

## X. THE BEHAVIOR PATTERNS OF DESERT RODENTS

by

J. F. EISENBERG

### *Introduction*

It is difficult to define a desert in a precise fashion. Arid to semi-arid areas may vary in the form of their vegetation; this ultimately reflects the variation of soil conditions, elevation, temperature, and periodicity of rainfall. Such variation in physical and vegetational features will be paralleled by variations in the species and diversity of rodent faunas exploiting them (ZAHAVI & WAHRMAN, 1957; CHEW & CHEW, 1970). Arid grasslands with intermixed *Artemisia* characterize a semi-desert habitat over much of the extreme western edge of the Great Plains of the United States. Semi-desert areas supporting mixed growth of low shrubs (termed chaparral) defines much of the semi-arid country in the southwestern, coastal portion of North America. True North American deserts have been classically divided into low elevation and high elevation life zones, the Lower Sonoran and Upper Sonoran respectively (MERRIAM & BAILEY, 1910).

To generalize, the true desert areas of the world are characterized by low stature, dispersed vegetation forms and extremely low rainfall. Hence, small rodents adapting to these environments are faced with scattered, unpredictable food resources, lack of continuous cover which would aid in predator avoidance, and a persistent shortage or absence of free water. The temperature of the world's deserts is highly variable depending on altitude and/or latitudinal position. The northern deserts may be bitterly cold during the winter when small mammals are confronted with heat conservation problems. In the lower latitudes, deserts may be subjected to extremely high daytime temperatures with concomitant problems of heat dissipation to be faced and solved by the diurnal mammalian inhabitants (SCHMIDT-NIELSEN & SCHMIDT-NIELSEN, 1952).

The world's deserts have their greatest distribution in the Eastern Hemisphere, in particular, North Africa, the Middle East, and Central Asia. These deserts cover a tremendous span of latitude and exhibit contrasting temperature extremes. Most of the Asian and African desert areas have counterparts in North America, for example, the Sahara-Sindian life zone (BODENHEIMER, 1935) is comparable to the Colorado desert of North America. Central and western Australia is dominated by

a variety of desert forms which are climatically and geophysically comparable to the North American and Asiatic series. Only South America exhibits a limited true desert area, the Atacama Desert confined to the coast of Peru and Chile. This desert is of relatively recent origin and does not display a series of Cricetine rodent forms exhibiting the diversity and degree of specialization that one finds among Heteromyidae of North America, and the Dipodidae and Gerbillinae of Africa and Asia.

When comparisons are made between desert rodents from two separate geographical areas, one is continually struck with the patterns of convergence. Similarities in color, form, ecology, and behavior demand some functional explanation, but equally intriguing are the differences. Attention will be focused on behavioral convergences but the importance of behavioral discontinuities begs that additional questions be posed.

Rodents are to be found in all of the world's desert areas; however, the most highly adapted desert rodents with the longest continual history of evolution and adaptation to desert life are to be found in North America and Asia. To a lesser extent, rodent evolution in Africa parallels the Asian adaptive radiation and (in part) the African desert rodent fauna is derivable from Asia's. The Australian desert rodent fauna shows some remarkable convergences toward that of the major continental radiations but the diversity of forms is lower.

In this review the major functional classes of rodent behavior patterns will be described for several species. I will employ a functional classification because I wish to emphasize that behavior patterns are mechanisms which serve to maintain the organism and allow selective exploitation of a suitable micro-habitat. Behavior patterns are adaptive strategies which are as much the products of natural selection as are the bones and muscles utilized as reference points by anatomists. The stereotyped, neuromuscular coordination patterns or 'fixed action patterns' which comprise a species' behavioral repertoire may be compared from one species to the other with useful inferences and predictions deriving from such comparisons (EISENBERG, 1967). For the purpose of this chapter, the behavior patterns of the heteromyid rodents will be taken as baselines to which comparisons of other species will be made.

### *The Evolution of Desert Adaptations*

#### ECOLOGICAL NICHES

If one turns to the semi-desert habitats of southwestern North America, a variety of rodent species exhibiting a variety of adaptations can be discerned. The following ecological niches can be described (see Tables 1 and 2).

Table 1. Semi-desert and Desert Rodent Faunas.

Libya (Mediterranean) <sup>1</sup>	California (Californian) <sup>2</sup>	Ground Squirrels	Libya (Saharan) <sup>1</sup>	California (Sonoran) <sup>2</sup>
—	Sciuridae <i>Citellus beecheyi</i>	—	—	Sciuridae <i>Citellus mohavensis</i> <i>Citellus leucurus</i>
Microtinae <i>Microtus mustersi</i>	Microtinae <i>Microtus californicus</i>	Voles	—	—
Spalacidae <i>Spalax ehrenbergi</i>	Geomyidae <i>Thomomys bottae</i>	Fossorial Forms	—	Geomyidae <i>Thomomys bottae</i>
Murinae	Cricetinae	Small Quadrupedal	Gerbillinae	Cricetinae
<i>Acomys cahirinus</i>	<i>Peromyscus boylei</i> <i>Peromyscus maniculatus</i> <i>Neotoma fuscipes</i>	Granivore/Insectivores	<i>Gerbillus gerbillus</i> <i>Gerbillus campestris</i> <i>Meriones crassus</i> <i>Meriones caudatus</i>	<i>Peromyscus eremicus</i> <i>Onychomys torridus</i> <i>Neotoma lepida</i>
Gerbillinae <i>Gerbillus eatoni</i> <i>Gerbillus henleyi</i> <i>Meriones libycus</i> <i>Pachyrhynchus duprassi</i> <i>Psammomys obesus</i>	Heteromyidae <i>Perognathus fallax</i> <i>Perognathus inornatus</i> <i>Perognathus californicus</i>	—	—	Heteromyidae <i>Perognathus formosus</i> <i>Perognathus penicillatus</i> <i>Perognathus longimembris</i>
Dipodidae <i>Allactaga tetradactyla</i> <i>Jaculus orientalis</i>	Heteromyidae <i>Dipodomys heermanni</i> <i>Dipodomys venustus</i> <i>Dipodomys agilis</i>	Bipedal Saltators	Dipodidae <i>Jaculus jaculus</i> <i>Jaculus deserti</i>	Heteromyidae <i>Dipodomys deserti</i> <i>Dipodomys merriami</i>

<sup>1</sup> Biotic Provinces and faunal elements from RANCK, 1968; BODENHEIMER, 1935.

<sup>2</sup> Biotic Provinces and faunal elements from DICE, 1952; INGLES, 1965.

Table 2. Micro-habitat Preferences for Some Desert Rodents

Substrate Type	Gaza, Israel <sup>1</sup>	Walker Lake, Nevada <sup>2</sup>
Rock	<i>Sekeetamys calurus</i> <i>Gerbillus dasyurus</i>	<i>Neotoma lepida</i> <i>Peromyscus crinitus</i> <i>Perognathus formosus</i>
Sand	<i>Jaculus jaculus</i> <i>Gerbillus gerbillus</i>	<i>Dipodomys deserti</i> <i>Microdipodops pallidus</i>
Soil	<i>Meriones crassus</i> <i>Gerbillus nanus</i>	<i>Perognathus longimembris</i> <i>Citellus leucurus</i> <i>Peromyscus eremicus</i> <i>Dipodomys microps</i>

<sup>1</sup> ZAHAVI & WAHRMAN, 1957; BODENHEIMER, 1935.

<sup>2</sup> Data from EISENBERG.

