210	0.069	0.071	0.105	0.335	0.398	0.187	0.411	0.077
PH					0.242	0.000	0.000	0.570	0.301	0.005	0.210	0.000
PR						0.000	0.000	0.202	0.268	0.007	0.237	0.000
PM							0.359	0.000	0.010	0.430	0.006	0.787
PI								0.000	0.009	0.625	0.018	0.335
EV									0.411	0.012	0.308	0.000
EI										0.064	0.670	0.010
EG											0.086	0.425
EL												0.009

Table 18.- Niche overlap in the Mapimí lizard community.CB - Coleonix brevis, CW - Crotaphytus wislizeni, SU - Sceloporus undulatus, CT - Cophosaurus texanus, HM - Holbrookia maculata, UE - Uma exul, PC - Phrynosoma cornutum, PM - Ph. modestum, US - Uta stansburiana, C - Cnemidophorus tigris, CS - C. scalaris, CI - C. innornatus.

	CW	SU	CT	HM	UE	PC	PM	US	C	CS	CI
CB	0.163	0.105	0.182	0.033	0.073	0.098	0.175	0.138	0.214	0.032	0.005
CW		0.179	0.125	0.005	0.001	0.081	0.283	0.136	0.303	0.047	0.000
SU			0.148	0.062	0.000	0.028	0.020	0.203	0.273	0.151	0.148
CT				0.001	0.000	0.013	0.262	0.105	0.242	0.022	0.000
HM					0.000	0.138	0.000	0.061	0.029	0.185	0.000
UE						0.000	0.000	0.298	0.288	0.000	0.000
PC							0.000	0.035	0.083	0.143	0.000
PM								0.073	0.203	0.010	0.000
US									0.580	0.049	0.004
C										0.046	0.000
CS											0.008

Partition of resources and general characteristics of communities.

In communities of lizards of the Bukhara desert, the partitioning of resource space occurs primarily along the first two discriminant axis. However, the explanatory power of the first axis is more than five fold that of the second axis (Table 19). The first of these axis is a complex gradient of increasing proportion of clay particles and gravel in the soil as well as a parallel reduction of the abundance of sod grasses and large shrubs. The second variable is a gradient of a increasing number of rodent burrows and the abundance of spring annual plants (Table 20).

Table 19.- Summary of multiple discriminant analysis of the niches of 13 species of the whole lizard community in Bukhara. *** P<.001.DF1, DF2 and DF3 are the first 3 possible discriminant functions. Mnemonics are from Table 2.

Information		**DF1**	**DF2**	**DF3**
Eigenvalue		3.655	0.663	0.220
Chi-square test for significance of discriminant function		4449***	738***	234***
Degrees of freedom		144	121	100
Percentage of discriminant information		75	14	5
Normalized eigenvectors (w)	DRB	0.751	0.987	0.785
	RCK	0.116	0.054	0.033
	GRW	0.095	-0.070	0.189
	CLY	0.536	-0.014	-0.219
	AGR	-0.051	0.018	-0.020
	FRB	0.072	-0.006	-0.021
	SAL	-0.049	0.031	-0.162
	AGF	0.014	0.018	-0.149
	PPG	-0.167	0.094	-0.216
	PSH	-0.163	0.070	-0.253
	SHV1	0.226	-0.038	0.350
	SHV2	-0.097	0.000	0.127

Table 20.- Linear correlation (r) between each discriminant function (DF1, DF2, DF3) and each habitat variable in the observation vector for the whole lizard community in Bukhara. Mnemonics are from Table 2.

Variable	DF1	DF2	DF3	Variable	DF1	DF2	DF3
DRB	0.417	0.854	0.246	SAL	0.370	-0.013	-0.668
RCK	0.484	-0.046	0.194	AGF	-0.134	0.662	-0.579
GRW	0.745	-0.148	0.162	PPG	-0.523	0.032	-0.055
CLY	0.916	-0.258	-0.115	PSH	-0.430	0.285	0.064
AGR	-0.278	0.609	-0.378	SHV1	-0.355	0.304	0.082
FRB	0.018	0.539	-0.585	SHV2	-0.699	0.273	0.125

In the lizard communities of Maplmí, the spatial partitioning of niches takes place mainly on the first three axis, but the contribution of each subsequent variable is approximately two times less than that of the previous one (Table 21). The first of these axis characterizes the gradient of a increasing proportion of clay particles in the soil and a parallel increase of the abundance of *S. kali.* The second variable also characterizes soil properties, but also shows a increasing proportion of rocks and gravel. The third variable reflects the abundance of perennial sod grasses and shrubs (Table 22).

Table 21.- Summary of multiple discriminant analysis of the niches of 13 species of the whole lizard community in Mapimí. *** P .001. DF1, DF2 and DF3 are the first 3 possible discriminant functions. Mnemonics are from Table 2.

Information		**DF1**	**DF2**	**DF3**
Eigenvalue		1.742	0.923	0.436
Chi-square test for significance of discriminant function		691***	335***	144***
Degrees of freedom		132	110	90
Percentage of discriminant information		49	26	12
Normalized eigenvectors (w)	DRB	-0.774	0.029	-0.579
	RCK	0.219	0.479	-0.032
	GRW	-0.089	0.270	0.079
	CLY	0.407	-0.032	0.086
	AGR	-0.108	0.149	-0.254
	FRB	-0.185	0.349	0.207
	SAL	0.131	0.006	0.018
	AGF	0.292	-0.430	0.029
	PPG	0.094	-0.104	0.280
	PSH	-0.050	0.278	0.272
	SHV1	-0.124	0.336	0.007
	SHV2	0.074	-0.406	0.624

Table 22.- Linear correlation (r) between each discriminant function (DF1, DF2, DF3) and each habitat variable in the observation vector for the whole lizard community in Mapimí. Mnemonics are from Table 2.

Variable	DF1	DF2	DF3	Variable	DF1	DF2	DF3
DRB	-0.068	-0.067	-0.021	SAL	0.702	-0.442	0.029
RCK	0.360	0.906	-0.074	AGF	0.709	-0.117	0.161
GRW	0.280	0.837	0.117	PPG	0.375	-0.065	0.674
CLY	0.854	-0.135	0.037	PSH	-0.475	0.442	0.414
AGR	0.487	0.209	0.069	SHV1	0.100	-0.149	0.801
FRB	0.312	-0.031	0.280	SHV2	0.049	-0.064	0.844

The displacement of niche centroids along the resource axis is shown in Figs. 8 and 9. At Bukhara, along the first axis (substrate) the centroids form two distinct groups - psammophiles, which include *C. eversmanni*, *T. scincus*, *Ph. mystaceus*, *Ph. interscapularis*, *E. grammica*, *E. scripta*, and sclerophiles, which includes all other species. The majority of species occupy a central position along the second axis (abundance of rodent burrows), with the exception of *Ph. reticulatus* which inhabits areas without burrows, and *G. caspius*, which is closely associated to burrows (Fig. 8).

There are no pronounced clusters of niche centroids along the first two axis in Mapimí. Along the first axis (from sandy to clay soils) there is a even displacement of niches in which on the one had, extreme positions are taken by strictly psammophylic *U. exul* and, on the other by *C. innornatus*, which is restricted by clay areas (Fig. 9 A,B). Niche centroids are also displaced evenly along the second axis (from rocky foothills to sandy and clay soils in hollows). Extreme positions on that gradient are take on the one hand, by *Ph. modestum* and *C. texanus*, which occur exclusively on the talus of foothills, and, on the other, by *C. innornatus*, occurring on pure clay soils (Fig. 9 A,C). The majority of species occupy the central position along the third axis (abundance of perennial vegetation), with the exception of *H. maculata*, which lives mainly in open sites, and *C. innornatus*, which is found in dense thickets (Fig. 9 B,C).

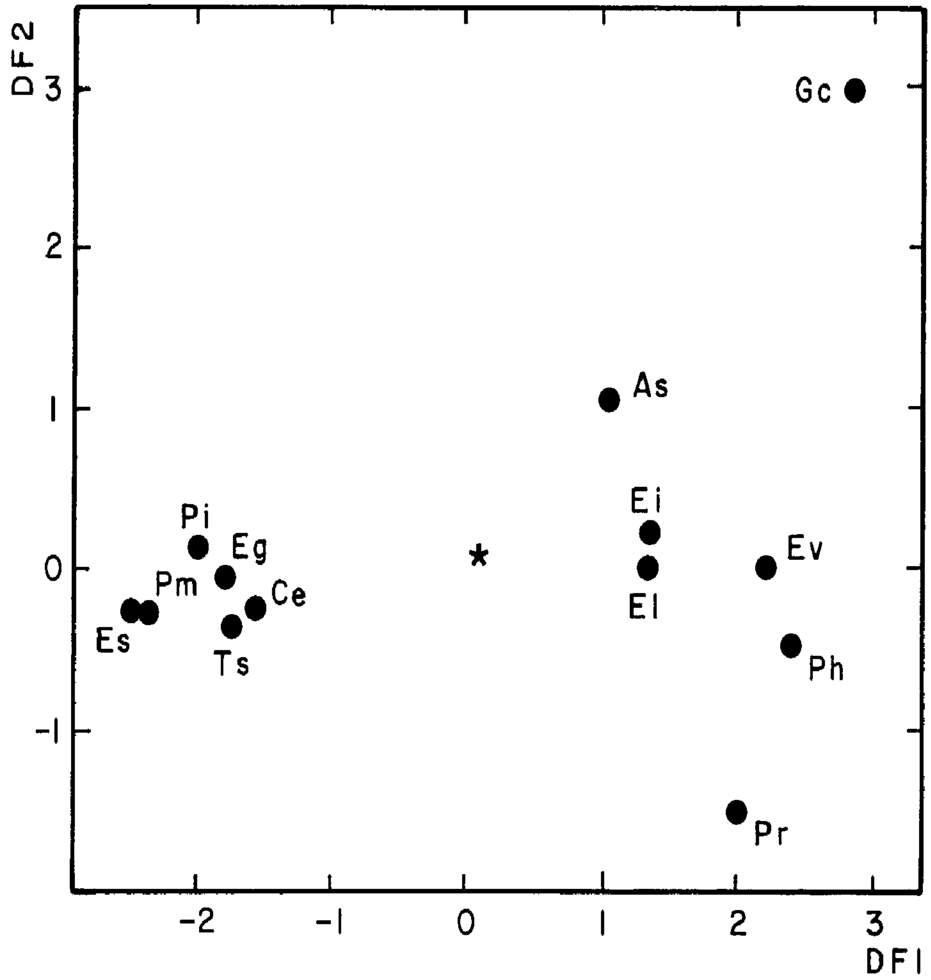

Figure 8.- Positions of species centroids in the two-dimensional discriminant space for the Bukhara lizard community. Community centroid is marked by asterisk. As - Agama sanguinolenta, Ce - Crossobamon eversmani, Eg - Eremias grammica, Ei - E intermedia, El - E. lineolata, Es - E. scripta, Gc - Gymodactylus caspicus, Ph - Phrynocephalus wenlios copus, Pi - Ph. interscapularis, Pm - Ph. mystaceus, Pr - Ph. reticulatus, Ts - Teratoscincus scincuss.

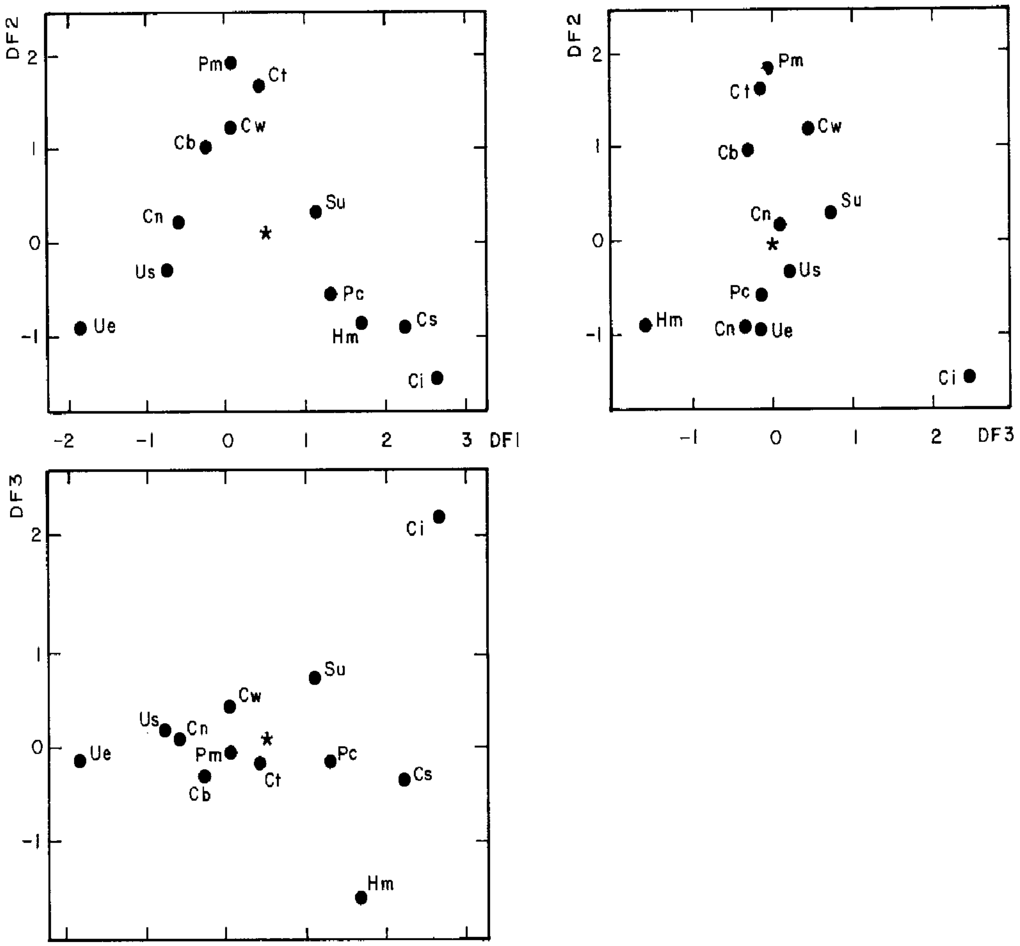

Figure 9.- Positions of species centroids on each pair of the first 3 discriminantaxis for the Mapimí lizard community. Community centroid is marked by asterisk. *Cb* - *Coleonix brevis*, *Ci* - *Cemidophorus innoratus*, *C* - *C. tigris*, *Cs* - *C. scalaris*, *Cw* - *Crotaphytus wislizeni*, *Ct* - *Cophosaurus texanus*, *Hm* - *Holbrookia makulata*, *Pc* - *Phrynosoma cornutum*, *Pm*. *P. modestum*, *Su* - *Sceloporus undulatus*, *Ue* - *Uma exul*, *Us* - *Uta stansburiana*.

Niche overlap parameters are give in Tables 17 and 18. The comparison of these data by the "analysis of the nearest neighbors" shows that the overlap of niches at Bukhara, at least for neighbors of the first order of clossesnes, is substantially higher than at Mapimí (Fig. 10). Dispersion of overlap with a decreasing rank of closeness (Fig. 11) decreases evenly at Mapimi, but it has a tendency to form a additional maximum at average ranks of closeness in Bukhara. This points to a even displacement of niches in the resource space at Mapimí and to the presence of spatial groups (guilds) in Bukhara.

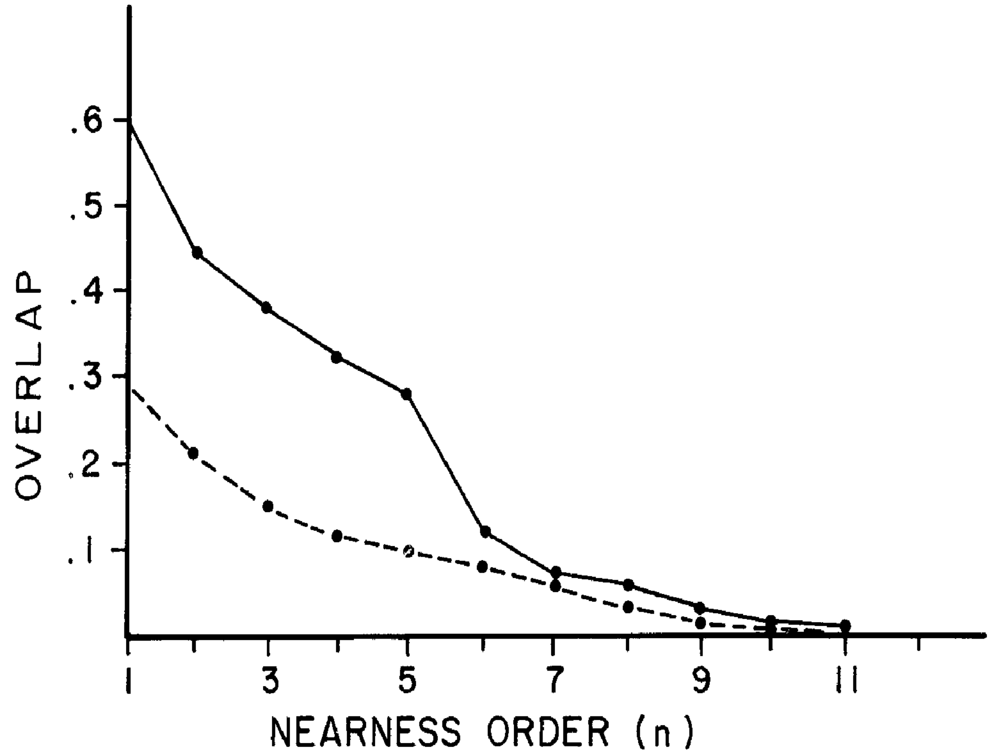

Figure 10.- Overlap of the first through the Sth nearest neighbors for the Bukhara (——) and the Mapimí (- - - -) lizard communities.