*Diurnal, surface foraging granivores*

This niche is occupied by various species of the genus *Citellus* (*Spermophilus*) including *Citellus mohavensis* and *C. leucurus* (see HUDSON, 1962, and BARTHOLOMEW & HUDSON, 1960).

*Nocturnal, insectivore-granivore*

This is a very specialized niche occupied by *Onychomys* in North America.

*Nocturnal, granivore-herbivore\**

a) Adapted to chaparral habitats; most species are dependent on free water in succulent plants. Examples: *Neotoma lepida*, *Peromyscus maniculatus*, *P. eremicus*, *Perognathus californicus*, *Dipodomys agilis* (see MACMILLEN, 1964, for a discussion of this rodent community). b) Adapted to flat, pebble deserts in extreme xeritic conditions. Examples: *Perognathus formosus*, *Dipodomys microps*, *Microdipodops megacephalus*. c) Adapted to sand deserts with spaced vegetation and a minimum of cover. Examples: *Perognathus penicillatus*, *Microdipodops pallidus*, *Dipodomys merriami*, *Dipodomys deserti*.

*Completely fossorial forms: herbivores*

Example: *Thomomys bottae*.

Such a series of forms may be found under similar ecological conditions

\* Some insects taken as prey.

Table 3. Convergent Evolution of Bipedal Saltating Rodent Genera in Arid Areas

Geographical Area	Family	Genera
Africa	Dipodidae	<i>Jaculus</i> <i>Allactaga</i>
Madagascar	Pedetidae	<i>Pedetes</i>
Asia	Muridae	<i>Macrotarsomys</i>
	Dipodidae	<i>Allactaga</i> <i>Alactagulus</i> <i>Euchoreutes</i> <i>Salpingotus</i> <i>Cardiocranius</i> <i>Pygerethmus</i> <i>Dipus</i> <i>Scirtopoda</i> <i>Paradipus</i> <i>Eremodipus</i> <i>Jaculus</i>
Australia	Muridae	<i>Notomys</i>
North America	Heteromyidae	<i>Microdipodops</i> <i>Dipodomys</i>

in Africa, including *Paraxerus* as a counterpart of *Citellus*, *Acomys* in place of *Peromyscus*; some species of *Meriones* and *Gerbillus* in place of *Neotoma* and *Perognathus*; and *Jaculus* in place of *Dipodomys*. A similar series of forms could be established for Asia, including *Citellus* and some species of *Meriones* as counterparts of *Citellus* in North America; *Acomys* as a counterpart of *Peromyscus*; *Gerbillus* as a counterpart of *Perognathus*; *Salpingotis* for *Microdipodops*, and a variety of the Dipodid genera, *Jaculus*, *Paradipus*, *Dipus*, and *Scirtopoda*, as counterparts of some species of the North American *Dipodomys*. In Australia, *Notomys*\*\* appears to be a reasonable counterpart of the smaller species of *Dipodomys* in North America (see Table 1).

The degree of convergence is a function of a) the different origins of the rodent stocks currently occupying the different continental areas, b) the length of time it has taken for divergence and adaptive radiation to occur, and c) the degree of similarity in the environments in which the adaptive radiations have taken place. Convergence in form and behavior results from not only physical similarities in environments but also from the similarity of associated species or populations which have been in competition with one another throughout the evolutionary history of their adaptations to desert areas. Suffice to say, however, that a remarkable convergence in niche occupancy has occurred as can be seen

\*\* *Macrotarsomys* of the south central desert region of Madagascar is very convergent with *Notomys*.

when rodent families are compared for the continental deserts of the world (see Table 3).

#### The Evolution of Desert Adaptations within the Family Heteromyidae.

Sometime during the Oligocene, the crust of the earth began to buckle initiating a period of mountain-building in North America and Asia. This process of elevation was followed by the development of grassy plains during the early Miocene replacing the wet forests of the Eocene and early Oligocene. From the beginning of this period, a gradual increase in aridity became the dominant trend. During the Pleistocene this drying-out oscillated with the advance and retreat of the glaciers, but the trend toward aridity persisted. In North America, a family of rodents, the Heteromyidae, was evolving in step with these environmental changes. The adaptive radiation culminated in a bipedal, ricochet form, the genus *Dipodomys*. Today the Heteromyidae consist of 5 genera, grouped into 3 subfamilies. The first subfamily, the Heteromyinae diverged in the early Oligocene and later in the Miocene split into two lines leading to each of the present genera, *Liomys* and *Heteromys*. The other stock diverged in the Miocene forming the lines giving rise to the Perognathinae and the Dipodomysinae. These first divisions corresponded to the more arid conditions of the middle and later Pliocene (WOOD, 1935).

Today the genera are distributed as follows: *Heteromys* is a tropical form confined to the moist areas of Central and South America. *Liomys* ranges in the subtropical, wet to semi-arid areas of coastal Mexico. *Perognathus* is divided into 2 subgenera 1) *Chaetodipus* of the more arid areas of the southwestern United States and Mexico, and 2) *Perognathus* ranging from the Lower Sonoran of the western United States well into the Great Plains. *Microdipodops* is confined entirely to the Great Basin. *Dipodomys* ranges all over the semi-arid and arid areas of western North America. This genus has also invaded the Transition life zone of California but in general is an inhabitant of the Sonoran life zone. Thus we have represented with this family a morphological spectrum from a relatively generalized rodent form in *Heteromys* to a very specialized form in *Dipodomys* (see Fig. 1). The trend toward specialization seems to indicate increased adaptation to an arid habitat culminating in *Dipodomys deserti* as a saltator of the sand dunes in California and Nevada (WOOD, 1935).

Bipedal saltating locomotion shown by *Dipodomys* and *Microdipodops* is one extreme specialization to desert life and has evolved convergently in all rodent populations found in the major deserts of the world (HATT, 1932; HOWELL, 1932) (see Table 3). Bipedal saltation is a means of gaining speed for short durations, but it is wasteful of energy since momentum may be lost when the animal strikes the ground. However, bipedal saltation permits the animal to change direction rapidly and this may be its chief selective advantage. Further the ability to spring upwards may be important in avoiding the strike of a snake. It would

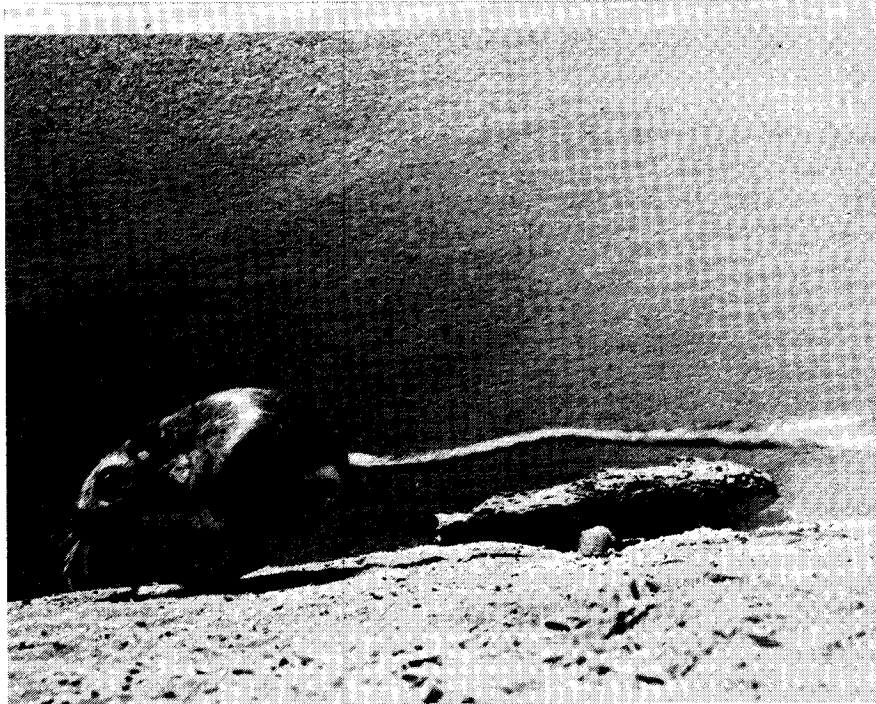


Fig. 1. Bipedal, ricochettal locomotion by *Dipodomys venustus*. Photograph of animal taken at the instant of impact. Note the prominent white tail tip and that the lateral white band on the tail forms an almost continuous line with the white hip stripe and white border of the ventrum. The long vibrissae are in contact with the substrate during slow, bipedal locomotion.

appear to me that predators (cursorial, avian, and reptilian) have been the primary selective forces in producing saltating forms whenever a rodent stock has begun to adapt to patterns of foraging in the open away from cover. Similarly predators have been responsible for the convergence in color patterns which one finds when desert rodents are compared from one continental area to the next.

To round out our discussion of morphological convergence among desert rodents, some mention should be made concerning the pinna and the tympanic bulla. The desert or steppe adapted rodents generally show a relative increase in either the size of the tympanic bullae (*Microdipodops* and *Dipodomys*) or the external ear (*Allactaga* and *Jaculus*). Occasionally some species show a proportionate increase in both the bulla and the pinna (OGNEV, 1959; HOWELL, 1932). It would appear that an enlarged pinna enhances the perception of low amplitude sounds by focusing sound energy at the external auditory meatus. The expanded bulla definitely increases the sensitivity of the ossicles in *Dipodomys* to

frequencies of 1 to 3 KHz and may aid in detecting predators (WEBSTER, 1960, 1962). Morphological changes in the cochlea correlating with the expanding tympanic bullae have been established for the Gerbillinae by LAY (1972) and for the Heteromyidae by PYE (1965). The exact manner in which the bulla functions to maintain sensitivity to low amplitude sounds is only partially understood but an hypothesis has been advanced by WISNER & LEGOUIX (WISNER *et al.*, 1954; LEGOUIX *et al.*, 1954). LAY (1972) should be consulted for a general review.

### *A Comparison of Behavior Patterns*

The behaviour patterns of desert rodents were first systematically studied and recorded by FERNAND LATASTE (1886–1889). After this pioneer effort, ethological studies of mammals were of sporadic occurrence until a renewed effort was made by I. EIBL-EIBESFELDT (1951). During the last decade rodent behaviour studies have increased greatly, and several summaries of behavioral repertoires are now available (EIBL-EIBESFELDT, 1958; EISENBERG, 1967). The following references will serve as a guide to the desert rodent literature: a) Interspecific relationships (MACMILLEN, 1964; WAGNER, 1961); b) the genus *Peromyscus* (EISENBERG, 1968; KING, 1968); c) the family Heteromyidae (EISENBERG, 1963a; EISENBERG & ISAAC, 1963); d) *Citellus* – general behavior (BALPH & BALPH, 1966; BALPH & STOKES, 1963); e) *Citellus leucurus* (HUDSON, 1962); f) *Citellus mohavensis* (BARTHOLOMEW & HUDSON, 1960); g) *Xerus* (EWER, 1965); h) *Onychomys* (RUFFER, 1968); i) *Gerbillus* (KIRCHSHOFER, 1958); j) *Meriones* (EIBL-EIBESFELDT, 1951; RAUCH, 1957; PETTER, 1961; BARAN & GLICKMAN, 1970; THIESSEN & YAHR, 1970; KUEHN & ZUCKER, 1968); k) *Jaculus* (KIRMIZ, 1962; HAPPOLD, 1970); l) *Notomys* (MARLOW, 1969; STANLEY, 1971); m) *Acomys* (DIETERLEN, 1962). Useful comments on the natural history of the Dipodidae are summarized by OGNEV (1959, 1963).

To maximize the utility of this brief review, I will choose only 5 rodent genera for intensive comparisons (i.e. *Gerbillus*, *Meriones*, *Perognathus*, *Dipodomys* and *Jaculus*). This series of forms includes species which are specialized for the exploitation of extremely arid habitats and offers a sample from both bipedal and quadrupedal forms. To avoid repetition in the description of behavior patterns, it should be emphasized that the basic behavioral repertoires for most rodent species are remarkably similar and behavioral inventories or ethograms for different species show a basic uniformity. Terminology and refined descriptions are included in EISENBERG (1967, 1968), EIBL-EIBESFELDT (1951, 1958), and GRANT & MACKINTOSH (1963).

### *Jaculus and Dipodomys*

Since the bipedal saltating rodents are an end point in adaptation to



desert habitats, I will confine the most detailed descriptions to these forms. In particular, I wish to compare and contrast *Dipodomys* with *Jaculus*. This is an instructive comparison since the animals are similar in external morphology but differ profoundly with respect to some of their behavior patterns.

#### *General Comparison*

*Dipodomys merriami* and *D. deserti* are roughly comparable in size to *Jaculus jaculus* and *J. orientalis*. All 4 species are adapted to extremely arid habitats. These animals can exist on metabolic water and require no succulent plants for maintenance of body weight (KIRMIZ, 1962). They are primarily granivores and forage at night for seeds and small arthropods. *Jaculus* displays torpor during cold periods and accumulates fat reserves which appear to supply it with energy during inclement periods. It caches very little. By contrast, *Dipodomys* is a persistent hoarder of seeds and, in common with all the Heteromyidae, possesses externally opening, fur-lined cheek pouches. These pouches are employed to transport seeds from collection points to caching areas in or near the burrow.

A further difference between *Jaculus* and *Dipodomys* concerns the gestation and development of the young. As noted in a previous publication (EISENBERG, 1963a) the genus *Dipodomys* shows both the longest gestation (29–33 d.) and on the average produces the smallest litters in the family Heteromyidae.\* The net result would appear to be the production of rather precocial young which show eye opening times from 12 to 17 days and weaning at 21 to 29 days. These data contrast sharply with the maturation data for the Dipodoidea. The primitive Zapodinae (*Sicista*) have long gestations (28–35 d.) and long developmental times for the young (eyes open at 28 days for *Sicista betulina*) (MOHR, 1954). Those specialized jerboas which have been studied indicate the retention of similar tendencies for both a long gestation and a long developmental period for the young. *Jaculus orientalis* has a gestation period of from 28 to 30 days as does *Dipus sagitta* (OGNEV, 1963). The eyes do not open until 5 weeks of age and coordinated locomotion with bipedal hopping does not occur before 6 weeks of age (see also KIRMIZ, 1962).

By contrast, coordinated bipedal locomotion manifests itself in *Dipodomys* from 3 to 3½ weeks of age. The rapid maturation of *Dipodomys* young results in early attempts at locomotion and the young of *D. nitratoides* begin to crawl in the maternal tunnel system at 10 days of age. The maternal retrieving response is highly developed in *Dipodomys* and errant young can be quickly re-assembled in the maternal nest. On the other hand, the young of *Jaculus orientalis* locomote very little, even at 4 weeks, and it would appear that the maternal retrieving response is very weak (see also PETTER, 1961).

\* *Notomys* exhibits a similar reproductive trend when compared to more typical Muridae.