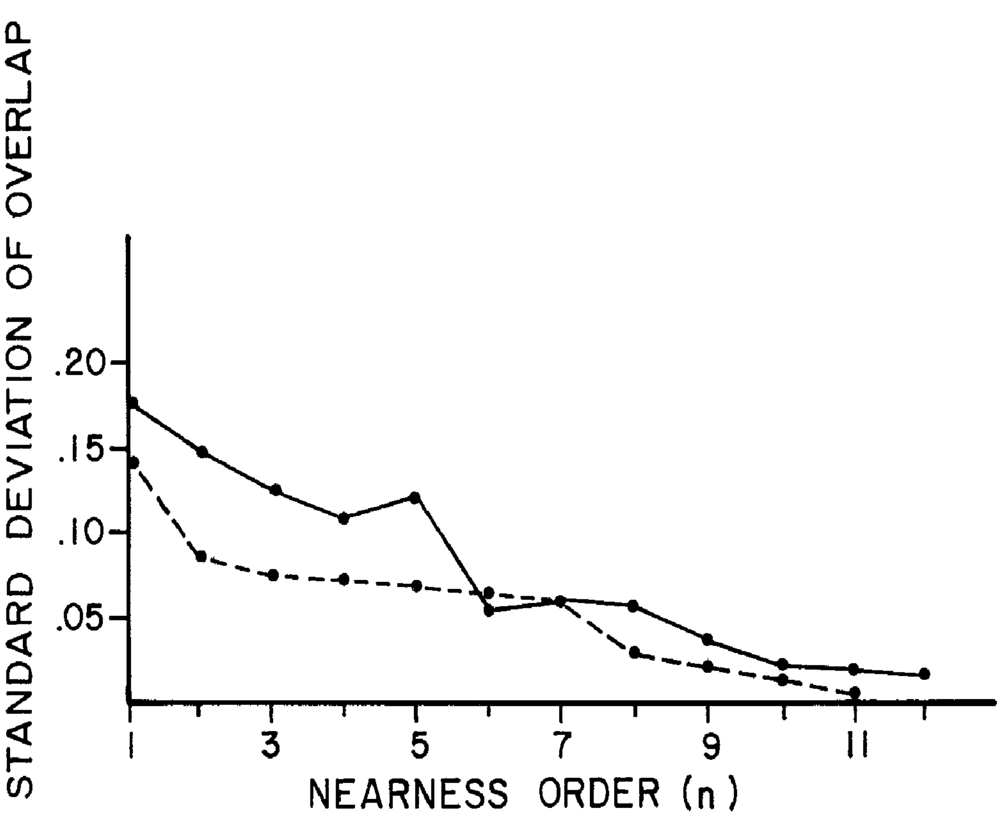

Figure 11.- Standard deviation of niche overlap between the first through the Sth nearest neighbors for the Bukhara (------) and the Mapimí (- - - -) lizard communities.

The relationships between the mai parameters of the niches of lizard communities in Bukhara and in Mapimí are give in Fig. 12. Both groups of communities have a negative although relatively weak correlation between niche breadth and niche position (distance from the center of resource space for the etire community) (Fig. 12 A,B). There is on relation between niche breadth and abundance of species in Bukhara (Fig. 12 C,E), and it is very weak and negative in Mapimí (Fig. 12 D,F). The relation between the niche position and the abundance of species in Bukhara is weakly negative, and observed only when biomass is used as then index of abundance (Fig. 12 G,I). In Mapimí this relation is also very weak, but positive, and is observed only wwhen twhen population desity is used as twhen index of abundance (Fig. 12 H,J). Abundance as assessed by population desity and by biomass is not correlated in Bukhara (Fig. 12 K) whereas in Mapimí there is a close positive correlation (Fig. 12 L).

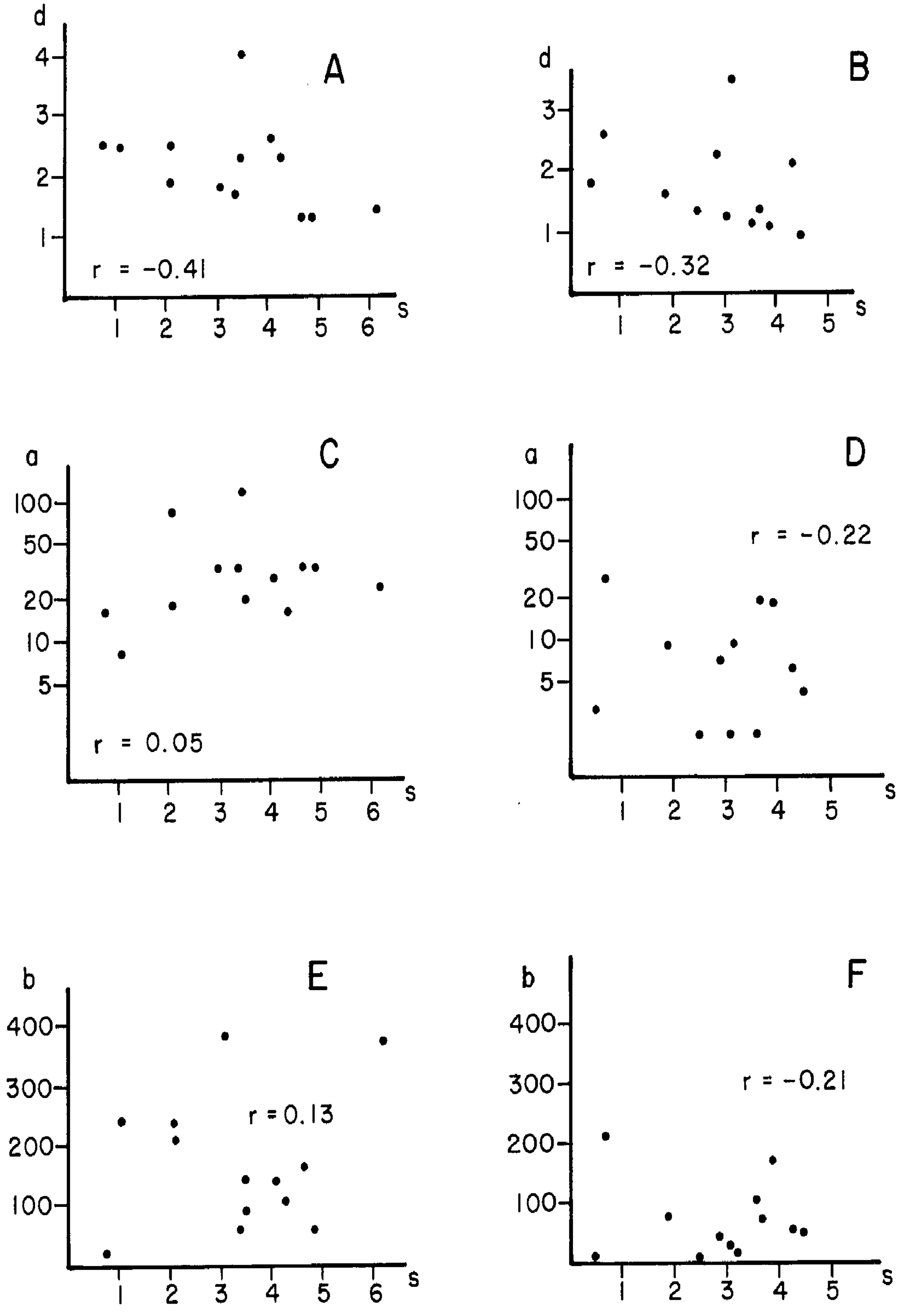

Figure 12.- Interrelation ships between niche breadth (s), niche position (d), maximal density (a: no/ha) and maximal biomass (b: g/ha) for the Bukhara (A,C,E,G,I,K) and then Mapimí (B,D,F,-H,J,L) lizard communities.

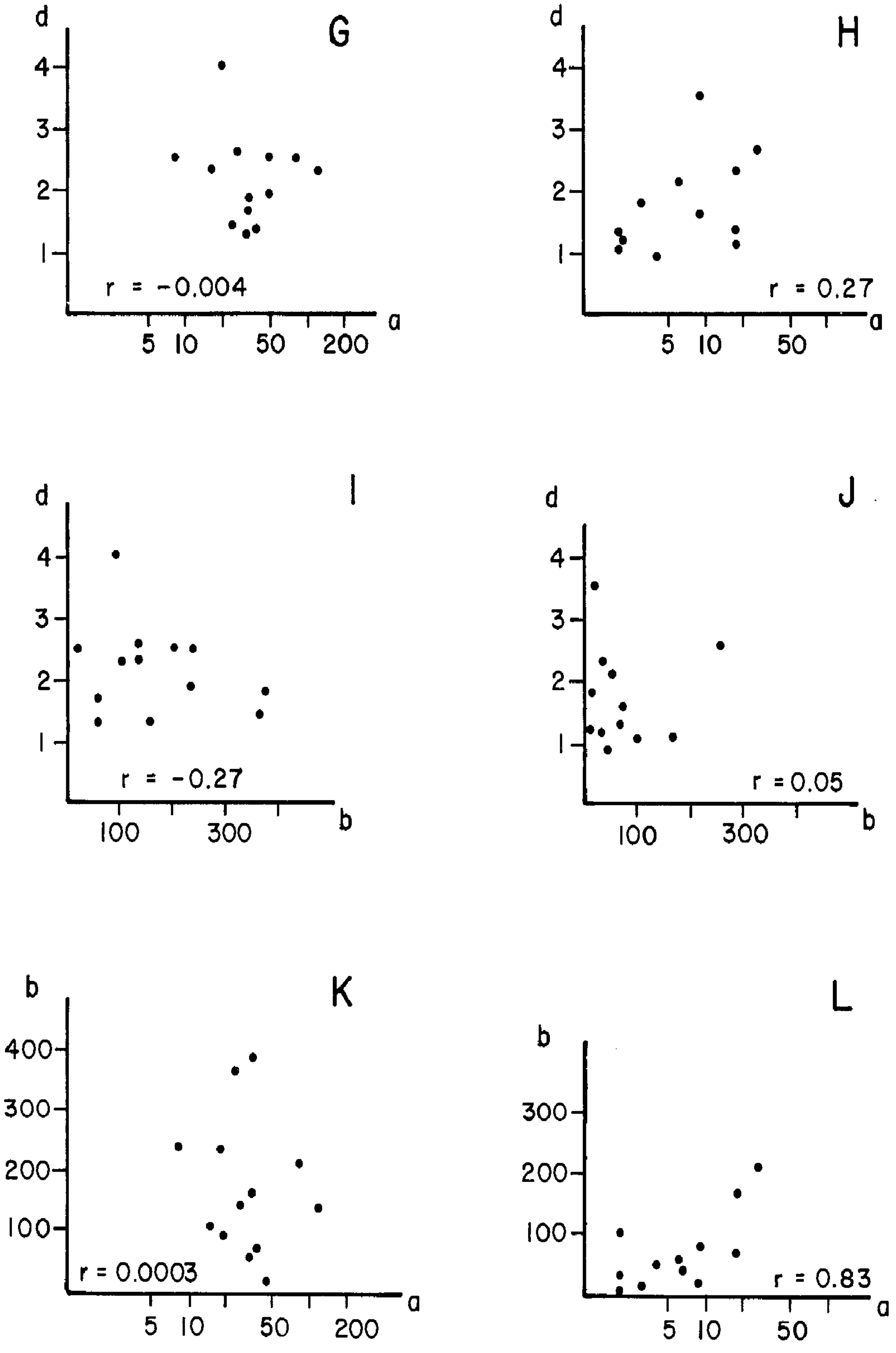

Figure 12.- Continuation.

Discussion

These results, as well as the analysis of the data published in the literature enable us to discuss which features of the organization of communities are universal, and which are specific for desert lizard communities as a whole or for particular communities within continents. However, we should first say something about how the basic quantitative indices may differ depending on the method of calculation.

In plotting a ecological space using the method of discriminant (canonical) analysis, a relative scale of these space variables reflects the contribution to the partitioning of resources by the species of the particular community (Green, 1971, 1974). If the ecological space is measured by analysing initial data on the structure of the environment (without the ocurrence of species) by the method of principal component analysis (Seagle and McCracken, 1986; Robey *et al.* 1987), the relative scale of these space variables corresponds only to the degree of variability of the structural components of the environment. It is therefore possible that the most variable environmental factors will be included in the first, most important axis, however little or on relation to the partitioning of space among coexisting species these may bear. Similarly, when this type of analysis is used, the estimated values of the niche breadth, that reflect the variability of certain combinations of environmental conditions can also be misleading or meaningless.

The meaning of the niche position index depends not only on the method of plotting a ecological space, but also on the method used to determine the center of the community. In using the analysis of initial data on the structure of the environment, by the method of principal component analysis in which the center of the community is assumed to be at the origin of coordiates, the niche position characterizes the displacemet of the microhabitat of a give species from the most widely represented type of habitat in the study area (Robey *et al.* 1987). In using the discriminant analysis in which the center of the community corresponds to the origin of the coordinates of the discriminant space, the niche position characterizes the distance of the microhabitat of a given species from the microhabitat of the most numerous species in the study area (Carnes and Slade, 1982; Van Horne and Ford, 1982). Finally, in using the discriminant analysis in which the center of the community is the center of gravity of the centroids of the species, as done in this article, them the niche position characterizes the distance of the microhabitat of a given species from the center of the physical gradients used by the entire community. Therefore, it quantifies the degree of ecological (in this case habitat) specialization of the given species.

Similarly. the interpretation of relationships between niche breadth and niche position can be quite different depending on the methods of analysis employed. By transforming the initial data on the structure of the environment using the method of principal component analysis, this relationship turns out to be positive (Robey *et al.* 1987).This can be attributed to the estimation of the niche breadth by resource partitioning variables of relatively low sigificace. I other analyses (Dueser and Shugart, 1979) this relation turns out to be more or less negative. The problem is that centroids of broad niches are always close to the center of the resource space, and as a consequence there is a negative correlation between the breadth and the position of the niche. Strong negative correlations should be observed only in the cases when the narrowing of niches continues as their remoteness from the center of resource space increases. For the desert lizard communities, analyzed in this paper, this regularity is somewhat disturbed by niches of average breadth, which tend to vary substantially in their displacement from the center of resource space.

Consistent relationships between niche breadth and abundance of species are not usually revealed, as is the situation in this work (Seagle and McCracken, 1986; Robey *et al.* 1987). At the same time, the majority of studies (Dueser and Shugart, 1979; Seagle and McCracken, 1986; Robey et al. 1987) show the presence of a strong negative correlation between niche position and the abundance of the species, however, this relationship was not found in this study. This can be explained by the differences in niche matrixes and by their different content. In these studies, niche position can be interpreted either as the distance of the microhabitat of a given species from the microhabitat of the most abundant species, in which case a negative correlation between niche position and abundance of the species occurs automatically as an artefact of calculation (Van Horne and Ford, 1982), or the niche position characterizes the degree of differentiation of a particular species from the habitat type most widely represented in the region, in which case a negative correlation of the niche position and abundance of the species is predicted by the theory of habitat selection (Rosenzweig, 1974). In our work, in which the niche position characterizes the degree of the habitat specialization of the species, the absence of this relationship indicates that different species use effectively different parts of complex gradients.

For both desert lizard communities (at Mapimí and at Bukhara), the main spatial structuring factors constitute two independent groups, in which the mechanical composition of the soil is most important and the abundance of shelter is of secondary importance. However, the contribution of particular structural factors to the axis of ecological space and thus the causal mechanisms are fundamentally different between the two communities. The first axis of ecological space in both cases corresponds mainly to the gradient of proportion of clay particles in the soil. But at Mapimí, a second important axis is the gradient that reflects the content of rocks and gravel, which essentially is of no significance at Bukhara. And, finnally, the second axis at Bukhara and the third axis at

Mapimí, characterizing the cover available in the habitats, are conformed by different structural factors: rodent burrows at Bukhara and perennial vegetation at Mapimí. These factor axis correspond to well know biological peculiarities of desert lizards. The effect of the substrate on the distribution of desert lizards over the habitat is usually so pronunced that it is described in terms of the distribution of types of biotopes or habitats distiguished on the basis of substrate (Barbault and Maury, 1981). Other analyses of the factors influecing the distribution and abundance of certain species have also showed that in the majority of cases the substrate is of primary importance (Shenbrot, 1988). As for other factors of secondary importance (the influence of vegetation, especially the abundance of shrubs and perennial grasses) on the spatial distribution and abundance of the Chihuahua desert lizards has already been emphasized (for instance, Degenhardt, 1974; Peterson and Whitford, 1987). The abundance of rodent burrows as the factor second in significance for the desert lizards of Central Asia has also been noted (Shenbrot, 1988).