### Maintenance Activities

Burrowing and nest construction are highly characteristic patterns for both *Dipodomys* and *Jaculus*. Basically the animals employ the forepaws and incisors to loosen soil. Soil which accumulates under the body is either kicked to the rear with the hind feet or the animal turns and pushes the earthen pile to the rear employing its forepaws and chest. In contrast to *Dipodomys*, the pro-odont dentition of many dipodids permits gnawing into a flat surface.

Burrow walls are typically packed by *Dipodomys* employing a pushing and patting motion with the forepaws. *Allactaga* and *Jaculus*, however, utilize the incisors and snout to 'tamp down' the soil by raising and lowering the head in the vertical plane thus bringing the snout and incisors in repeated, forceful contact with the soil. Typically both *Jaculus* and *Dipodomys* plug the entrances to their burrows with earth at the cessation of their nocturnal activity cycle.

The construction of a nest from dried plant material varies from species to species in *Dipodomys* and the dipodids (EISENBERG, 1963a, 1967); however, females with young typically build a nest.

Assembly of foodstuffs differs markedly in *Dipodomys* and *Jaculus*. Whereas *Jaculus* will gather some plant material into its burrow system, all species of *Dipodomys* collect and cache seeds and plant parts. Most species of *Dipodomys* form small, surface caches in the vicinity of the burrow and in addition cache seeds in special chambers within the burrow. The kind and magnitude of the caches vary from species to species (EISENBERG, 1963a). It is worth re-emphasizing that the reduced caching tendency in the dipodids is probably correlated with their capacity for assuming hibernation or torpidity. Thus, the ability to establish fat reserves in the dipodids may be an alternative to caching as a means of passing through periods of food scarcity.

### LOCOMOTION, DAILY ACTIVITY, AND EXPLORATION

Moving on a plane surface may involve 3 basic patterns in small rodents 1) diagonal limb coordination when the contralateral limbs are in synchrony, 2) quadrupedal saltation where the forelimbs alternate with the hind limbs in striking the ground simultaneously, and 3) bipedal locomotion which may be expressed as either a) the walk where the hind limbs support the weight alternately, or b) bipedal saltation when the hind limbs strike the ground simultaneously after each successive hop (HATT, 1932; EISENBERG, 1963a).

*Dipodomys* and *Jaculus* employ quadrupedal saltation when moving slowly or foraging for seeds but bipedal saltation predominates as a mode of rapid forward progression. When foraging for seeds the animals may shuffle in a bipedal walk.

Both *Jaculus* and *Dipodomys* are nocturnal. Upon awakening in the burrow, the animal generally yawns and stretches and shakes itself. It may then proceed to a special chamber in the burrow system and urinate. If some scraps of food have been cached in the burrow system, these may be nibbled or alternatively the animal may move up the tunnel to the burrow entrance where it pauses before leaving and beginning to explore. Exploration of a foreign environment generally involves cautious departures from the nest only to return to the safety of the burrow before proceeding out again. Once the animal has become reasonably confident in a new environment, it will begin exploratory activity. Initially the body may be tensed either in a quadrupedal or in an upright stance. As it becomes more relaxed, the animal will assume more rounded body contours and its movements will become more purposive.

Upon leaving the burrow, the animals generally sandbathe at a specific locus. This serves to dress the pelage and serves also to mark the sandbathing spot with odors from glands situated at various points on the body. Once the animal has settled down in a new environment, it generally initiates foraging behavior. From time to time while moving about the environment, the animal will depress the hind quarters bringing the ano-genital region into contact with the substrate. This 'marking behavior' is very similar in both *Dipodomys* and *Jaculus*.

#### CARE OF THE BODY SURFACE

Auto-grooming (washing) occupies an important role in the activity of most small rodents (BÜRGER, 1959), since grooming activities involving the teeth, forepaws, and tongue serve to remove ectoparasites from the animal's fur. Bipedal desert rodents, such as *Dipodomys* and *Jaculus*, generally have shortened forelimbs when contrasted with their quadrupedal counterparts. The shortened forelimbs impose certain restrictions upon the animals when they wash their face, since wiping movements behind the ears generally cannot be performed simultaneously by both forepaws. Instead, the head must be turned alternately to one side to allow the short, ipsilateral forelimb to sweep behind the ear and over the face nearest to it.

The sequence of movements employed during washing are very similar for *Jaculus* and *Dipodomys*. The tongue is used to lick the forepaws and fur while the teeth are generally used to nibble the coat. Forelimbs are employed in 2 ways 1) the fur may be brushed by the inside of the wrist and forearm as it is passed over the surface of the body, and 2) the claws and digits are used to manipulate the tail, comb at the fur, and grasp while wiping the nose, ears, and vibrissae. In general the forepaws are first held under the mouth and licked and then the nose and vibrissae are wiped. Employing lateral up-and-down strokes, the animal may wipe its face with the inner sides of its forelimbs; gradually lengthening the

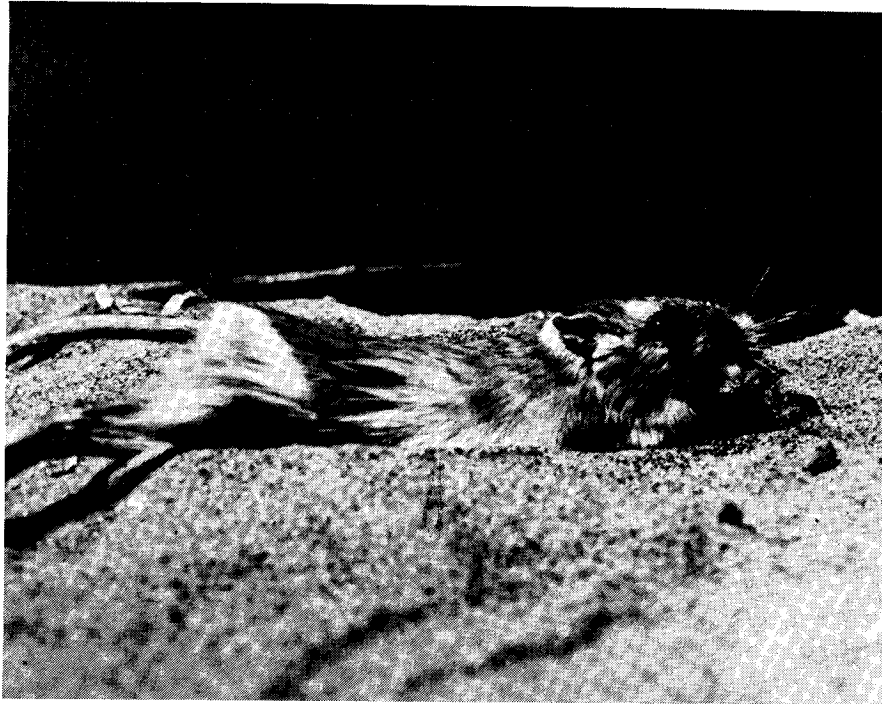


Fig. 2. Extension on the ventrum during the ventral-rubbing phase of sandbathing by *Dipodomys merriami*.

strokes until they reach behind the ears. The combing movements of the forelimbs are then extended to the flank and belly areas and often the combing movements of the forelimbs are combined with licking and nibbling. A complete washing sequence usually ends when the animal grasps the tail and brings it up to its mouth, licking and nibbling the tail from base to tip.

In addition to the typical washing sequence, the animal may intersperse washing bouts with scratching. The hind limb is moved with rapid pendular strokes and directed at various parts of the animal's body. When scratching, the head generally receives the most attention. The nails of the hind foot are usually cleaned with the animal's tongue and incisors between bouts of scratching.