The presence of the second axis of resource space at Mapimí, that reflect the gradient of rockiness of the substrate and the absence of this factor in Bukhara, is apparently explained by geomorphological differences between these regions. At Mapimí, where low mountain ridges are regular elements of the topography, the gradients of the rock content of the substrate are a important phenomenon. Correspondingly, the differentiation on these gradients could be a essential factor in the evolution of the communities at Mapimí. Similar elements in the topography at Bukhara are rare and less pronunced and, in this connection they apparently do not play a major role in niche differentiation. Differences between the Bukhara and the Mapimí desert lizard communities in the character of used shelters are apparently explained by the differences in the general biotic situation. A number of species of lizards in Bukhara are closely associated with shrubs, but these are species which use shrubs as a perch for prey waiting (*A. sanguinolenta*) or which hunt in the crowns of shrubs (*E. scripta* and, partially, *E. lineolata*). It seems that the absence in Bukhara of such large, thick and thorny perennial plants as *Prosopis* and *Opuntia* does not allow lizards to effectively use shrubs as shelters the way they do in Mapimí. In Mapimí a number of lizards are closely associated with rodent burrows (*C. wislizeni* - to burrows of *Dipodomys nelsoin*; *S. undulatus* and *S. magister* - to N*eotoma* nests); however, the abundance of rodent burrows and the degree of their complexity at Mapimí canot be compared with extremely complicated and numerous burrows of gerbils, especially of *Rhombomys opimus*, which in Bukhara are reliable shelters for reptiles.

The spatial organization of the Bukhara and the Mapimí desert lizard communities differs substantially in the pattern of the internal structure. While at Mapimí the niches of the species are distributed more or less evenly in the ecological space, in Bukhara there are two distinct groups: the psammophilic and the sclerophilic species. Only one species (*U. exul*) is psammophilous at Mapimí, whereas the other two, which frequently occur on sands (*U. stasburiana* and *C.*

tigris) are not strict psammobionts and also occur on other substrate. In Bukhara 6 species are rather strict psammophiles and other 2 species (*A. sanguinolenta* and *E. lineolata*), while not strict psammophiles, nevertheless occur widely on sands. These differences can be explained by differences in the age of sand landscapes. Sands in the Chihuahua desert are very young (they were formed in the mid Pleistocene as a result of wind action on coastal deposits of lake basins; Axtell, 1974). By cotrast, sand landscapes of Central Asia were largely developed in the upper Pliocene (Fedorovich, 1975); therefore, the psammophilous fauna of Central Asia had much more time for independent evolution.

Finally, these communities differ in the degree of spatial overlap of niches. In Bukhara this is generally higher than in Mapimí; this can be observed in the analyses of the communities and of the separate foraging guilds. Apparently, this can be largely explained by differentiation of the body size of the species in Bukhara, which facilitates the co-ocurrence of species of the same foraging guild, because of the different size of the prey they catch. These differences are indirectly cofirmed by the absence of a correlation between the population density and the biomass of the species in Bukhara and by the presence of a strict positive correlation between these variables in Mapimí. The presence of spatial (biotopic) guilds at Bukhara and their absence at Mapimí may be important in determinig differences in the degree of overlap between species of different trophic guilds. The presence of more pronunced body size differentiation withing trophic guilds in the Bukhara lizard communities apparently indicates a more prolonged evolution of the latter as compared with the Mapimí communities.

To conclude, it will be expedient to assess the possibilities of distinguishing eco-equivalent species in the communities of the different continents. Direct quantitative measurements of similarity for distinguishing eco-equivalents, (Fuentes 1976) are alomst impossible to obtain in this case, because the niches of species are arranged in a ecological space, specific for each community. More acceptable might be a partially qualitative approach in wich we could evaluate the general similarity in the position of the species in the structure of comunitites (Shenbrot, 1982); in this case the similarity in the distribution of species niches along resource axis, should reflect the gradients of similar habitat variables. It would be appropriate from this point of view to compare these communities by the first and second axis of resource space at Bukhara and by the first and third axis for Mapimí (Fig. 8, 9B). This comparison allows us to identify the probable eco-equivalent pairs of species *Ph. interscapularis -U. exul* and *E. grammica - C. tigris* (Gallina *et al.* 1985). However, considering the substantial differences in body size withing the first pair of species and the differences in the breadth of niches in the second pair this proves to be somewhat complicated. Besides these two pairs of species we may tentatively distinguish two more pairs of eco-equivalents, although they will also be controversial: *C. scalaris - E. velox* and *Ph. reticulatus - H. maculata.* There is also a similarity in the spatial position of *G. caspius* in Bukhara and *C. innornatus* in Mapimi, but these forms cannot be considered as eco-equivalents, because they belong to different foraging guilds.

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CHAPTER 6

MARKING BEHAVIOR IN DESERT RODENTS. STRUCTURAL ANALYSIS OF THE SEQUENCE OF MOVEMENT

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Abstract

Time relations of elements of behavior during orientation and familiarization were studied in representatives of eight species of desert rodents with different distribution of specific skin glands. In all species sandbathing is isolated from positively interrelated washing and fur cleansing on the one hand and anus-genital touching of the substrate on the other. Sandbathing activity is considered as an intermediate stage in the evolution of the specific skin gland for marking behavior in rodents.

Introduction

Rodents of different taxonomic groups have specific skin glands on the sides, belly and back. These glands play a highly important role in chemical communication (Sokolov, 1973). Rodents leave their secretion by rubbing themselves on the ground or on protruding objects. This is known as marking behavior and is viewed as evidence of the involvement of the specific gland in chemical communication (Johnson, 1973).

Similar movements, are known as "sandbathing" (Eisenberg, 1963a), and viewed as a comfort behavior (Eisenberg, 1963a; Borchel *et al.*, 1976). Sandbathing is particularly widely spread among rodents which have an extremely thin and thick fur and an intensive secretion of the sebaceous glands is typical of their skin (Quay, 1965; Sokolov, 1973). Excessive fat secretion provides constant lubrication of the skin and prevents the organism from profuse evaporation. The fat secretion also impairs the thermoinsulation properties of the fur. The adaptive meaning of sandbathing as well as the entire comfort behavior is explained by way of keeping the thermoinsulation properties of the fur as well as removal of ectoparasite. However the odor left by rodents during sandbathing and perceived by conspecifics may cause a response in the shape of a similar behavior. Bathing sites play the role of non-specific marks in territorial species of rodents indicating the presence of a mate (Eisenberg, 1963a; Laine and Griswold, 1976; Randall, 1981; Rogovin, 1979).

The relation between sandbathing, grooming and marking behavior in different species remains obscure. If marking behavior is in fact aimed at leaving specific signal markings, it should be manifested in situations other than comfort behavior and be negatively related to the latter or independent of it in time. The present paper deals with testing this hypothesis by analyzing time relations of different behavioral elements of a set of comfort and marking activity in different species of rodents distinguished by the presence and location of specific skin glands.

Material And Methods

Observations of individual behavior of eight species and three families of desert rodents provided a basis for the present paper. The list of species and families is given below: Heteromyidae two species (*Dipodomys merriami*, *Perognathus penicillatus*); Dipodidae: four species (*Euchoreutes naso*, *Salpingotus crassicauda*, *Allactaga bullata*, *Dipus sagitta*); Cricetidae: two species (*Meriones meridianus, Phodopus roborovskii*).

The behavior of the selected species is fairly well descriptive of the groups analyzed which is confirmed by preliminary observations of 18 representatives of the families of organisms kept in captivity (Table 1). In addition the selected species are the least sensitive to experimentation and of similar temperament such that their behavior was fully demonstrated under laboratory conditions. Experiments were conducted with males captured in nature and preliminary kept in separate cages for a week. A day prior to the experiment the sand was removed from the cages, thus making the fur greasy. During the experiments the animals were placed into 60x60x40 cm plastic open-air cages for small species and 1x1x1 m for larger ones. A 2 cm layer of clean sand was put on the bottom of the cage. The movement patterns of the animal were registered while it examined the unfamiliar area. Registration was conducted with a tape recorder for 10 min. Time recording was initiated from the moment the animal began to move on the open-air cage.

Table 1.- Elements of behavior of male desert rodents during examination of an open-air cage, while taking care of the fur and marking.

Species	Elements of behavior				Location of specific skin glands
	1	2	3	4	
Heteromyidae					
Dipodomys deserti	-	+	+	+	Dorsal glands
D. merriami	-	+	+	+	Dorsal glands
D. nelsoni	-	+	+	+	Dorsal glands
Perognathus nelsoni	-	+	+	?	not pronounced
P. pennicillatus	-	+	+	?	not pronounced
P. flavus	-	+	+	?	not pronounced
Dipodidae					
Euchoreutes naso	-	+	+	+	not pronounced
Cardiocranius paradoxus	-	+	+	-	not pronounced
Salpingotus crassicauda	-	+	+	+	not pronounced
Allactaga bullata	-	+	+	+	not pronounced
Dipus sagitta	-	+	+	+	not pronounced
Cricetidae					
Rhombomys opimus	-	+	+	+	midventral gland
Meriones meridianus	-	+	+	+	midventral gland
Phodopus roborovskii	+	+	+	?	midventral gland
Onichomys torridus	+	+	+	+	midventral gland
Peromyscus eremicus	-	-	-	+	not pronounced
Neotoma albigula	-	-	+	+	midventral gland

Notes: 1 - back-rubbing (roll over the back);
2 - side-rubbing;
3 - belly-rubbing (roll over the belly);
4 - sand-touching with anus and genitals

The following patterns of behavior were registered:

Washing - licking of the front paws and wiping the head with them.

Cleansing - combing of the fur with front and hind paws, nibbling of the fur.

Side rubbing - movements with rhythmic curving of the axis of the body, lying on the side, and also turning over to the back.

Belly-rubbing - rhythmic movements, lying on the belly, sometimes with an alternate thrusting forward and stretching backward movement of the hind paws; crawling was also observed as well as stretching and lying on the belly.

Touching sand with the anus and genitals - peculiar squatting while moving along the open-air cage, leaving drops of urine and, probably secretions from glands of the anal-genital region typical of all species. Urine marking, however, was not registered in *P. pennicillatus*, and *Ph. roborovskii*, which is practically explained by the difficulty in distinguishing this pattern of behavior in small quadrupedal animals.

Digging sand with the front paws and raking it up under the belly and throwing it away.

Other activities - all other patterns with the exception of the already mentioned (movements on an open-air cage, sniffing, half-rising on the hind paws in the process of movement).

The analysis was performed as follows: the number and probability of ties between two patterns were calculated for each species, based on primary matrixes of the number of transition of each pattern into another one by all experiments.

The tetrachoric coefficient was used as a measure of conjugation in time of two patterns:

$$r = (ad - bc) / \sqrt{} (a+b)(c+d)(a+c)(b+d)$$

where *a* is the number of ties of elements of behavior *A* and *B*; *b* is the number of ties between element *A* and other elements without *B*; *c* is the number of ties between element *B* and other elements without *A*; *d* is the number of ties between all other elements without *A* and *B*. The significance of the coefficient can be simply checked by the X^2 criterion ($X^2 = nr^2$), where *n* is the number of all pairs of patterns with degrees of freedom: v=1 (Plokhinsky, 1970).

The pair-group method of the cluster analysis without weighing was used to depict graphically the relations obtained and the establishment of the groups of interrelated patterns of behavior (Bailey, 1970).

Estimations of the significance of the differences in the probability of relations between two patterns in different species are given by Student's criterion using Fisher's transformation (Terentiev and Rostova, 1977).

Results And Discussion

Rubbing of different sections of the body on the substrate are typical patterns of behavior among all desert rodents (Table 1). The presence of these movements in a species does not depend on the availability or absence of the specific skin gland on the body or on its site of location. For instance *Dipodomys* with dorsal specific glands (Quay, 1953) do not show back-rubbing and roll over the belly. The majority of other rodents do not rub their backs on the substrate. It is only *Phodopus roborovskii* and *Onichomys torridus* that while sandbathing roll over their back although well developed specific glands are located on the belly. Two basic scent marking patterns are indicative of all the species with the exception of *Peromyscus eremicus*. These are mainly side- and belly-rubbings. The absence of these movements in the behavior of *P. eremicus* could be explained by the absence of well developed specific body skin glands. However, both types of movements are indicative of the representatives of the jerboa family which do not possess specific skin glands on the body (Sokolov and Skurat, 1974).

Preliminary observations have shown that in the absence of social stimulation the representation of the behavior repertoires of rubbing on the substrate by different parts of the body is not an indicator of activity of the specific skin gland. A more detailed structural analysis of behavior was conducted by us on the representatives of families of desert rodents. Fig. 1 shows the diagrams of the probability of co-occurrence of behavioral patterns among species while examining an unfamiliar cage area. The analysis of these diagrams shows the existence of a great diversity in the organization of the same set of behavior patterns of different species.

The probability of occurrence of each element of behavior in various species is different; in the scheme it is represented by the total thickness of the lines that run off the designations of patterns of behavior. For instance, two patterns: side- and belly-rubbings and side-rubbing prevail in the majority of species. Belly-rubbing is more indicative of *E. naso* and *M. meridianus*.

The prevalence of belly-rubbing in *E. naso* over side-rubbing can be explained by the high frequency of scent marking with urine and soiling the belly with it (Sokolov and Rogovin, 1981). Belly-rubbing in *M. meridianus* can be explained by the presence of an actively functioning abdominal gland. However, in *Ph. roborovskii* (also possessing the abdominal gland) the probability of side-rubbing is higher. In *D. merriami* (with the dorsal gland) the probability of each of these two patterns is approximately similar. In this way, it is not only the presence, but

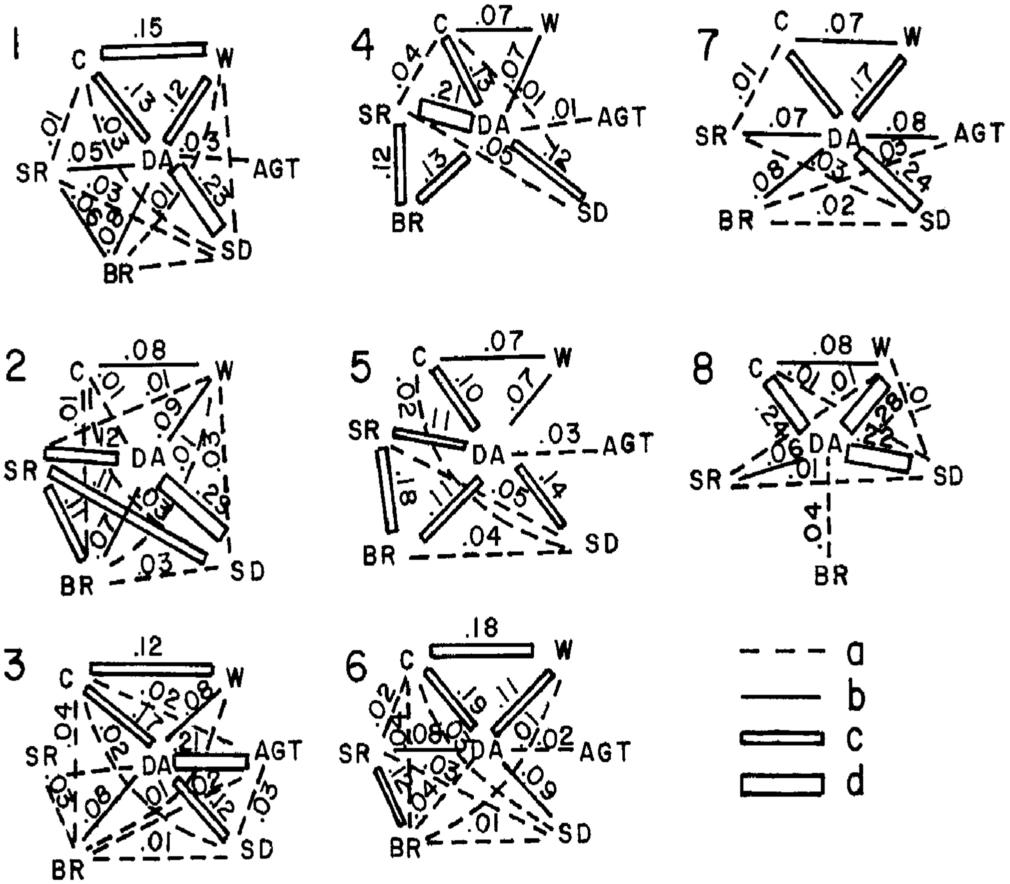

Figure 1.- Probabilities of the co-occurrence of patterns in the explorative behavior of rodents in an unfamiliar cage area: cleansing by paws; W - washing; SR - side-rubbing; BR -belly-rubbing; SD - sand-digging; AGT - anus-genital touching; OA - other activity. Probability of co-occurrence: a- <0.05; b - 0.05-0.1; c - 0.11-0.2; d - >0.2. Species: 1 - Dipodomys merriami; 2 - Perognathus penicillatus; 3 - Euchoreutes naso; 4 - Salpingotus crassicauda; 5 - Allactaga bullata; 6 - Dipus sagitta; 7 - Meriones meridianus; 8 - Phodopus roborovskii.

also the probability of occurrence of this or other type of body-rubbing on the substrate which do not depend on the presence and site of location of the specific skin gland on the body.