Sandbathing in desert rodents is a method of dressing the pelage and has the derived function of marking. There are 3 distinct components: 1) the animal initiates a sandbathing bout by digging in the substrate with its forepaws and then rubbing either its side or its ventrum in the sand. 2) The side-rub consists of lowering the side of the face to the substrate and gliding forward by extending the body; the body is then

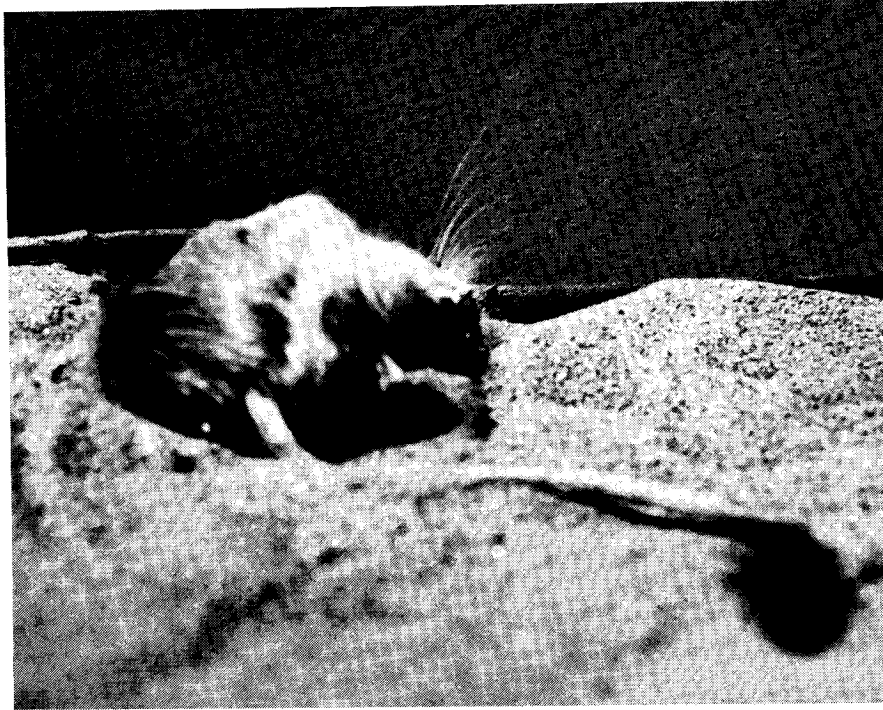


Fig. 3. Flexion on the side during the side-rubbing phase of sandbathing by *Dipodomys merriami*.

alternately flexed and extended while the animal remains on its side. 3) In the ventrum-rub the body is extended and flexed while the animal lies with its ventrum pressed against the substrate. Typically *Dipodomys* shows sandbathing by combining ventrum- and side-rubs into a rather predictable sequence (EISENBERG, 1963b) (Figs. 2 and 3). On the other hand, the dipodid rodents, including *Jaculus* and *Allactaga*, almost invariably show sandbathing involving the side-rub alone and the ventrum-rub is either shown rarely or may be shown independently in combination with other marking behaviors (EISENBERG, 1967).

#### ANTI-PREDATOR BEHAVIORS

The jerboas and kangaroo rats are relatively large in size when compared to the other nocturnal rodents which share the same microhabitats. As a result they are somewhat more conspicuous. Perhaps the origin of bipedality is in some way a result of predator selection for a species which can exhibit greater speed when under attack by an aerial or terrestrial predator. No doubt the remarkable convergence in the color patterns of desert rodents from the various areas of the world has resulted from

predator selection since there is a strong correlation between the reflectance of the pelage and the soil from which the species has been obtained.

The eyes of jerboas and kangaroo rats are reasonably large and visual detection of predators may be important in predator avoidance. Mention has already been made of the tendency for either an increased pinna size or inflated mastoid bullae; it may be that these modifications are related to predator detection. Indeed, the experiments of WEBSTER (1962) indicate that the ability to perceive low-frequency sounds of low amplitude produced by rattlesnakes is related to the presence of an inflated mastoid bulla.

Predator avoidance involves the ability to detect the presence of the predator and then to follow through with several alternative courses of action. The bipedal ricochet permits kangaroo rats and jerboas to leap into the air, thus avoiding the strike of a terrestrial predator. At the same time, bipedality permits the animals to move rapidly and change direction quickly, thus avoiding both aerial or terrestrial pursuit.

Other predators, especially snakes, can be avoided by plugging the burrow. Of course, plugging the tunnels in the burrow is probably also related to the maintenance of a high humidity within the burrow system to reduce water loss. However, burrow-plugging also occurs in terrestrial rodents not adapted to arid environments.

When disturbed by a mild stimulus in their burrow, such as falling sand grains in the tunnel system, kangaroo rats and jerboas frequently approach the source of the disturbance. Upon approaching such a minor tunnel disturbance, the animal will generally begin digging and kicking back and pushing and patting at the walls of the tunnel. This can serve 2 purposes: 1) it can reinforce the tunnel walls during incipient cave-ins, and 2) the digging and pushing activity can serve to plug the burrow. Thus burrow-plugging and the maintenance of burrow walls are inter-related activities elicited by minor disturbances to the soil of the tunnel walls. Such a disturbance could be caused 1) by a predator attempting to enter the burrow, and 2) by slight earth movements occurring from the cracking and drying of the tunnel walls.

When mildly disturbed on the surface, jerboas and kangaroo rats have a tendency to approach a novel object and to pause at a certain distance surveying it. If the stimulus does not induce flight, the animal may exhibit displacement activities including digging. In the kangaroo rat, *Dipodomys deserti*, this behavior pattern is ritualized and has become an anti-predator mechanism. The presence of novel objects will elicit not only digging but the directed kicking back of sand or soil onto the stimulus. If a snake is involved, it may strike (whereupon the kangaroo rat avoids the strike by leaping up) or move away to avoid the sand storm. Hence, kicking sand at a novel stimulus has adaptive value in that it forces the

predator to reveal its identity through movement or to move away. Such ritualized sand-kicking has not been noted as yet for *Jaculus*.

Kangaroo rats and jerboas have characteristic responses to both conspecifics and small predators which invade their home range, including the assumption of an alert posture, pilo-erection, and tooth-chattering. *Jaculus* and *Dipodomys* will also thump with the hind foot while facing a variety of alien animals. This tooth-chattering, pilo-erection, and thumping form part of an intimidation display. Of course, any sustained attack by a small predator produces immediate escape flight. Drumming by *Dipodomys deserti* is highly ritualized, including at least 3 variants: slow drumming, fast drumming, and the roll. These form a graded series and probably represent different levels of arousal (EISENBERG, 1963a).

#### COMMUNICATION MECHANISMS

Before moving on to a discussion of social behavior, we must establish a basic assumption; namely, that posture, sound, and marking behaviors have a significance in communicating information to conspecifics. The inference that information transfer occurs, results from observations of 2 animal encounters where predictable responses occur in the presumptive receiver to known activities of the presumptive sender. The investigation of communication mechanisms requires much more experimentation before the exact significance of many behavior patterns can be ascertained (EISENBERG, 1963a; 1967).

Many of the configurations shown by 2 interacting animals involve the exchange of tactile information but this is very difficult to distinguish from the exchange of chemical information. Thus, the 2 modalities may be combined.