The preliminary analysis of the probabilities of co-occurrence of patterns provides initial information on their intentional combination and the presence of interrelated patterns separated by other activities. Two main groups of patterns are distinguished: 1) cleansing-washing of the face; 2) side- and belly-rubbing. Cleansing in all species is often accompanied by washing. Side-rubbing occurs often parallel to belly-rubbing in *D. merriami, P. penicillatus, S. crassicauda, A. bullata, D. sagitta*. However, during the analysis of the probabilities of co-occurrence of behavioral patterns in *M. meridianus* and *Ph. roborovskii* the "side- and belly-rubbing" cluster could not be identified. This cluster is neither observed in *E. naso*.

Sand digging may occur in combination with any pattern in different species; these patterns are observed separately while an animal moves along an open-air cage. The same is indicative of the combinations of touching the substrate with anus-genitals and of other patterns.

More detailed information on the combination of patterns of behavior in different species can be obtained by analyzing the tetrachoric coefficients matrixes of these elements (Tables 2-5). These coefficients help to demonstrate more clearly the value and the direction of patterns, since they consider all possible combinations of the patterns analyzed in a species.

The analysis of matrixes of coefficients show that the positive values are indicative of the pair of patterns of "cleansing - washing of the face" in all species with the exception of *M. meridianus* and *Ph. roborovskii*. Positive "other activity - sand digging" relations are indicative of the two species of the Heteromyidae family; whereas "other activity - - sand touching with anus and genitals" are positive relations of all species of the Dipodidae family. However in *M. meridianus*, belly - rubbing is positively related to anus-genitals touching (insignificant weak negative correlation) and are independent of side-rubbing. In *Ph. roborovskii* (in which urine markings were not registered during experiments) belly-rubbing on the substrate turned out to be also independent of side-rubbing. Sharp differences between *M. meridianus* and *Ph. roborovskii* from other species by the probabilities of relation between side-rubbing and belly-rubbing are shown in Table 6.

Table 2. Time conjugation of different elements of behavior in *Dipodomys merriami* (over the diagonal) and *Perognathus pennicillatus* (under the diagonal).

Elements of behavior	Washing	Scratching	Side-rubbing	Belly-rubbing	Sand digging	Touching sand with anus and genitals	Other activity
Washing	-	+0.20***	-0.26***	-0.22***	0.38***	-0.13*	-0.36***
Cleansing	+0.07	-	-0.25***	-0.17**	-0.51***	-0.16**	-0.34***
Side-rubbing	-0.33***	-0.26***	-	+0.27	-0.15***	-0.06**	-0.30***
Belly-rubbing	-0.22***	-0.12	+0.15*	-	-0.21***	-0.09	-0.23***
Sand-digging	-0.38***	-0.23***	-0.26***	-0.40***	-	-0.07	+0.07
Touching sand with anus and genitals	-	-	-	-	-	-	+0.03
Other activity	-0.18***	-0.39***	-0.38***	-0.33***	+0.07	-	-

Over the diagonal: number of experiments - 10, number of transitions - 330; under the diagonal - number of experiments - 9, number of transitions - 282. Evaluation of statistical significance by X^2 see also Table 3-6: * - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$.

Table 3.- Time conjugation of different elements of behavior in *Euchoreutes naso* (over the diagonal) and *Salpingotus Crassicauda* (under the diagonal).

Elements of behavior	Washing	Scrat-ching	Side-rubbing	Belly-rubbing	Sand-digging	Touching sand with anus and genitals	Other activity
Washing	-	+0.19***	-0.12***	-0.18***	-0.25***	-0.32***	-0.36***
Cleansing	+0.19***	-	-0.15***	-0.17***	-0.28***	-0.39***	-0.37***
Side-rubbing	-0.35***	-0.32***	-	+0.20***	-0.09**	-0.13***	-0.19***
Belly-rubbing	-0.31***	-0.33***	+0.34***	-	-0.24***	-0.12**	-0.43***
Sand-digging	-0.27***	-0.25***	-0.10*	-0.16***	-	-0.06	-0.07
Touching sand with anus and genitals	-0.09*	-0.13**	-0.08	-0.07	-0.06	-	+0.05
Other activity	-0.26***	-0.23***	-0.27***	-0.38***	-0.003	+0.13**	-

Over the diagonal: number of experiments - 23, number of transitions - 1043; under the diagonal: number of experiments - 15, number of transitions - 595.

Table 4. Time conjugation of different elements of behavior in Allactaga bullata (over the diagonal) and Dipus sagitta (under the diagonal).

Elements of behavior	**Washing**	**Scrat-ching**	**Side-rubbing**	**Belly-rubbing**	**Sand-digging**	**Touching sand with anus and genitals**	**Other activity**
Washing	-	+0.27***	-0.33***	-0.28***	-0.25***	-0.09*	-0.10*
Cleansing	+0.13**	-	-0.37***	-0.33***	-0.19***	-0.11*	-0.11*
Side-rubbing	-0.37***	-0.45***	-	+0.20***	-0.20***	-0.15**	-0.37***
Belly-rubbing	-0.31***	-0.33***	+0.34***	-	-0.24***	-0.12	-0.43***
Sand-digging	-0.27***	-0.25***	-0.10*	-0.16***	-	-0.06	-0.07
Touching sand with anus and genitals	-0.09*	-0.13**	-0.08	-0.07	-0.06	-	+0.05
Other activity	-0.26***	-0.23***	-0.27***	-0.38***	-0.003	+0.13**	-

Over the diagonal: number of experiments - 18, number of transitions - 467; under the diagonal: number of experiments - 18, number of transitions - 558.

Table 5. Time conjugation of different elements of behavior in Meriones meridaianus (over the diagonal) and Phodopus Roborovskii (under the diagonal).

Elements of behavior	**Washing**	**Scratching**	**Side-rubbing**	**Belly-rubbing**	**Sand-digging**	**Touching sand with anus and genitals**	**Other activity**
Washing	-	+0.04	-0.18**	-0.23***	-0.37***	-0.35***	-0.18**
Cleansing	-0.23***	-	-0.13*	-0.24***	-0.29***	-0.22***	-0.23***
Side-rubbing	-0.17***	-0.21***	-	-0.11	-0.03	-0.14*	-0.22***
Belly-rubbing	-0.19***	-0.17***	-0.01	-	-0.15*	+0.14*	-0.12*
Sand-digging	-0.43***	-0.37***	-0.09*	-0.10*	-	-0.20***	-0.03
Touching sand with anus and genitals	-	-	-	-	-	-	-0.14*
Other activity	-0.28***	-0.29***	-0.18***	-0.02	-0.01	-	-

Over the diagonal: number of experiments - 6, number of transitions - 271; under the diagonal: number of experiments - 8, number of transitions - 472.

Table 6. Interspecific differences in the probabilities of interrelationship between side- and belly-rubbing on the substrate.

Species	Total of side-rubbings	Frequency of co-occurrence of side- and belly rub-	T-criterion and the significant of differences in species behavior (* P<0.05; ** P<0.01; *** P<0.001)						
			P.p.	E.n.	S.c.	A.b.	D.s.	M.m.	Ph.r.
D.merriami	55	0.36±0.06	0.5	1.7	1.0	1.6	0.9	5.2***	7.0***
P.penicillatus	101	0.32±0.05	-	2.5*	0.6	2.6**	1.8	5.3***	5.8***
E.naso	56	0.52±0.07		-	3.2**	0.5	1.2	6.7***	7.2***
S. crassicauda	254	0.29±0.03			-	4.0***	2.9**	5.4***	6.0***
A.bullata	174	0.48±0.04				-	0.9	7.3***	8.1***
D.sagitta	157	0.43±0.04					-	6.7***	7.4***
M.meridianus	31	0.03±0.01						-	0.1
Ph.roborovskii	42	0.05±0.03							-

Rather important is the fact that touching of the substrate with the anus and genitals (usually interpreted as a marking behavior; Eisenberg, 1967), proved to be independent or negatively related to side- or belly-rubbing in all species with this type of behavior with the exception of the already mentioned *M. meridianus*. Significant negative relations in that group of patterns are indicative of *E. naso* as well, distinguished by a high frequency of urine markings. Although this species is characterized by an increased frequency of substrate belly-rubbing, these movements are accompanied by touching sand with anus and by genitals and urine markings.

The functional significance of cleansing is more or less clear. In all cases, cleansing is significantly negative related to side and belly-rubbing.

All this is illustrated by dendrograms derived from the cluster analysis of matrixes of tetrachoric coefficients of conjugation of behavioral units (Fig. 2). These dendrograms show the hierarchy of relations among the coefficients. Clusters are distinguished by the principle of maximum relations and represent separate blocks of positively related behavioral units.

Since we analyzed the patterns of behavior whose purpose could be considered as clear (cleansing and washing on the one hand, and touching with anus and genitals on the other), it is possible to formulate hypotheses for the functional significance of the behavior still barely understood. These hypotheses, quite naturally, are limited by the approach used by us namely: the analysis of the relations between behavioral patterns when the subjects examine on unfamiliar cage area. Nevertheless these hypotheses seem to be reasonable in the light of the information present in the literature on the nature of comfort and marking activity of rodents.

In species that have no specific skin glands (Jerboas), side and belly-rubbing represent a specific behavioral complex which can be called sandbathing activity.

The main function of these patterns is to care for the fur. The presence of two patterns in the sandbathings complex in jerboas has been already studied (Eisenberg, 1967; Sokolov and Rogovin, 1981). The functional significance of sandbathing in jerboas could be determined only experimentally. Besides cleansing (that removes the secretions from sebaceous glands), these movements may have the meaning of nonspecific marking behavior, it will be shown that the scent at bathing sites influences the behavior of conspecifics. Currently only data for *S. crassicauda* are available_(Rogovin, 1979).

In species that posses actively functioning abdominal specific glands (in our analysis they are *M. meridianus* and *Ph. roborovskii*), belly-rubbing on the substrate is not directly related to side-rubbing on the substrate and can be viewed as specific marking movements, aimed at leaving the scent of these glands. Side rubbing on the substrate is of similar function in jerboas. They either show the cleansing behavior or it might be a nonspecific marking function different from belly-rubbing. Belly-rubbing in gerbils and hamsters is usually unrelated to space with the bathing sites and occurs in other situations. Their

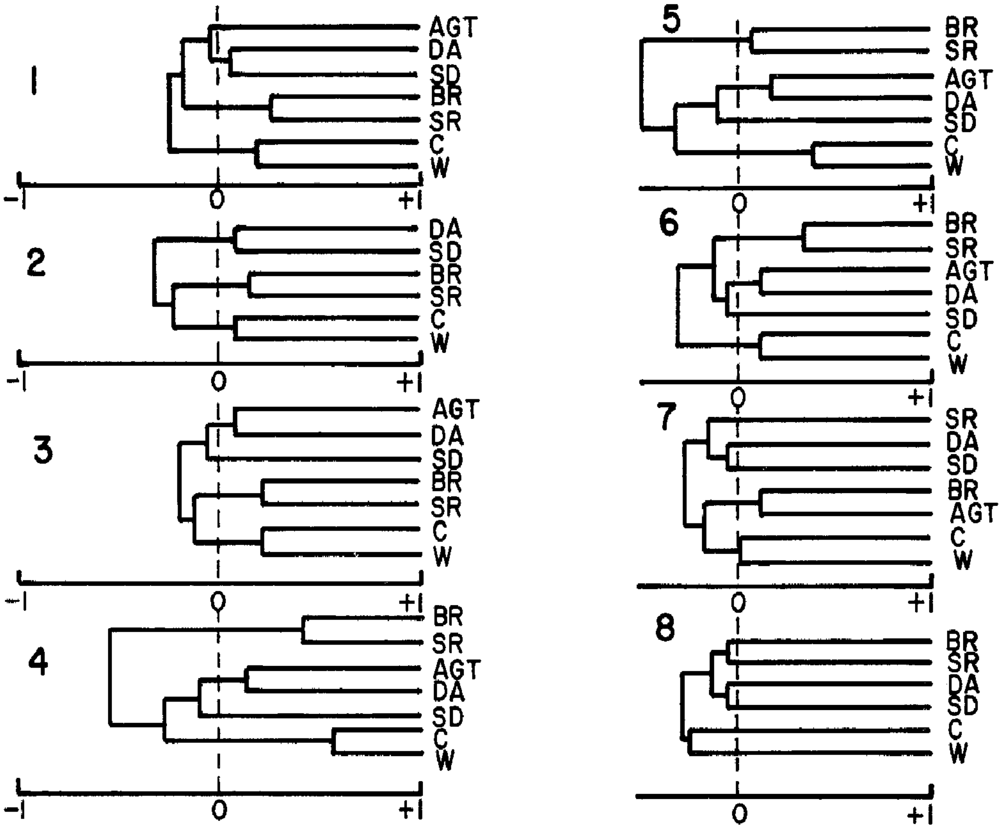

Figure 2.- Structure of the relationships between the patterns of behavior of rodents during examination of an unfamiliar cage area. Design as in Fig. 1.

frequency sharply increases in the presence of a conspecific which is not the case of side rubbing in gerbils and of side- and back-rubbings in hamsters. In addition, an indication to a specific marking function of belly rubbing in *M. meridianus* is the positive interrelationship of these movements with urine markings while touching the substrate with anus and genitals.

Marking behavior in the form of belly-rubbing on the substrate has been repeatedly described in different species of gerbils (Eisenberg, 1967; Thiessen, 1968; Goltzman *et al.*, 1982; Kumari and Prakash, 1981; Paskhina and Lapin, 1982; Idris and Prakash, 1982). For instance Thiessen showed that in *M.unguiculatus* there is a relation of dependence between this behavior and the level of sexual hormones in the blood (Thiessen *et al.*, 1968, 1970; Thiessen and Lindzey, 1970;) and that it is possible to simulate or inhibit this behavior by social partners (Nyby *et al.*, 1970; Thiessen *et al.*, 1971). All these facts point to a specific marking function of belly-rubbing in gerbils. Marking behavior does not depend on the state of the fur (the level of oiling); however, with regard to sandbathing this relationship has been demonstrated (Tortora *et al.*, 1974).

The structure of the interrelationship of behavioral patterns of the representative heteromyids is similar to that of jerboas. Since side- and belly-rubbing in Heteromyidae represent a single complex of movements, and since back rubbing or turning from side to side across the back are not indicative, there is no evidence therefore to consider that sandbathing in *D. merriami* is related to the presence of the dorsal specific gland. Most workers (Eisenberg, 1963a, 1963b; Borchelt *et al.*, 1976; Laine and Griswold, 1976; Griswold *et al.*, 1977) noted that in the Heteromyidae side and belly-rubbing are joined into one single complex sandbathing behavior. A non-specific marking function of sandbathing has been shown in *Dipodomys spectabilis* (Laine and Griswold, 1976). Bathing sites may cause a response in the form of sandbathing among conspecific in *D. merriami* and in *D. microps* (Randall, 1981). Sandbathing in *Dipodomys* can be simulated by tactile stimulation of the body (Griswold *et al.*, 1977) and their frequency of response depends on the soiling of the fur and the intensity of the functioning of the sebaceous glands of the skin (Randall, 1981a). The hormonal regulation of sandbathing has not been studied profusely. However it has been demonstrated that in *D. merriami* the frequency of the occurrence of this form of behavior after castration does not change (Lepri and Randall, 1983); in *D. spectabilis* an inverse dependence on the frequency of sandbathing has been observed in the levels of sexual steroids (Randall, 1986). An indirect indication that sandbathing in *Dipodomys* plays the role of grooming the fur, is the dependence of its frequency on the quality of the substrate which is less indicative of a specific marking behavior (Borchelt *et al.*, 1976).

The results of the analysis of the interrelationship in time of different patterns of behavior show the probability of the following path for the occurrence of specific marking behavior. This type of behavior developed parallel to the transformation of a part of the sebaceous skin glands into specific glands together with the activity of their secretory function. Side and belly-rubbing that are present in repertoires of behavior of the majority of species are primarily initiated by mainly peripheral stimuli and serve to remove foreign objects or the excess of fat from the fur. Further, part of these movements become independent and begin to play the function of marking behavior. Such an isolation of some movements is related to a change in the pattern of their motivation. The initiation of the activity of the specific marking behavior may be dependent either on internal causes (physiological state of the organism), or on external social stimuli. Apparently, there may be a further change of the form of specific marking body movements *per se* (slowed down crawling or spreading in the sand at the site where the secretion of the specific skin gland is left, etc.).

The fixation of the function of nonspecific marking behavior in a number of species with sandbathing and its isolation from cleansing and washing makes it possible to view sandbathing as an intermediate stage in the evolution of the specific marking behavior of rodents.

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CHAPTER 7

THE ECOLOGICAL ORGANIZATION OF A HIGHLY DIVERSE DESERT LIZARD COMMUNITY IN MEXICO

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Abstract

The ecological structure of a highly diverse desert lizard guild located in the State of Sonora, México, was studied during 1982, 1983 and 1984. The community is composed of 17 species and the habitat, microhabitat and daily temporal prey taxa and prey size utilization were analyzed. It was found that the diurnal rhythms of the most common species were very similar during the same season, but varied extensively from Summer to Autumn. These rhythms were obviously dependent on the thermal constraints of the environment; these constraints were so restrictive that they led to an almost identical activity pattern in all species.

It was also observed that highly specialized species showed a very low variation in food habits; the opposite occurred with more eclectic predators. Food specialization can also sway the expected correlation between the size of the predator and the size of their prey. Food niche overlaps, analyzed to insect's family level, both at taxonomical and prey volume level were persistently low. Thus food niche structuring could play a determining role in organizing this lizard guild. Habitat selection plays also a determining role in the organization of this lizard guild, which is attained by the microhabitat niche segregation. The determinant role that selection of species plays in the use of the three main axis of the niche and by the way of the structuring of this community as well as its ecological meaning are discussed.

Introduction

The importance of resource partitioning in reducing the potential competition among the species that constitute a guild and so contributing to the species richness, has been reiteratively outlined by many authors during the past twenty years since the homage to Santa Rosalía, Hutchinson (1959), classic work. For a short review of the studies on lizards, the reader is referred to: Barbault, 1977, 1981; Barbault and Grenot 1977; Barbault and Maury, 1981; Huey and Pianka, 1977; Mellado, 1980; Pianka, 1975; Schoener, 1968, 1975; Simon and Middendorf, 1976.

Usually, resource partitioning is studied on three niche dimensions: space (Barbault and Grenot 1977; Ortega *et al.*, 1982;), time (Barbault, 1977; Ortega, *et al.* 1984;) and food (Barbault *et al.* 1985; Mou and Barbault, 1986). It has been assumed that the space partitioning is by far the most common way to promote ecological segregation between co-occurring species, followed by direct food partitioning and temporal segregation (Schoener, 1974). However, in the case of desert lizard communities it has been observed that the ecological organization among sympatric species (on the three main axis of the niche) is not the result of the dynamics of competitive interactions alone but reflects the ecological constraints of each species (Barbault and Maury, 1981; Barbault *et. al.*, 1985; Ortega *et. al.*, 1984; Toft, 1985).

To better understanding the constraints that shape lizard communities, one can resort to broad comparisons among large communities that evolved independently (Orians and Solbrig, 1977, Pianka, 1986). It is also possible to deal with more detailed studies concerning a well defined community, in a shorter spatial and temporal scale (Barbault and Maury, 1981). Conceived in such form, and as part of a more general comparative study of desert lizard guilds, the main objective of this work is the analysis of resource partitioning along the three main axis of the niche in one desert lizard guild of México.

Material and Methods

The study area

The field work was carried out during 1981-1983 in the region of the El Pinacate (31 ° 52' N, 112 ° 51' W) which is the most arid part of the most arid desert of México: the Sonora Desert (Fig. 1). Annual precipitation varies between 64 mm and 200 mm with rainfall patterns highly unpredictable (Ezcurra, *et al.*, 1982). The rainfall seasonal cycle and monthly temperature for the two years of study are shown in Fig. 2.

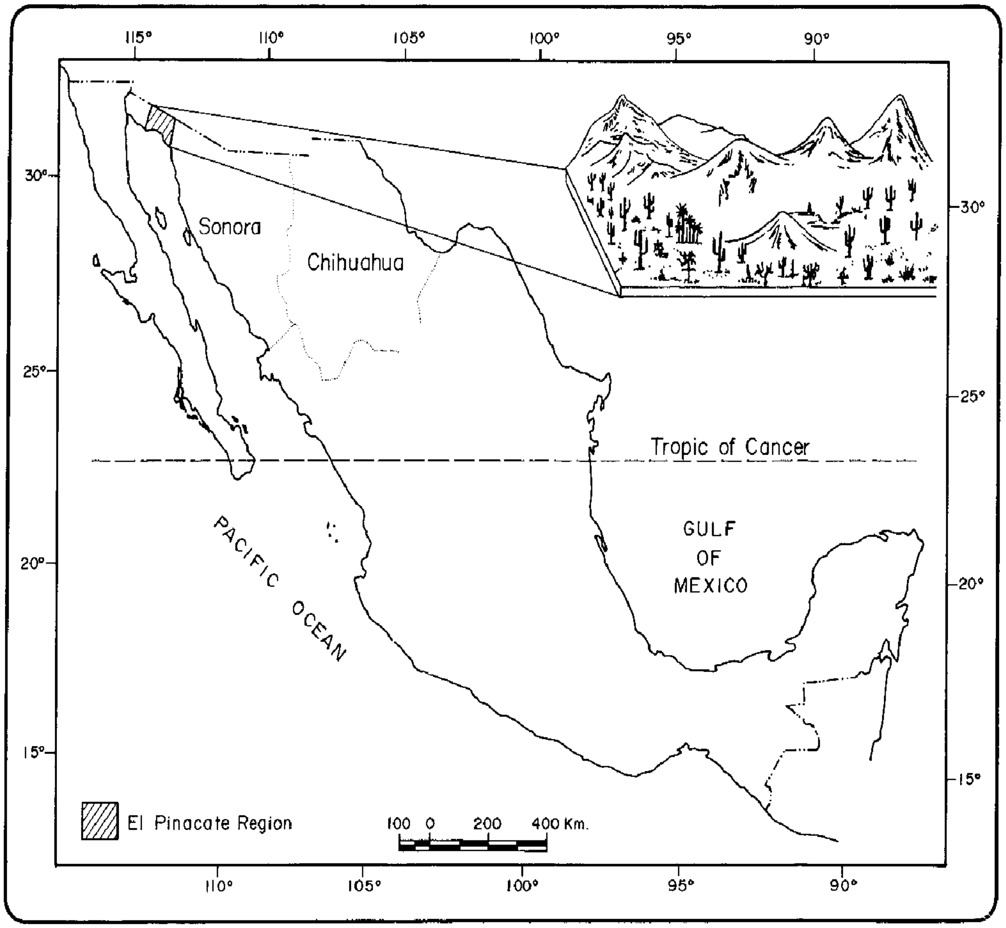
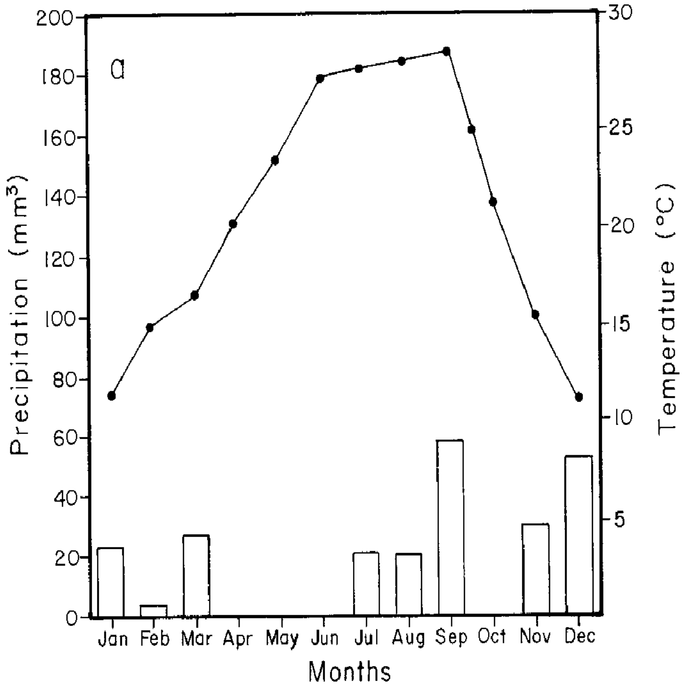


Figure 1.- Localization of the El Pinacate Región.



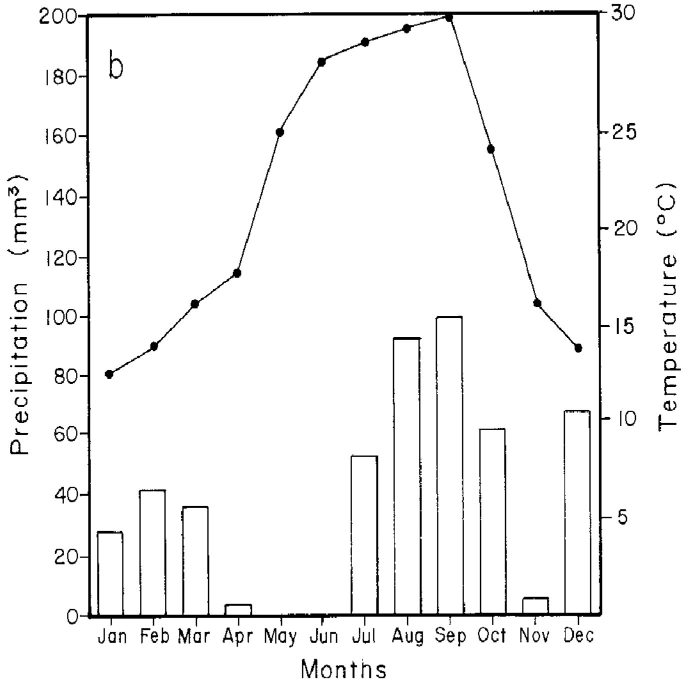


Figure 2.- Mean montlyprecipitationand temperaturefor 1982 (a) and for 1983 (b)in the studyzone.

The species

The complete lizard guild of El Pinacate comprises 17 species (censuses carried out during several years by González-Romero), although only 12 were observed on the studied transects (marked with *).

- 13 Iguanidae: *Callisurus draconoides* *, *Crotaphytus collaris* *, *Dipsosaurus dorsalis* *, *Gambelia wislizeni* *, *Phrynosoma solare, P. m'calli* *, *P. platyrhinos* *, *Sauromalus obesus* *, *Sceloporus magister* *, *Uma notata* *, *Urusaurus graciosus, U. ornatus * and Uta stansburiana* *.

-1 Teiidae: *Cnemidophorus tigris* *.
-1 Xantusidae: *Xantusis vigilis*
-1 Gekkonidae: *Coleonyx variegatus*
-1 Helodermatide: *Heloderma suspectum*

Among the potential predators of lizards in the study zone, the following were observed: snakes: *Masticophis flagellum, Pitouphis melanoleucus, Salvadora hexalepis, Lampropeltis gelulus;* mammals: *Canis latrans, Urocyon cyneroargenteus, Vulpes macrotis, and Basariscus astutus*; birds of prey: *Buteo jamaicensis, Parabuteo uncintus, Falco sparverius and Circus cianeus*; rattlesnakes: *Crotalus atrox, C. cerastes and C. scutulatus*. However, at present we have not data on the impact of predation over the lizard populations.

Methods

After various prospective surveys (A. González-Romero in 1980 and 1981), two study sites were censused during October 18 to 28, 1982 and during June 16 to 28, 1983. (Ortega *et al.* 1986). Seven types of habitats were distinguished along the two transects: mountain basis, mountain slope scrub or bajada, lava flows and dunes in the La Sierra Blanca transect, and river-shore scrub in the Rio Sonoyta transect (Fig. 3).

In each habitat two of us (Alfredo Ortega and Robert Barbault during 1982; Alfredo Ortega and Alberto González during 1983) walked along randomly from 07:00 to 20:00 hrs. for one hour census periods. We walked keeping a distance of 7 m between us and looking for lizards within this 7m wide path. Such distance was chosen in function of the visibility conditions. For each observed lizard we recorded the following data: species, hour and microhabitat. Twelve types of microhabitat were recognized (González-Romero *et. al.*, 1989): ground, ground under shrub, ground under tree, sand, sand under shrub , sand (in), rocks, lava, fallen branches, scrub basis, tree and crevice (in). During the same days time was dedicated to collecting the available adults of each species in order to analyze the stomach content. The lizards were fixed in 10% formalin.

The stomach content was extracted in the laboratory and observed under a binocular stereoscopic microscope. The food items of the insectivorous lizards were identified to the level of family. Each item was also measured with an ocular micrometer.

Habitat and microhabitat niche breadth as well as trophic and temporal niche breadths were calculated using the diversity measure of Simpson (Levins, 1968):

$$B = (\Sigma\ p_1^{2} -)^{-1}$$

were p_i is the proportion of individuals found in the i^{th} substrate or habitat. For the daily activity: p_i was (for each species), the proportion of the individuals observed during the hour interval i to the total number recorded over the 13 time spans distinguished. For the trophic axis: p_i was the proportion both by taxonomical level and by size of the preys consumed by each species in relation to the total items consumed by the species under analysis.

Habitat and microhabitat niche overlap among species were measured using Pianka's index (Pianka, 1973):

$$O_{jk} = \frac{\Sigma\ P_{ij}\ .\ \Sigma\ P_{ik}}{\sqrt{\Sigma\ P_{ij}^{2}\ .\ \Sigma\ P_{ij}^{2}}}$$

where Pij and Pik are the frequencies of utilization of the i^{th} habitat or microhabitat by the j^{th} and k^{th} species.

Trophic and temporal overlaps were similarly estimated For the case of trophic overlap among species, Pij and Pik represent the frequencies of utilization of the i^{th} taxon or prey size by the j and k species. For the overlap of the temporal niche Pij and Pik represent the proportion of active individuals to the time i^{th} by the species j and k respectively.

As emphasized by Ricklefs and Lau (1980) there are no simple statistical methods to calculate the confidence limits of such estimates, which does not present our results from being discussed.

Results

Species abundance

The five most commonly recorded species in the study area are *Uta stansburiana, Cnemidophorus tigris, Dipsosaurus dorsalis, Uma notata and Callisaurus draconoides*. They represent 96 % of all sighted individuals in 1982, and 95 % in 1983.

The censuses along the transects during the hours of highest activity of diurnal lizards *(Ortega et. al, 1986)* provide rough estimates of population densities. The average distance walked per hour was 3,600 m which corresponds to a surface of 25,200 m^2. The densities calculated in this way are minimum densities (mean number of active individuals per ha.) and were corrected by multiplying the abundances of *Cnemidophorus tigris* by a factor of two, because it has been observed that the abundances calculated form censuses during periods of lizard maximum activity correspond to approximately half of the real densities (measured by mark-recapture methods on quadrants) for the "sit and wait" species, but only to one quarter for the widely foraging species (Barbault and Maury, 1981). From Fig. 3, it follows that each Sierra Blanca habitat is mainly dominated by only one or two species: *Uma notata* on the dunes and the pair *Uta stansburiana/Cnemidophorus tigris* elsewhere. The Sonoyta communities are enriched by *Callisaurus draconoides*, a new common species near the river bank, while density of *Uta stansburiana* is dropping sharply.

Spatial distribution of the Species

The spatial distribution of the main species are shown in Fig. 4 and their spatial niche width are presented in Table 1. It can be seen that three out of the five most common species recorded in the area are widely distributed (*Uta stansburiana, Cnemidophorus tigris and Dipsosaurus dorsalis*) while the other two (*Uma notata and Callisaurus draconoides*) seem to be restricted to one habitat only (sand dunes for the former and river shore brush for the latter). Concerning the less frequently observed species we can also observe that *Sceloporus* magister is strictly confined to riparian "forest"; *Sauromalus obesus* to lava flows; *Crotaphytus collaris* to mountain slopes and *Gambelia wislizenii* to bush-landscapes (brushes or fixed dunes) near rivers.

The overlap values of spatial niches between the main species are given in Table 2. There is a high overlap (> 0.80) between *Uta stansburiana and Cnemidophorus tigris,* as well as among *Dipsosaurus dorsalis, Sceloporus magister and Callisaurus draconoides.*

Further analysis of these data show how these species use the various microhabitats or substrates (Table 3). Since the species distribution over the microhabitat range did not change significantly from 1982 to 1983, the data for the two sampled periods were pooled together. While *Uta stansburiana* and *Cnemidophorus tigris* appear as poorly specialized, most species seem mainly restricted to a well defined microhabitat category: *Uma notata* to sandy substrates; *Sceloporus magister* and *Urosaurus ornatus* to trees; *Crotaphytus collaris* to rocky outcrops; *Sauromalus obesus* to basaltic flows and *Dipsosaurus dorsalis* to bushes covered areas.