Visual communication mechanisms are probably of minimal importance in nocturnal rodents. However, the eye is quite large in *Dipodomys* and *Jaculus* and certainly on moonlit nights, movement can be perceived. There is a remarkable convergence in the marking patterns on the body of jerboas and kangaroo rats. Regardless of the color of the dorsal pelage, the ventrum is white and the terminal tuft of the tail generally consists of one, proximal, black band demarcating a white tail tip (see Fig. 4). This contrasting white portion on the tip of the tail would appear to serve as an orientation point for a male when engaged in the sexual pursuit of a female.

The white ventrum is displayed during the ritualized upright postures employed in fighting and in courtship. The display of this white ventrum produces a sharply contrasting, reflective surface and may aid orientation during a sequence of mutual uprights and sparring behavior; however, the use of the white ventrum as a signal is not unique for either the kangaroo rat or the jerboa (EISENBERG, 1967).

Aspects of auditory communication involve 3 classes of sounds: a)

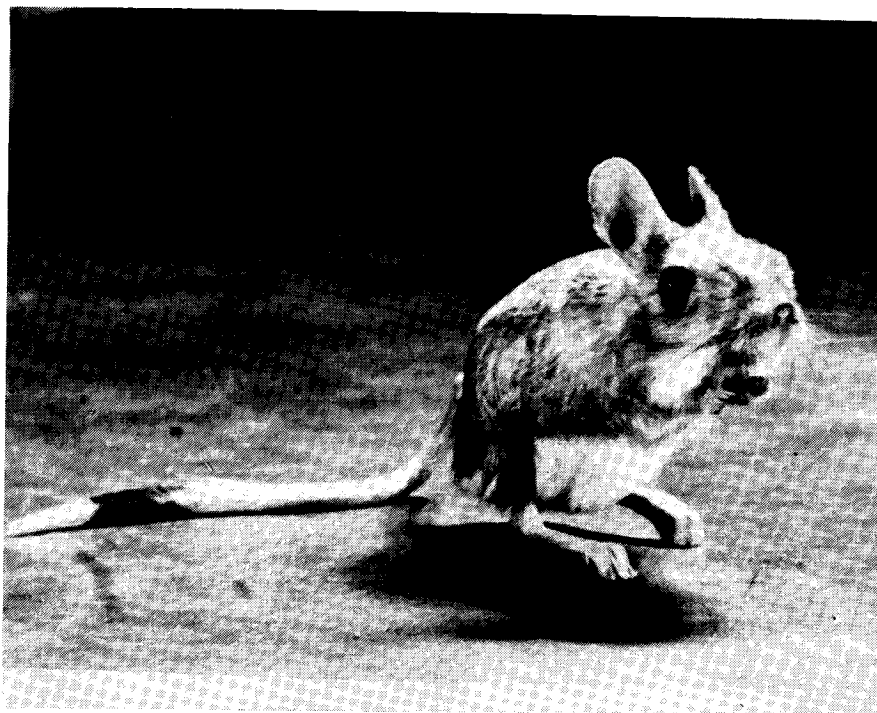


Fig. 4. *Jaculus orientalis*. Note the white tail tip bordered proximally with black. When relaxed, the animal sits with the heel touching the substrate. When hopping bipedally, the animal rises on its toe tips as is indicated by the position of the left foot as the animal prepares to move.

sounds produced by the activities of the animals themselves, namely, the sounds of digging and kick-back. These may have incidental communicatory significance. b) Non-vocal communication by ritualized movement patterns including tooth-chattering or drumming with the hind feet. As indicated in the previous section, drumming with the hind feet is generally shown when the animal is suddenly startled or is in a thwarting context. Tooth-chattering generally occurs in a threat situation. c) The production of vocalizations by expelling air through the animal's glottis.

In both the jerboa and the kangaroo rat, one can distinguish 5 classes of vocalizations: 1) a high squeal which may be shown in a defensive situation; 2) a low grunt; 3) a cry emitted in a young animal when alone, cold, and isolated; 4) a growl or buzzing sound which may be given by an aggressive animal; and 5) a 'comfort' peeping produced by the neonate when the female grooms it.

Male dipodids, including *Allactaga* and *Jaculus*, are prone to produce a 'courting sound'. It tends to be of a buzzing quality in *Jaculus*; however, in *Alactaga*, the sound consists of a buzz component followed by



Table 4. Some Rodent Vocalization for *Dipodomys* and *Jaculus*.<sup>1</sup>

Species	Sound	Context(s)	Implied Function	Sample (N)	Structure of Sound	Frequencies with Greatest Energy (Hz)	Duration of Pulse (sec.)
<i>Dipodomys panamintinus nitratoides</i>	1. Squeal High intensity	When injured, when defensive	Inhibits attack	N.R.	—	—	—
	Chirp	When defensive	?	10	Harmonic	1500-2500	.18-.21
	2. Growl	Thwarting situations	Warning of attack	10	Blurred harmonics to no harmonics	800-1800	.07-.09
	3. Grunt	Startle	?	N.R.	—	N.R.	N.R.
<i>panamintinus</i>	4. Cry of abandoned young (Day 1)	Young out of nest	Induces retrieval	9	Harmonic repetitive	2000; 3000	.1 -.21
	<i>Jaculus orientalis</i>	1. Squeal High intensity	When injured, when defensive	Inhibits attack	N.R.	—	N.R.
Low intensity		Thwarting situations	?	N.R.	—	N.R.	N.R.
2. Growl or Buzz (Courting)		Thwarting situations	Warning of attack	4	Non-harmonic repetitive	1000-1800	.1 -.2
3. Grunt		?	?	N.R.	—	N.R.	N.R.
4. Cry of abandoned young (Day 22)	Young cold	Induce return of female	2	Harmonic repetitive	1500; 3000	N.R. .22	

? = Function incompletely understood.

N.R. = Not recorded.

<sup>1</sup> = All recordings analyzed to 20 KHz only.

a high squeal. This sound appears to have similarities to sounds produced in clearly agonistic situations. Kangaroo rats rarely produce a courting sound, although occasionally during courtship pursuit the female will produce a rather grating, chirp sound. Table 4 compares the sounds of *Dipodomys panamintinus* and *Jaculus orientalis* with respect to the neonate abandoned cry and the 'courtship call'. A remarkable similarity exists between these 2 genera since the fundamental frequency and the frequencies emphasized are roughly the same for both species. The calls have a harmonic structure in the young animal although the harmonics may be blurred in the adult, thus giving rise to the buzzy or noisy quality of the sounds. It is interesting to note that the fundamental frequency and greatest energy concentration in the sound tends to be concentrated at the level to which the ear is most sensitive in *Dipodomys* (see WEBSTER, 1962).

Olfactory communication is undoubtedly of great importance in coordinating the social behavior of rodents (MYKYTOWYCZ, 1970; WHITTEN & BRONSON, 1970). Marking by dragging the ano-genital area over the substrate appears to impart information of use to conspecifics. Furthermore, sandbathing at the same locus establishes an area where odor traces of the sandbather can be left behind for conspecifics to find. The repeated use of the same locus for sandbathing by an individual and the frequent sandbathing of other individuals at the same locus reinforces the conviction that some form of chemical communication is going on (EISENBERG, 1963a; 1967). Marking by depressing the ano-genital region is often accomplished at this same spot. This permits not only leaving traces from the genitalia and/or urine at the marking spot but also implies that the animal may mark its own fur with such traces.