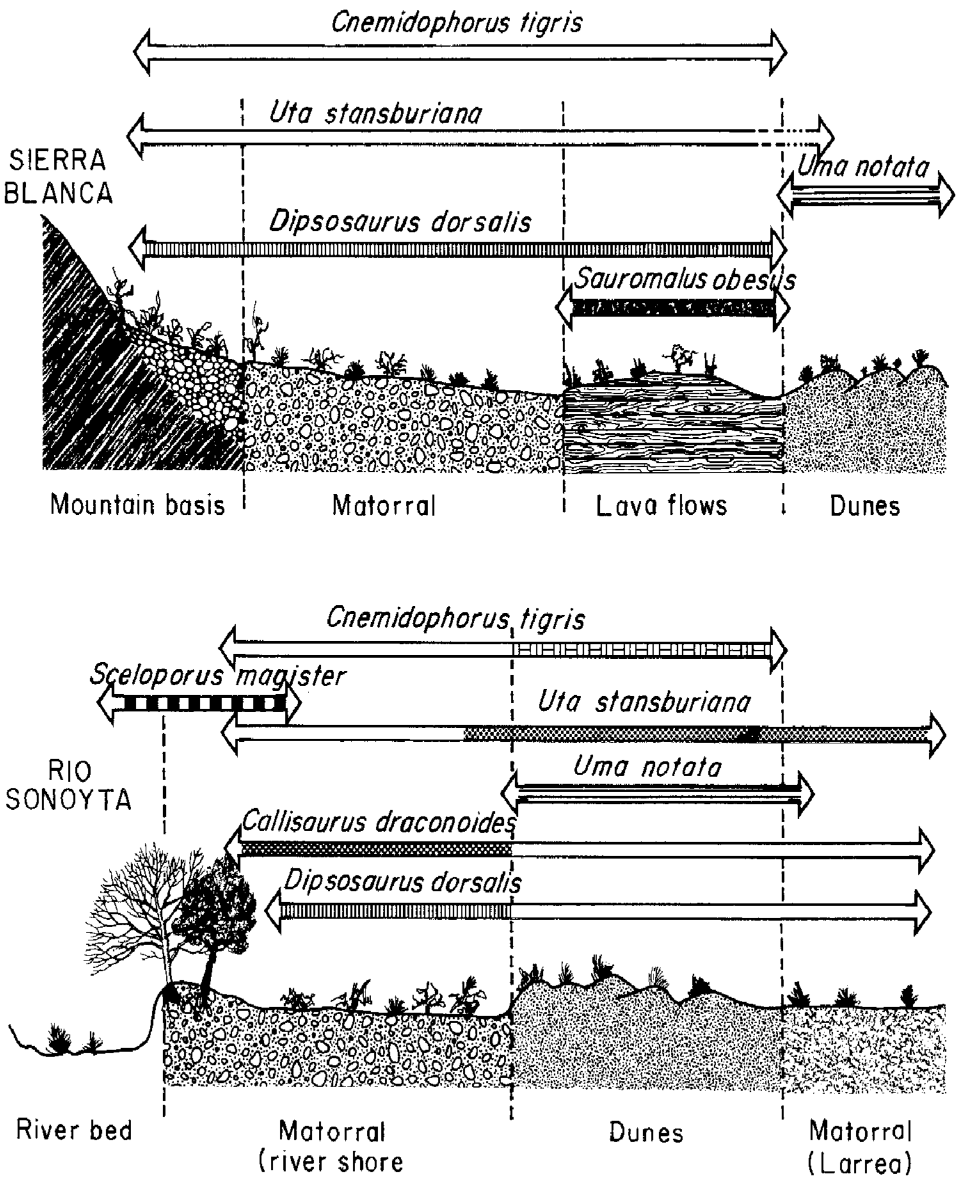


Figure 3.- Distribution of lizard species along the two topographic gradients.

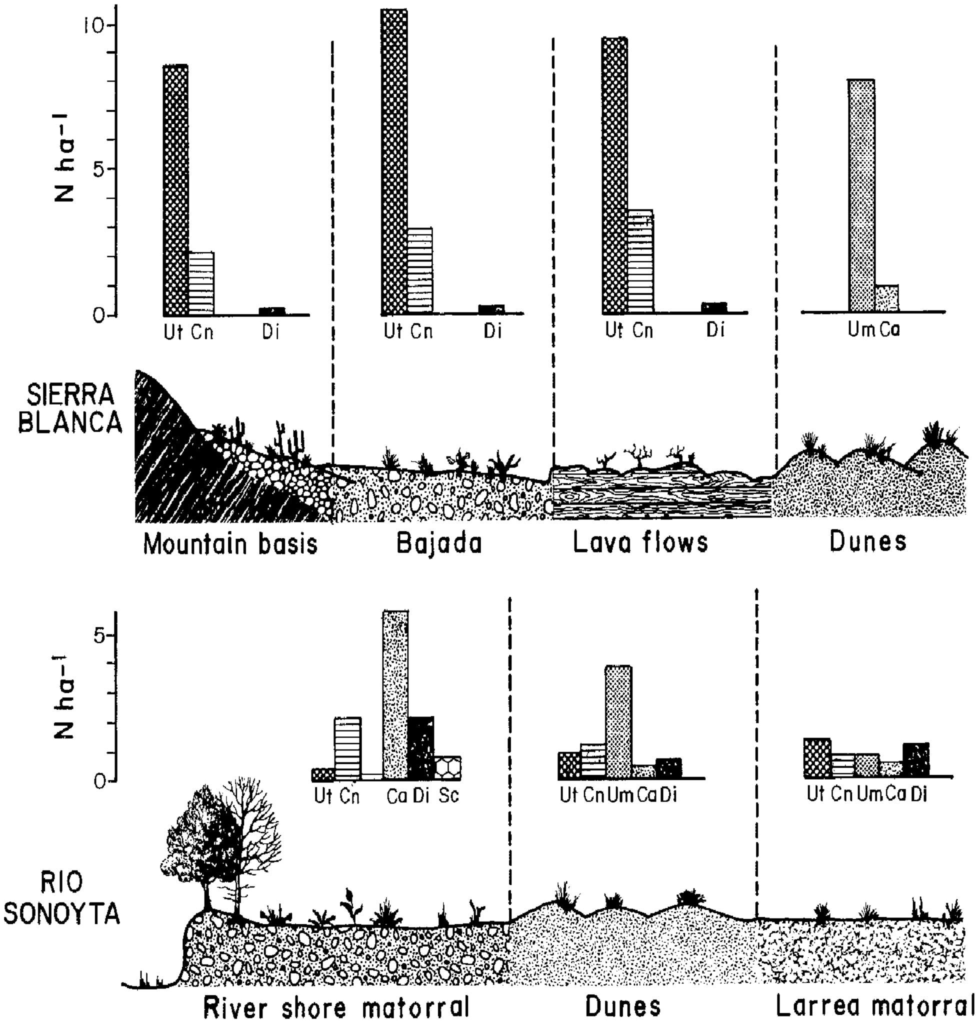


Figure 4.- Number of individuals per ha for the most common species recorded along the two transects during the hours of highest activity.

Table 1.- Habitat niche breadth (B) for the 12 species in 1982 (7 habitats sampled) and 1983 (6 habitats sampled) and mean standarized habitat niche breadth (B).

	1982		1983		
	counted	B	counted	B	B
U. stansburiana	574	3.49	336	3.13	0.42
C. tigris	105	4.46	62	4.31	0.62
U. notata	192	1.93	146	1.73	0.15
C. draconoides	111	1.19	86	1.71	0.09
D. dorsalis	38	3.78	55	1.86	0.32
S. magister	22	1.00	12	1.55	0.05
P. platyrhinos	6	3.01	0		0.34
C. collaris	0		5	1.00	0
G. wislizeni	0		10	1.00	0
S. obesus	2	2.00	1	1.00	0.08
U. ornatus	3	1.00	0		0

Table 2.- Habitat niche similarityvalues between the main species in 1982 (first line) and 1983 (second line).

	S. stansburiana	*C. tigris*	*U. notata*	*C. draconoides*	*D. dorsalis*	*S. magister*
Uta	-	0.843	0.062	0.030	0.472	0.024
stansburiana	-	0.934	0.018	0.021	0.130	0.026
Cnemidophorus		-	0.057	0.524	0.723	0.515
tigris		-	0.058	0.184	0.293	0.233
Uma			-	0.023	0.085	0
notata			-	0.300	0.109	0.196
Callisaurus				-	0.561	0.998
draconoides				-	0.929	0.928
Dipsosaurus					-	0.525
dorsalis					-	0.986
Sceloporus						-
magister						-

The overlap values at the level of microhabitats show (Table 4) that large values are found between *Uta stansburiana* and *Cnemidophorus tigris; Callisaurus draconoides* and *Dipsosaurus dorsalis*, and also *Cnemidophorus tigris* and *Callisaurus draconoides* and *Dipsosaurus dorsalis*.

Considering both aspects of the spatial dimension and then calculating the mean overlap values between the paired species as the product of the habitat and microhabitat indices, it can be seen (Table 5) that the only large overlap values recorded are those between *Uta stansburiana* and *Cnemidophorus tigris* (0.79 in 1982 and 0.88 in 1983) and, to a lesser extent those between *Dipsosaurus dorsalis* and *Cnemidophorus tigris* (0.52 in 1982, but only 0.21 in 1983).

Table 3. - Relative distribution of the recorded individuals over the various microhabitats or substrates, and corresponding niche breadth of species (B).

	N	a	b	c	d	e	f	g	h	i	j	k	l	B
U. stansburiana	959	.354	.267		.004	.005		.032	.211	.045	.081			3.99
C. tigris	173	.493	.321		.005				.065	.005	.112			2.76
Uma notata	346				.580	.260	.160							2.33
C. *draconoides*	201	.773	.112	.004	.017	.013	.043			.026	.013			1 .63
D. dorsalis	106	.263	.638	.038	.013				.013		.038			2.09
S. magister	34		.114	.800							.029	.057		1.52
P. m'calli	10	.600	.100		.200	.100								2.38
P. platyrhinos	5	.600						.200	.200					2.27
C. collaris	10							1						1.00
G. wislizeni	3	1											.875	1.00
S. obesus		7								.125			.875	1.28
U. ornatus	3										1			1.00

Caption to microhabitats: a = Open ground, b = Ground under shrub, c = Ground under tree, d = Open sand, e = Under shrub, f = In shrub, g = Rock, h = Lava, i = Fallen branches, j = Shrubs basis, k = Tree, l = In cervice.

Table. 4.- Microhabitat niche similarityvalues between the main species.

	S. stansburiana	*C. tigris*	*U. notata*	*C. draconoides*	*D. dorsalis*	*S. magister*
Uta Stansburiana	-	0.939	0.011	0.780	0.777	0.081
Cnemidophorus tigris		-	0.007	0.888	0.720	0.082
Uma Notata			-	0.039	0.017	0
Callisaurus draconoides				-	0.508	0.026
Dipsosaurus dorsalis					-	0.186
Scalaris magister						-

Daily temporal activity of the species

Fifty six transects (3.6 km) were sampled during one hour periods during October, 1982 and 53 transects during June 1983. Respectively 1,106 and 749 lizards pertaining to 10 species were recorded. Only those species observed more than 50 times during each season were considered for analysis. Table 6 shows that there is a close resemblance in the daily activity rhythms among the species during each season which is evidenced by the difference among the rhythms between the Summer and the Fall (Fig. 5).

Among all the pairs considered, the temporal overlap among the five most frequent observed species was always higher than 0.83 during 1983 and 0.73 during 1982 (Table 7).

Table 5.- Mean spatial niche overlap values between the main species in 1982 (first line) and 1983 (second line).

	S. stansburiana	*C. tigris*	*U. notata*	*C. draconoides*	*D. dorsalis*	*S. magister*
Uta	-	0.792	0.001	0.023	0.367	0.002
Stansburiana	-	0.877	0	0.016	0.002	0.081
Cnemidophorus		-	0	0.465	0.521	0.042
tigris		-	0	0.163	0.211	0.019
Uma			-	0.001	0.001	0
Notata			-	0.012	0.002	0
Callisaurus				-	0.285	0.026
draconoides				-	0.472	0.024
Dipsosaurus					-	0.098
dorsalis					-	0.183
Sceloporus						-
magister						-

Food consumption

Prey taxa consumption

According to the diversity of the contribution of all prey taxa to the diet of each species by numbers of prey items (Table 8), as well as by the volume of prey (Table 9), it is possible to observe that there are highly specialized species that resort to a small range of food resources, just like *D. dorsalis* (plants); and species like *C. draconoides* and *U. stansburiana*, that show more diversified alimentary habits. In spite that *U. notata* showed a preference for ants during one of the years studied, it can be considered as a generalists species if the three years and both measures, number and volume are taking into account. *C. tigris* shows a relative specialization considering the number of prey items in relation to termite consumption, but if the prey volume is considered, the diet seems to

Table 6.- Average numbers of observed lizards per hour during October of 1982 and June of 1983.

Transect begining (h)		7	8	9	10	11	12	13	14	15	16	17	18	19	
Number of transects	1982	2	2	2	6	6	9	7	5	8	3	2	2	2	D
	1983	5	4	5	5	5	2	2	2	2	5	6	5	5	S
Uta	1982			14	28	23	21	27	29	26	28				0.56
Stansburiana	1983	12	22	13	7						9	13	1		0.40
Cnemidophorus	1982			1	7	6	3	4	2						0.30
tigris	1983	2	3	3	2						2	1			0.37
Uma	1982		7	16	13	13	19	24	28	25					0.51
notata	1983	3	6	6	2						8	7	2		0.42
Callisaurus	1982		6	10	24	17	14	11	7	4					0.44
draconoides	1983	2	4	6	3						2	2			0.31
Dipsosaurus	1982		2	5	4	2	1	1							0.26
dorsalis	1983		3	3	2	1					1	2	1		0.34

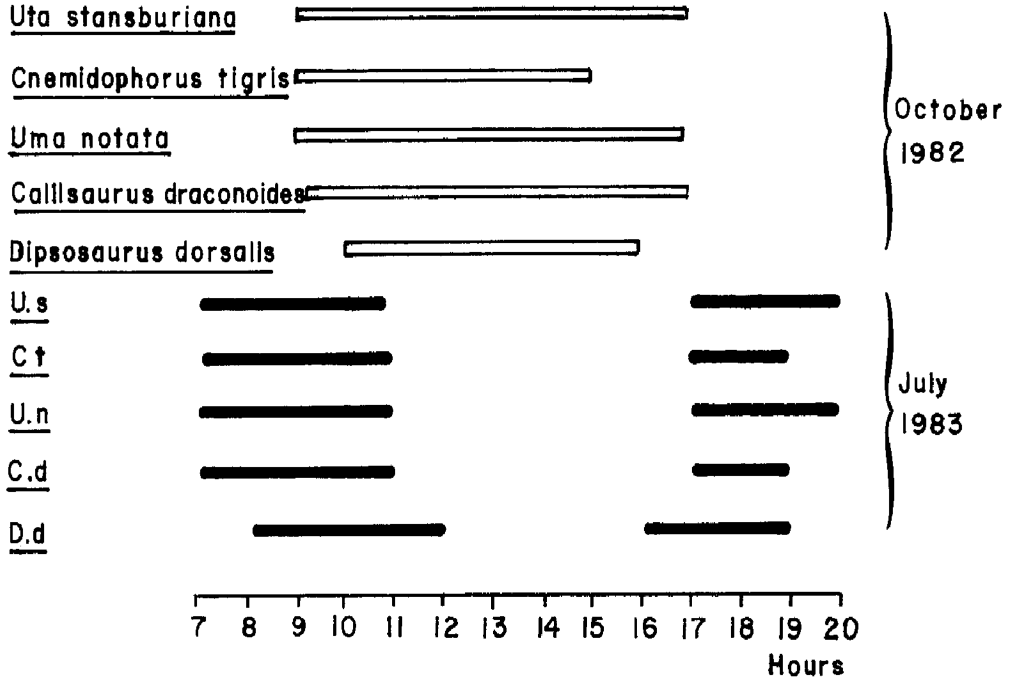


Figure 5.- Daily activity cycles for the main lizard species of the zone for the two studied seasons.

Table 7.- Daily activity cycles for five species during October, 1982 and June, 1983.

	U.s	*C.t*	*U.n*	*C.d*	*D.d*
Uta	-	0.78	0.97	0.74	0.73
Stansburiana		0.95	0.91	0.89	0.89
Cnemidophorus	0.78	-	0.73	0.89	0.88
tigris	0.95		0.87	0.96	0.90
Uma	0.97	0.73	-	0.71	0.71
notata	0.91	0.87		0.83	0.82
Callisaurus	0.74	0.89	0.71	-	0.96
draconoides	0.89	0.96	0.83		0.91
Dipsosaurus	0.73	0.88	0.71	0.96	-
dorsalis	0.89	0.90	0.82	0.91	

Tables 8 and 9 also show that there is a relation between specialization of the diet and the stability of type and volume of prey items consumed: the species with high specialization show a very low variation among the years. This is the case of *D. dorsalis* and *C. tigris.*

The other three species show the broadest differences among the type and volume of prey items consumed: *C. draconoides*, *U. notata* and *U. stansburiana* show higher values of diversity of preys consumed during 1982 and 1983 than during 1984. Such difference is much more noticeable in the case of *U. stansburiana.*

Fig. 1 shows the average values of temperature and precipitation during the years of 1982 and 1984. Even when no data are available for 1984, it can be seen that the values of temperature are more stable among the years and also more predictable.

Prey size utilization

Fig. 5 shows that the four insectivorous species predate mainly upon relatively small prey items (1 to 20 mm^3). Such size specialization is more evident in *C. tigris* and *U. stansburiana* but not so in the case of *U. notata* and *C. draconoides.*

Table 8.- Composition of the Diet by Prey Taxa (Total frecuency) for the Studied Species.