#### AGONISTIC BEHAVIOR

In bipedal rodents, such as *Jaculus* and *Dipodomys*, the upright posture is frequently employed. An animal in a low crouch generally has a high tendency to attack. An extreme upright posture at almost 90° to the substrate, however, indicates an animal in an ambivalent motivational state which is not likely to attack an opponent immediately (EISENBERG, 1963a). Assumption of an extreme upright posture is often accompanied by hopping back and forth on the hind legs, termed jockeying. A highly aggressive animal may hop immediately toward an opponent inducing flight behavior. If both animals clash together, they may lock together gripping one another while kicking and biting. Fights are extremely brief and generally a subordinate animal will move away. Under confined conditions of captivity, however, severe wounding and death can result from fighting (EISENBERG, 1967).

## Contact to Sexual Behavior *Dipodomys*

### 1. Contact

### 2. Precopulatory Interaction

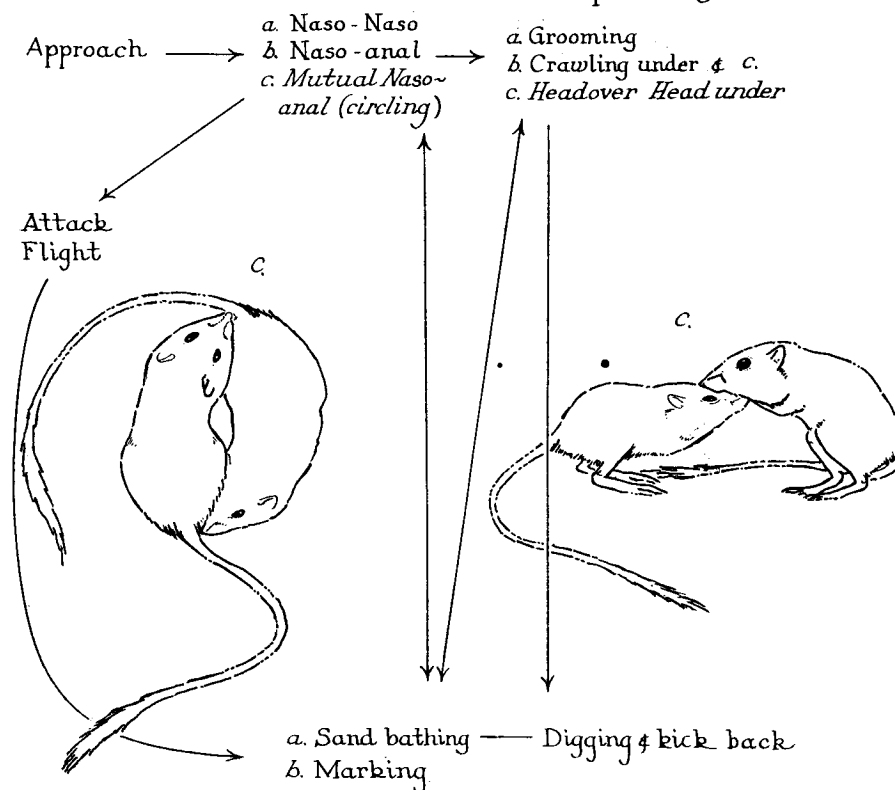


Fig. 5. Contact and precopulatory interaction by *Dipodomys*. Two common contact-promoting postures are illustrated including mutual naso-anal investigation and head-over head-under (from EISENBERG, 1963a).

### COURTSHIP AND MATING

Courtship behavior generally involves interactions which promote contact. Certain elements of agonistic behavior may be shown in the initial phases of courtship but in general contact is established between the 2 animals. Prominent in contact-promoting behavior is the slow approach of one animal to another, placing the head of a subordinate animal beneath the head of a dominant, and then either crawling under the dominant animal or submitting to grooming by the dominant. Initial phases of contact often involve naso-anal investigation by the partners which may be mutual (Fig. 5). Sexual behavior generally involves a driving process where the male will approach the female, touch nose-to-

### 3. Sexual Behavior

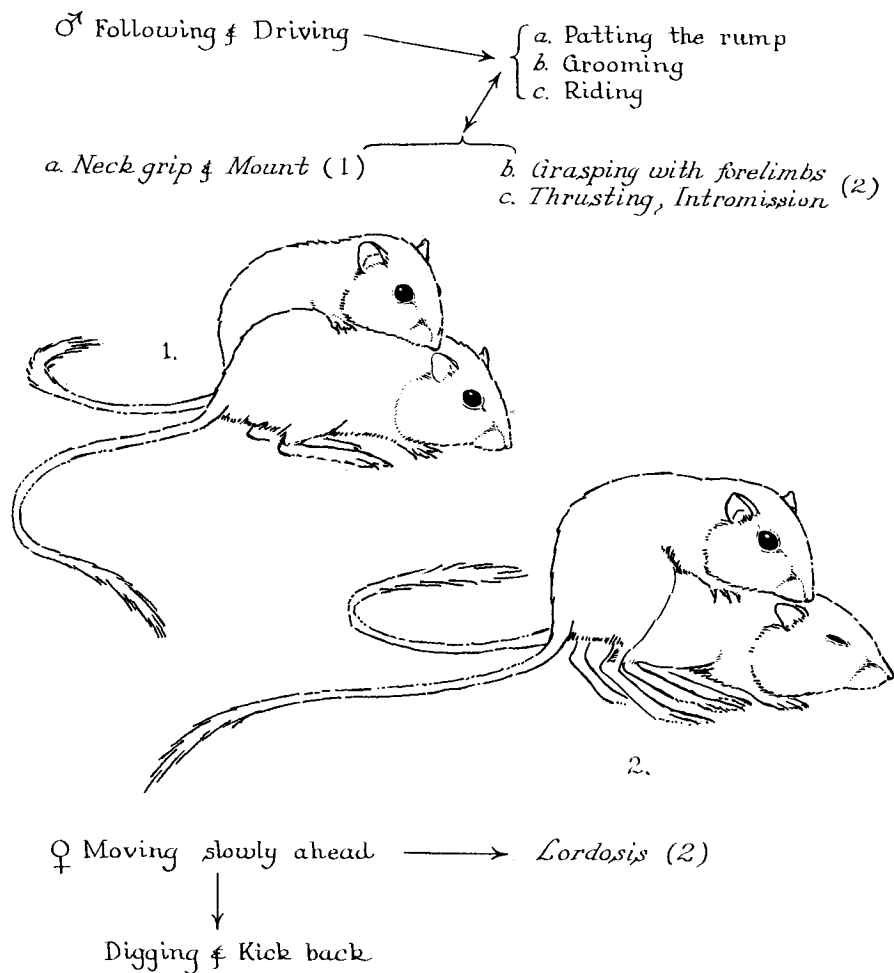


Fig. 6. Sexual behavior in *Dipodomys*. Preparation for mount involves a neck grip by the male. During mounting behavior the female assumes a lordosis posture and moves her tail to one side (from EISENBERG, 1963a).

nose, then proceed to the rear of the female to perform a naso-genital investigation. If the female is slightly unreceptive, she may move away, giving rise to the driving pattern whereupon the male follows the female. If the female is receptive, she will stop suddenly and assume a lordosis posture, remaining quadrupedal but raising the hind leg. Upon the assumption of lordosis, the male will generally attempt to mount (Fig. 6). A neck grip is employed by the male kangaroo rat to secure the female but such a behavior pattern is not generally shown by the male *Jaculus*. Vast

differences in the temporal patterning of copulatory behavior may be noted when various rodent species are compared (EISENBERG, 1963a; 1967), but an exact quantification of the copulatory patterns for *Jaculus* remains to be done.