SPECIES	**D. dorsalis**			**C. draconoides**			**U. notata**			**U. stansburiana**			**C. tigris**		
YEAR	82	83	84	82	83	84	82	83	84	82	83	84	82	83	84
Number of stomach	10	21	9	34	33	10	39	34	10	67	37	19	38	41	20
Number of items	13	27	4	436	269	33	590	1403	218	732	471	184	2469	960	690
Order Family															
Coleoptera															
Indetermined					.033	.121	.002	.003	.014	.012	.023	.022	.001	.015	.007
Chrysomélidae				.087			.034							.001	
Curculiónidae		.021		.009	.004	.015		.001		.003	.023	.005	.002		
Tenebriónidae		.042					.005	.003	.028	.026	.036	.005	.002	.027	.010
Cupédidae			.004				.002	.002	.133	.001		.005	.002	.003	.013
Carabidae							.002								
Rhysodidae													.001		
Scolytidae											.002		*		
Meloidae								.001					.007	.001	
Coccinelidae					.015			.006							
Allecullidae					.004										
Corylopnidae								.001							
Scaphidiidae								.001							
Histeridae									.005						
Orthoptera															
Indetemined				.005	.011		.003			.011		.016	.002		.004
Acrididae				.005	.011	.030	.003	.001		.001	.002		.001	.016	.004
Gryllidae													.001		
Blatellidae													.004	.001	
Polyphagidae											.002		*	.001	.001
Lepidoptera															
Indetermined	.08			.009	.007		.010	.001		.018	.002		.001	.001	.001
Pyralidae				.069			.002								
Gracilariidae				.055			.036	.001		.003	.002	.071	.021		.014
Noctuaidae				.002			.012			.003		.011	.007	.003	.014
Incurvariidae				.009											
Pterophoridae										.001					
Mycropterisydae						.030						.005	.002		
Sesiidae					.007										
Coleophoridae								.001							
Gelechiidae											.002				
Hymenoptera															
Indetermined	.08	.063	.06	.062	.112	.061	.088	.008	.009	.048	.023	.005		.001	.003
Formicidae	.08	.271		.010	.104	.212	.085	.193	.798	.074	.503	.424		.004	.001
Braconoidae				.007			.012								
Icheneumonidae				.005											
Andrenidae				.016		.015									
Halictidae				.007		.002									
Sphecidae				.011	.033	.030	.075	.004		.014	.008	.011		.001	

Table 8.- Composition of the Diet by Prey Taxa (Total frecuency) for the Studied Species. (continuation).

SPECIES		**D. dorsalis**			**C. draconoides**			**U. notata**			**U. stansburiana**			**C. tigris**		
YEAR		82	83	84	82	83	84	82	83	84	82	83	84	82	83	84
Number of stomach		10	21	9	34	33	10	39	34	10	67	37	19	38	41	20
Number of items		13	27	4	436	269	33	590	1403	218	732	471	184	2469	960	690
Order	Family															
	Cephycidae						.003				.001					
	Xyelidae						.002									
	Vespidae		.037				.007				.003					
	Multillidae										.001					
	Collectidae										.001					
	Pompillidae					.015			.001							
	Gasteruptiidae					.004										
	Apidae								.001			.011				
	Tiphiidae								.001							
	Evaniidae								.001							
Hymenoptera																
	Tenthedinidae											.002				
Hemiptera																
	Indetermined		.021		.032	.089	.121	.020	.004		.051	.013	.011	.002		.001
	Lygaedidae		.021		.466	.297		.246	.421	.005	.257	.023	.005	.009	.018	
	Pyrrhocoridae				.007	.007		.049	.004		.005	.019			.004	
	Pentatomidae		.021		.002	.007		.005	.005		.012			.004	.003	
	Miridae							.041	.028							
	Cydnidae							.002	.023			.021			.001	
	Hydrometidae									.001					.001	
	Coreidae								.012			.011		*		
	Tinginidae								.001							
Diptera																
	Intermined				.007		.121	.007	.001		.003			.001		
	Empididae				.002											
	Asilidae				.005			.002						.001		
	Muscidae				.030			.002			.001					
	Phoridae							.002								
	Therevidae											.004				
	Cecidomyiidae								.001						.001	
Homoptera																
	Indetermined															
	Cicadellidae				.005	.145	.152	.168	.247	.005	.135	.011	.147	.031	.131	.007
	Ortheziidae													*		
	Dyctyopharidae													*		
Isoptera																
	Termitidae				.057	.011	.061	.010			.083	.225	.223	.890	.750	.897
Neuroptera																
	Indetermined					.007					.001			*		
	Myrmeleontidae				.009	.030	.030	.014	.011	.005	.005	.004	.011	.009	.005	.001
	Osmilidae							.003	.010		.008			.001		

Table 8.- Composition of the Diet by Prey Taxa (Total frecuency) for the Studied Species. (continuation).

SPECIES	**D. dorsalis**			**C. draconoides**			**U. notata**			**U. stansburiana**			**C. tigris**		
YEAR	82	83	84	82	83	84	82	83	84	82	83	84	82	83	84
Number of stomach	10	21	9	34	33	10	39	34	10	67	37	19	38	41	20
Number of items	13	27	4	436	269	33	1590	403	218	732	471	184	2469	960	690
Order Family															
Acari				.001	.004					.204	.001		*		
Araneida															
Indetermined					.004	.020		.001		.003	.008				
Theraphosidae				.009	.033		.003	.001		.004	.011	.005	.002	.008	.013
Diplura					.014					.003					
Solpugida										.001		.005	.003		.001
Dermaptera															
Indetermined												.011			
Labirudirae													.001		
Scorpionidae															
Isópoda													*		
Thysanoptera															
Indetermined		.063													
Thripidae		.021													
Scolopendromorpha											.002				
Vegetals	.760	.438	1.00												
U. stansburiana														.002	
C. tigris														.001	
D 1.67	3.59	1.00	4.12	6.86	8.10	8.49	3.60	1.53	6.90	3.24	3.89	1.26	1.72	1.	2 4

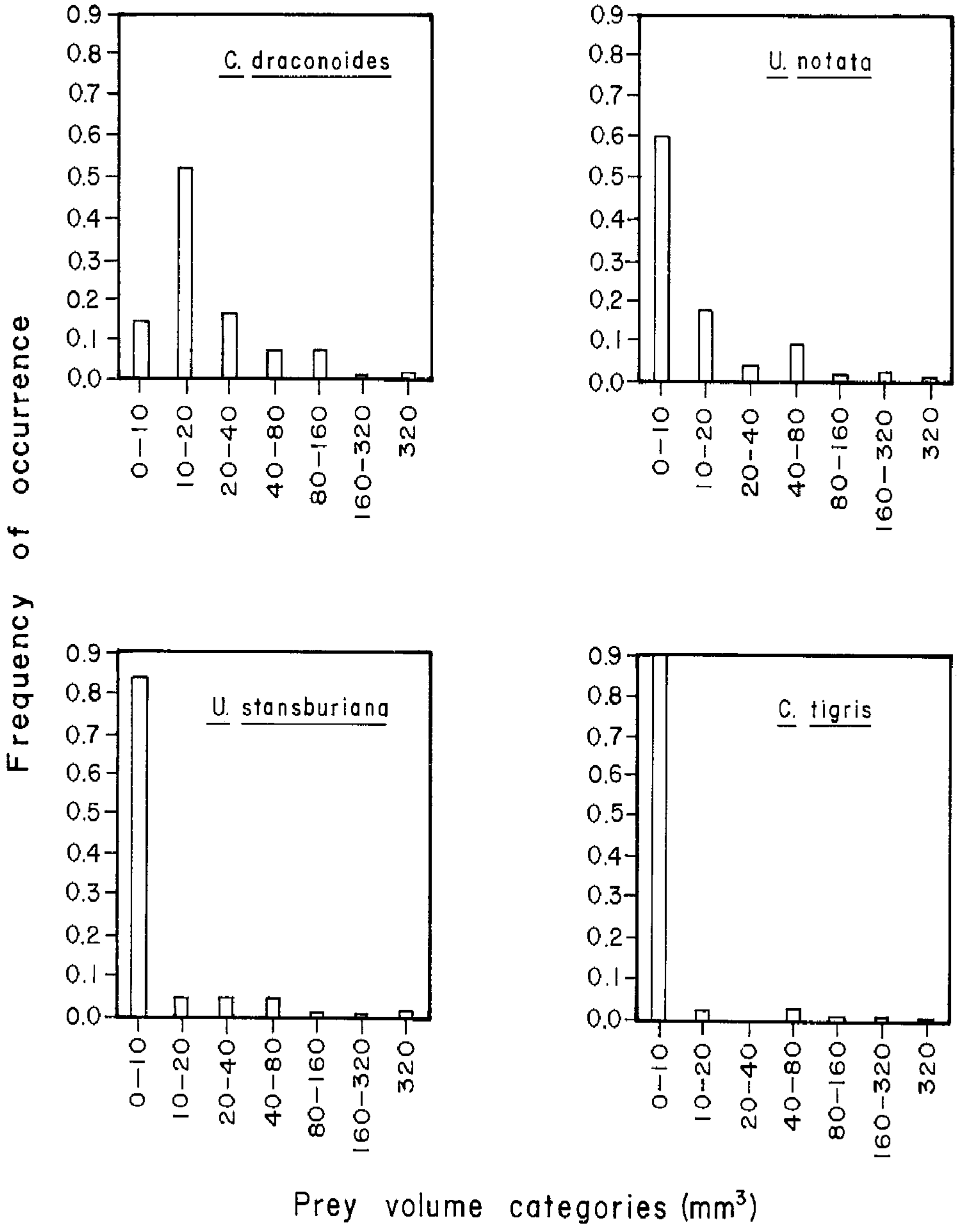


Figure 6.- Frequency distribution by volume of major prey taxa consumed.

Table 9.- Composition of the Diet by Prey Volume (frecuency by volume) for the Lizard's studied species.

SPECIES	**D. dorsalis**			**C. draconoides**			**U. notata**			**U. stansburiana**			**C. tigris**		
YEAR	82	83	84	82	83	84	82	83	84	82	83	84	82	83	84
Number of stomach	10	21	9	34	33	10	39	34	10	67	37	19	38	41	20
Number of items	13	27	4	436	269	33	590	1403	218	732	471	184	2469	960	690
Order Family															
Coleoptera															
Indetermined				0.022	*	*	*	*	*	*	.02	.002	.055	.037	
Chrysomélidae			.034			.013							*		
Curculiónidae	*		.012	*		.017	*		.012	.007	*	.043			
Tenebriónidae		*					.017	*	*	.060	.190	.002	*	.107	.022
Cupédidae					*		.003	.005	.071	*		*	.001	.024	.007
Carabidae							*								
Rhysodidae													.003		
Scolytidae											*		*		
Meloidae								.011					*	.003	
Coccinelidae					.021			.015							
Allecullidae				*											
Corylopnidae								*							
Scaphidiidae								*							
Histeridae								.018							
Orthoptera															
Indetermined				*	*		*			.061		*	.005		*
Acrididae				.138	.236	.391	.024	*		.068	.010		.006	.195	.215
Gryllidae												.114			
Blatellidae													.161	.010	
Polyphagidae											.009		.003	.016	.051
Lepidoptera															
Indetermined	*			*	*		.014	*		.066	*		*	*	.009
Pyralidae				.085			*								
Gracilariidae				.233			.002	.014		.015	*	.825	.067		.206
Noctuaidae				.003			.014			*		.052	*	*	.145
Incurvariidae				.019											
Pterophoridae										.001					
Mycropterisydae						.440						*	*		
Sesiidae					.002										
Coleophoridae								*							
Gelechiidae											.001				
Hyrnenoptera															
Indetermined	*	*		*	.060	*	*	*	*	.135	*	*		*	
Formicidae	*	*		.013	.073	.045	.010	.363	.882	.038	.047	.050		.001	*
Braconoidae				.001			.004								
Icheneumonidae				.001											
Andrenidae				.008		.158									
Halictidae				.054		*									
Sphecidae				.024	.010	*	.480	*		.016	.094	.01		*	

Table 9.- Composition of the Diet by Prey Taxa (Total frecuency) for the Studied Species. (continuation).

SPECIES		**D. dorsalis**			**C. draconoides**			**U. notata**			**U. stansburiana**			**C. tigris**		
YEAR		82	83	84	82	83	84	82	83	84	82	83	84	82	83	84
Number of stomach		10	21	9	34	33	10	39	34	10	67	37	19	38	41	20
Number of items		13	27	4	436	269	33	590	1403	218	732	471	184	469	960	690
Order	Family															
	Cephycidae							*			.007					
	Xyelidae						.002									
	Vespidae		*				.011				.001					
	Multillidae										*					
	Collectidae										.009					
	Pompillidae					.075			.001							
	Gasteruptiidae					.001										
	Apidae								.012			0.040				
	Tiphiidae								.005							
	Evaniidae								.001							
Hemiptera																
	Tentheinidae											*				
Hemiptera																
	Indetermined	*			*	*	.029	*	.007		*	*	*	.001		*
	Lygaedidae	*			.181	.228		.051	.163	.022	.237	.022	*	.083	.062	
	Pyrrhocoridae				.067	.003		.019	.005		.012	.142			*	
	Pentatomidae	*			*	.029		.022	.096		*			.023	*	
	Miridae							.035	.030							
	Cydnidae							.001	.128			.038			*	
	Hydrometidae										*					*
	Coreidae								.016			.030		*		
	Tinginidae								*							
Diptera																
	Indetermined				*		*	.082	.006		*			*		
	Empididae				*											*
	Asilidae				.009			*								
	Muscidae				.108			.003			.036					
	Phoridae							*								
	Therevidae											.88				
	Cecidomyiidae								*						*	
Homoptera																
	Indetermined															
	Cicadellidae				*	.037	.078	.012	.013	*	.087	.007	.005	.022	.064	.004
	Ortheziidae													*		
	Dyctyopharidae													*		
Isoptera																
	Termitidae				*	.005	*	.001			.043	.211	.023	.346	.163	.304
Neuroptera																
	Indetermined					*					*			*		
	Myrmeleontidae				.212	.091	*	.001	.002	.008	.024	.014	*	.002	.149	*
	Osmilidae							.002	.006		.022					

Table 9.- Composition of the Diet by Prey Taxa (Total frecuency) for the Studied Species. (continuation).

SPECIES	**D. dorsalis**			**C. draconoides**			**U. notata**			**U. stansburiana**			**C. tigris**		
YEAR	82	83	84	82	83	84	82	83	84	82	83	84	82	83	84
Number of stomach	10	21	9	34	33	10	39	34	10	67	37	19	38	41	20
Number of items	13	27	4	436	269	33	590	1403	218	732	471	184	469	960	690
Order Family															
Acari				*	*					.026	*		*		
Araneida															
Indetermined					*	.017		*		*	.002				
Theraphosidae				.003	.016		.001	*		.006	.034	*	.007	.144	.001
Diplura							*			*					
Solpúgida										.017			.034		*
Dermaptera															
Indetermined												.022			
Labirudirae													*		
Scorpionidae													.077		
Isópoda													*		
Thysanoptera															
Indetermined		*													
Thripidae		*													
Scolopendromorpha											.009				
Vegetals	1.00	1.00	1.00												
U. stansburiana															.016
C. tigris															.057
D	**1.00**	**1.00**	**1.00**	**7.38**	**5.42**	**2.81**	**3.72**	**5.03**	**1.28**	**9.45**	**7.95**	**1.46**	**5.51**	**8.85**	**4.84**

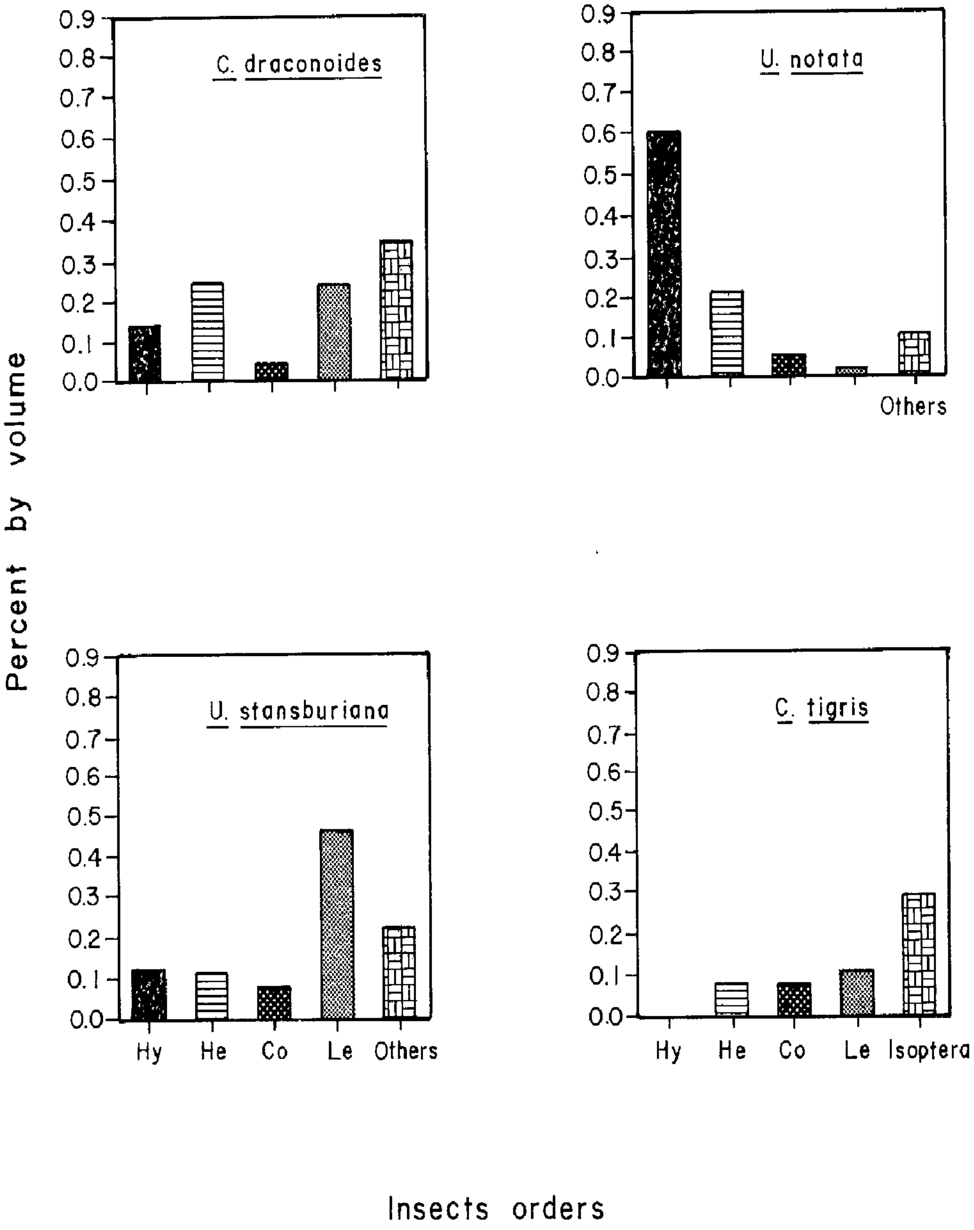


Figure 7.- Prey size (volume of items, mm^3) consumption spectra for the six studied species.

Considering the volume of the main insect groups consumed (Fig. 6) it is remarkable that the results are coincident with those showed in table IX. *C. tigris* shows that in the distribution of the prey volume categories, the highest values represent one insect group (isoptera). *U. notata* shows a slight concentration hymenoptera in the stomach contents. *C. draconoides* and *U. stansburiana* show a more diversified spectrum of consumption of orders insect.

Considering the volume of the four groups of insects consumed more frequently by the four lizards, we can observe that there is a weak tendency or relationship between the size of the lizard and the size of the prey item consumed (Fig. 8); however, it is not significative ($r = -0.17$; $y = 73.46x - 0.04$; $p > 0.05$ N.S.).

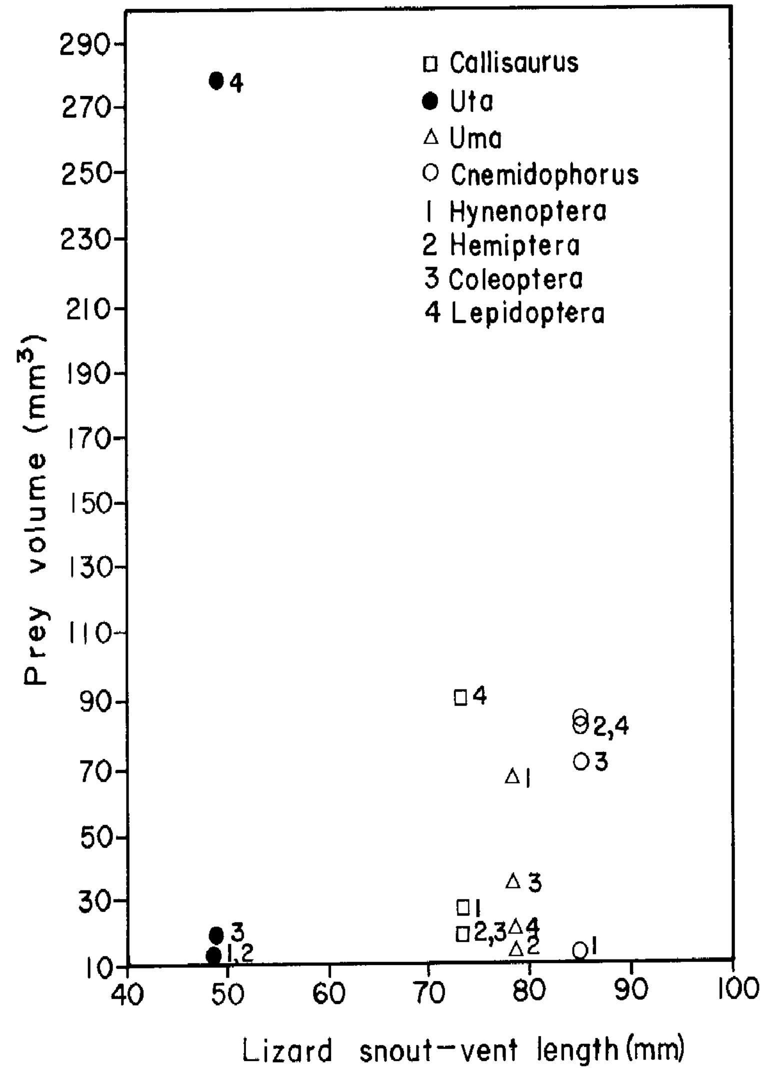


Figure 8.- Relationship between average prey volume and average body length among the studied species.

It is well known that there is a correlation between the size of the predator and the size of the prey item consumed and also between their diversity (Barbault *et. al.*, 1978, 1985; Khodadoost *et al.* 1987). However, the data obtained in this study show that this statement is valid for generalists predators only, (*e.g. U. stansburiana and C. draconoides*). However, from this study it follows that it does not seem to be the rule in the case of noticeable specialized species in the use of resources: for instance *C. tigris* is a larger lizard as compared to *U. stansburiana* and *C. draconoides*; but *C. tigris* (as most species of the genus *Cnemidophorus*) is a predator specialized in the consumption of termites, which are a relatively small items.

Niche overlap

Table 10, shows the values of trophic niche overlap for the five species studied during the three years considered. It is possible to see that the overlap values can be drastically altered if not only the quantity of preys consumed but also their relative volume are considered. Table 10 shows that the overlap values are higher considering only the frequency by numbers of prey items consumed and also that these values are reduced according to the volume of each prey. It is also evident that there is a higher overlap among the more generalists species: *C. draconoides*, *U. notata* and *U. stansburiana* in relation to the other two specialized species.

The data of Table 10 were concentrated for a simple analysis in Tables 11, 12 and 13 in which it can be observed that with the exception of U. stansburiana the other four species show higher overlap values among the individuals of the same species during the three years, than among the individuals of this species with the others. It can also be seen that the highly specialized species show this general pattern more clearly.

Discusion

Concerning the daily temporal structuring of this lizard guild, the results reflect the constraint characteristics of the climatic conditions that are dominant in this desert ecosystem. In the hot Summer, all species try to avoid the mid-day torrid hours, while in the Fall they take advantage of the warmer hours of the day (9 to 16 hrs.). Thus, the daily cycle niche is generally narrower during the Summer than during the Fall, with a remarkable convergence of the diversity values (Ds) (around 0.37 during the Summer and around 0.40 during the Fall), which is true even far completely ecologically different species, such as the "widely foraging" *Cnemidophorus tigris* and the "sit and wait" foragers of the genus *Uta, Uma* and *Callisaurus*.

Table 10.- Values of trophic niche overlap for the five species and for the three years of study. The upper part shows the values considering volume contribution of prey taxa by volume) and the lower part the values considering the frequency by numbers.

	D. dorsalis			C. draconoides			U. notata			U. stansburiana			C. tigris		
	1982	1983	1984	1982	1983	1984	1982	1983	1984	1982	1983	1984	1982	1983	1984
D. dorsalis 1982	-	1.00	1.00	0	0	0	0	0	0	0	0	0	0	0	0
D. dorsalis 1983	.828	-	1.00	0	0	0	0	0	0	0	0	0	0	0	0
D. dorsalis 1984	.984	.829	-	0	0	0	0	0	0	0	0	0	0	0	0
C. draconoides 1982	.016	.065	0	-	.563	.251	.147	.232	.046	.518	.138	.634	.205	.251	.467
C. draconoides 1983	.061	.214	0	.807	-	.514	.117	.313	.184	.114	.105	.14	.131	.166	.373
C. draconoides 1984	.081	.345	0	.093	.515	-	*	*	.076	.180	*	*	.016	.274	.309
U. notata 1982	.57	.193	0	.768	.929	.465	-	.073	.022	.148	.288	.007	.027	.052	.034
U. notata 1983	.039	.223	0	.771	.910	.710	.907	-	.820	.434	.179	.084	.095	.127	.015
U. notata 1984	.104	.510	0	.028	.281	.313	.255	.371	-	*	.134	.060	*	.017	*
U. stansburiana 1982	.037	.154	0	.698	.797	.951	.764	.783	.201	-	.286	.063	.282	.429	.223
U. stansburiana 1983	.098	.480	0	.113	.334	.509	.299	.376	.895	.312	-	.027	.503	.545	.440
U. stansburiana 1984	.087	.432	0	.100	.376	.662	.395	.449	.826	.377	.942	-	.179	.014	.491
C. tigris 1982	.003	*	0	.127	.053	.337	.056	.023	*	.236	.406	.453	-	.468	.625
C. tigris 1983	*	.007	0	.138	.117	.258	.134	.102	.008	.296	.411	.488	.989	-	.543
C. tigris 1984	*	.002	0	.117	.006	.181	.036	.004	.004	.222	.047	.455	.999	.985	-

Table 11.- Average values of trophic niche overlap for the five species considering the frequency contribution of each Prey categorie.

	D. d.				
D. dorsalis	0.880	*C. d.*			
C. draconoides	0.087	0.472	*U. n.*		
U.notata	0.125	0.575	0.511	*U. s.*	
U. stansburiana	0.143	0.504	0.554	0.554	*C. t.*
C. tigris	0.001	0.148	0.041	0.334	0.991

Table 12.- Average values of trophic niche overlap for the five studied species considering the volume contribution of each Prey Taxa category.

	D. d.				
D. dorsalis	1.000	*C. d.*			
C. draconoides	.0	0.443	*U. n.*		
U.notata	.0	0.124	0.305	*U. s.*	
U. stansburiana	.0	0.189	0.137	0.125	*C. t.*
C. tigris	.0	0.244	0.041	0.345	0.545

Table 13.- Average values of the producto of two components measures of trophic niche overlap.

	D. d.	*C. d.*	*U. n.*	*U. s.*	*C. t.*
D. dorsalis	0.940				
C. draconoides	0.044	0.458			
U.notata	0.063	0.350	0.408		
U. stansburiana	0.072	0.347	0.346	0.335	
C. tigris	0.001	0.196	0.041	0.340	0.760

Thus, it can be reasonable assumed that the severe climatic constraints that are characteristic of the study site compel the species to limit their activities to a reduced portion of the day, therefore, preventing any possibility of daily temporal segregation. In this way this community is far from the general rules admitted for the case of lizards, and even for reptiles in general; these rules establish that the temporal segregation of heterothermal individuals is the main factor contributing to their ecological separation (Schoener, 1974; Toft, 1985).

Two outstanding features of this lizard community that have to be emphasized is that the average overlap values in food niches are never higher than 0.58 among the members of the guild when the frequency of contribution of each prey taxa category is considered and, also, that the highest value considering the volume contribution of each prey taxa category are never greater than 0.34. This means that these species, in spite of the ecological variability among years, show a good separation through their food habits, therefore indicating that the potential competition for food is probably an important factor in the ecological organization of this assemblage of species. Thus the observed trophic specializations could be a key factor that permit the high diversity of species of this community.

Food specialization is generally assumed to be a less important factor in the ecological segregation observed among one guild members (Schoener, 1974). Such general assumption is also claimed for the particular case of the reptiles (Toft, 1985) and for the lizards (Barbault and Maury, 1981; Mou, 1987; Mou and Barbault, 1986).

There is, however, one fundamental difference between this study and others that deal with the food niche relationships of lizards (Barbault *et al.*, 1985; Ballinger and Ballinger, 1979; Pianka and Huey, 1978; Smith and Milstead, 1971) that is the fact that we performed the analysis of the prey items over the Family level, whereas other authors have done their analysis on the level of Order.

Of course, the analysis performed on the Order level could display a 100% overlap between two species consuming Coleoptera, while one species might mainly feed on Carabidae and the other on Chrysomelidae, therefore, overlaping very slightly.

If we could go further in the analysis performed (at genus and even species level) we would obtain a more accurate vision of the food niche relationships. Evidently there must exist a balance between the need for performing a precise analysis and the real possibilities to do it. However, care must be exercised in the interpretation of the food niche data when a precise level of prey identification has not been achieved.

Regarding spatial segregation, the overall of the lizard guild of the Pinacate region appears to be spatially subdivided into different subsets of only three or four common species (Fig. 3). In this line of thought, *Uma notata* and *Sauromalus obesus* are clearly restricted to only one kind of microhabitat and thus separated from the cluster of species at this level.

Coexisting species within each of these sub-groups are also ecologically separated by the differential utilization of the microhabitat; for example *Crotaphytus collaris, Gambelia wislizeni, Urosaurus ornatus, Callisaurus draconoides* and *Sceloporus magister* are highly specialized in the use of one kind of microhabitat. Thus, the microhabitat spatial overlap values were highly reduced between the individuals of the last two species in relation to all the others.

At the spatial level there are two pairs of highly syntopic species: *Cnemidophorus tigris* with *Uta stansburiana*, on one side and the former with *Dipsosaurus dorsalis* on the other. However if we consider the trophic axis, there are no risks of competition: *Cnemidophorus tigris* is a widely foraging lizard, feeding mainly on termites, while *Uta stansburiana* has a much more diverse diet of a reduced range of the size of preys items on account of being a small predator. The last one, *Dipsosaurus dorsalis* is a large herbivorous species not included in the insectivorous guild here discussed.

What about competition?

From the obtained results it is clear that all the species differ mainly in the way they use the spatial resources, both in the microhabitat as well as in the habitat, and also in how they use the food resources offered by the environment.

The close relationship between species and habitat results generally from the substrate specificity shown by every species, *i.e. Uma notata*, which is restricted to the Sierra Blanca and the Río Sonoyta dunes on account of being a sand-dweller; *Sceloporus magister* (an arboreces species) is therefore restricted to the Sonoyta river bank due to the fact that it is the only place provided with trees, the preferred substrate of this species.

D. dorsalis, C. tigris and *U. stansburiana* (species not separated at the spatial level), are further ecologically separated by their feeding habits, which in the case of the two insectivorous species, results from their different foraging strategies: "widely foraging", consisting in actively and intensively searching for the prey (*C.* tigris); and the "sit and wait" tactic of a stalking predator (*U. stansburiana*). Each strategy exposes the predator to a different range of prey items: for instance "sit and wait" hunters are able to prey upon winged insects when they land near them, while "widely foraging" species are more successful with apterous insects.

Although the theory establishes that the heterotherm organisms of different species could be ecologically separated on the temporal axis (Schoener, 1974; Toft, 1985), this is not the case at El Pinacate. In this most arid zone of México, where the prevailing temperatures are so radical there are no possibilities of partitioning on this axis: all the species must be active over the same time span.

Now it is clear that substrate specialization is neither necessarily nor likely to be a phenomenon competitively induced (Barbault and Maury, 1981; Barbault *et al.*, 1985; Ortega *et al.*, 1982). In fact, lizards may depend strongly upon close substrate adaptation in order to avoid predators, to thermoregulate efficiently or to be successful in mating and defending territory. Thus, the substrate selection and specialization may be a response evolved to cope with a complex combination of various selective pressures and not only with the pressure exerted by the interspecific competition (Ortega, *et al.*, 1982).

However the interspecific competitive risks are minimized as a by-product of microhabitat specialization. Moreover the ecological complementary resulting from the patchy coexistence of the species allows a more efficient use of the available space and should optimize the exploitation of resources. So, the segregation at the microhabitat level should be an important key in explaining the apparent ecological organization of the whole community. Thus, the diversity of richness of this guild is probably achieved through spatial segregation but in close interaction with feeding segregation.

Effective competition between species could prevail in some circumstances. For instance the scarcity of *Uta stansburiana* in the river bank matorral suggests a true competitive exclusion effect. This habitat, characterized by a well developed bush vegetation should be very favorable for side-blotched lizards, so that their scarcity could be tentatively attributed to the very abundant *Callisaurus draconoides*. However the only way to assess firmly the competitive effect of *Callisaurus draconoides* over *Uta stansburiana* is to experimentally exclude the former from this area; an experiment that remains to be made. The only way to test the relative force of the competitive pressures on the organization of this guild is through experimental work, which deserves further attention.

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