#### PARENTAL CARE BEHAVIOR

The genus *Dipodomys* is characterized by a high intraspecific aggressiveness. The parturient female generally drives the male out of the burrow and raises the young alone. Although pair tolerance is higher in *Jaculus jaculus* and *J. orientalis*, the female still has a tendency to nest alone during the early development of the young. Nest-building behavior generally increases after the birth of the young and the female spends a great deal of time crouching over the young keeping her back arched to prevent crushing them. This allows the young to nurse while they are kept warm. The female shows a high level of grooming activity, licking the young and removing the feces and urine from the anal and genital regions. The retrieving response is highly developed in the genus *Dipodomys* but only weakly shown in *Jaculus*. During retrieving a pup that has wandered out of the nest is picked up by a fold of the skin with the incisors and carried back to the nest site.

#### GENERAL SUMMARY

Several remarkable convergences can be noted when the dipodids are compared with heteromyids. Considering *Jaculus* and *Dipodomys*, one notices a convergence in the locomotor patterns with corresponding morphological modifications including shortening of the neck, shortening of the forelimbs, and lengthening of the hind foot and tail. Color patterns including the white tail tip bordered by black and the white ventrum show remarkable similarity between the 2 genera. The expansion of the tympanic bulla in the 2 genera seems to indicate a similar function in predator detection. Marking by depressing the ano-genital region on the substrate and marking by means of sandbathing appear to be convergently evolved in the 2 genera although the integration of the patterns and the form of the patterns are slightly different.

The construction of burrows and the plugging of burrows is no doubt related to survival in the arid, hot desert areas but burrow plugging would appear to be a possible anti-predator response to snakes. The food-caching behavior of *Dipodomys*, although strongly developed is not paralleled by a similar development in *Jaculus* which appears to rely more on fat reserves for passing through periods of food scarcity.

The tonal structures of adult and neonatal vocalizations in *Jaculus* and *Dipodomys* show similarities. The development of the young in *Jaculus* is conservative reflecting some of the trends manifest in more primitive

dipodids such as *Sicista*. Development of the neonate in *Dipodomys* shows a specialized advance over more primitive members of the family Heteromyidae (EISENBERG, 1963a). Differences in food-caching behavior appear to be reflected in the social behavior, since the pair tolerance of *Jaculus orientalis* is higher than that displayed by *Dipodomys deserti*. In *Dipodomys* the social system appears to be predicated on individual defense of a burrow system and defense of associated caches.

*A Comparison of Behavior Patterns in:  
Meriones, Gerbillus and Perognathus*

*Gerbillus* and *Meriones* are members of the subfamily Gerbillinae which show close affinities with the Cricetinae. Four species were studied by the author, *Gerbillus nanus*, *Gerbillus gerbillus*, *Meriones unguiculatus*, and *Meriones hurrianae*. *Meriones unguiculatus* is the best studied of the gerbilline rodents and a rather extensive literature has accumulated within the past 10 years (GULOTTA, 1971). Unfortunately very little is known concerning its ecology in the wild. The genus *Perognathus* has been the subject of a variety of field studies and behavior investigations. In the main my remarks will be confined to *Perognathus parvus* and *Perognathus californicus* (see Figs. 7, 8 and 9).

GENERAL COMPARISONS

*Perognathus californicus* and *P. parvus* are comparable in size to *Gerbillus gerbillus* and *G. nanus*. The species of *Meriones* are somewhat larger animals and some species (e.g., *M. hurrianae*) resemble the smaller ground squirrels, such as *Citellus leucurus* of the Sonoran Life Zone in North America. In behavior and ecology, *Gerbillus nanus* and *Perognathus parvus* resemble one another more closely than is the case when either *Perognathus* or *Gerbillus* species are compared with the genus *Meriones*.

Certain species of the 3 genera exhibit the capacity to exist on metabolic water alone. *Meriones unguiculatus* can survive without free water (WINKELMAN & GETZ, 1962; KUTSCHER, 1968). A similar ability has been demonstrated for *Gerbillus gerbillus* (BURNS, 1956). Comparable phenomena are reviewed for *Perognathus* by SCHMIDT-NEILSEN & SCHMIDT-NIELSEN (1952). *Gerbillus* and *Perognathus* very strongly exhibit the trait of caching seeds. The 2 species of *Meriones* which were studied, although caching seeds, exhibited more variability and less persistence in the formation of caches in their burrow systems.

Reproduction is quite similar for the 3 genera. *Meriones* typically shows a gestation of approximately 25 days; eye-opening time in the young may be from 14–19 days of age. *Gerbillus nanus* shows a gestation of 23 days with eye-opening from 14–15 days of age. *Perognathus* shows gestation periods of 24–25 days with eye-opening times from 14 to 16 days of age.

No profound difference appears to exist in the development of the young as was the case when *Jaculus* was compared with *Dipodomys*.

#### MAINTENANCE ACTIVITIES

Gerbils, jirds, and pocket mice construct extensive tunnel systems for caching food and constructing nests. A given individual may build more than one burrow system, some of the systems being quite simple and used only occasionally. Parturient females apparently construct more extensive burrow systems, as has been reported for *Gerbillus nanus* (KIRCHSHOFER, 1958) and *Perognathus parvus* (SCHEFFER, 1938). Digging in the substrate involves the teeth, forepaws, and hind limbs. Once tunnels have been excavated, the tunnel walls are packed by pushing and patting with the forepaws. *Meriones* differs somewhat from the smaller species of *Gerbillus* and *Perognathus* in that the walls of the tunnels are packed by employing both the forepaws and the nose. The whole body of *Meriones* is jerked back and forth while holding the forepaws rigid on either side of the nose; thus, the nose pad and forepaws strike the soil and serve to tamp it firmly into place. *Gerbillus* and *Perognathus* push and pat with the forepaws as the principal method for reinforcing the tunnel walls. Nests are generally constructed within the tunnel system by assembling dried plant material. The tendency for nest building increases at the time of parturition.

As noted in the previous section, all species of the 3 genera assemble foodstuffs and cache it within the tunnel system. The species of *Meriones* are prone to cut vegetation into small pieces for caching. This tendency to bite vegetable matter, stalks, roots, and pods into small pieces has been termed Häckseln by EIBL-EIBESFELDT (1951). This pattern has been noted by the author in *Meriones unguiculatus*, *M. hurrianae*, and *Tatera indica*.

#### LOCOMOTION AND EXPLORATION

In contrast to the bipedally adapted dipodids and kangaroo rats, pocket mice, gerbils, and jirds do not habitually locomote bipedally. Instead, they perform either the diagonal limb coordination pattern or saltate quadrupedally where the fore and hind limbs alternately strike the ground. Although these species can stand erect bipedally, bracing the body with the tail and occasionally shuffle forward in a bipedal walk, sustained bipedal saltation is not exhibited.

*Gerbillus* and *Perognathus* are typically nocturnal whereas both *Meriones hurrianae* and *M. unguiculatus* show tendencies to be active during the early morning and early evening. Although the species of *Meriones* avoid strong light, they may be said to be semi-diurnal or at least crepuscular in their activity (NAUMAN, 1968). This is in keeping with their apparent convergence toward a ground-squirrel-like ecological niche.

Sandbathing may be shown by all 4 species either at the entrance to the burrow or upon leaving the burrow. As with the jerboas and kangaroo rats, this behavior pattern serves to dress the pelage and, additionally serves to mark the sandbathing spot with odors from glands situated at various points on the body. Marking by dragging the ano-genital area over selected points on the substrate (perineal drag) while depositing urine traces or exudates from glands associated with the anus or genitalia is characteristic for these rodent species. *Meriones*, however, has a very specialized marking movement involving extending and flexing while depressing the ventrum to the substrate. This serves to bring the large gland located on the ventrum of this genus into contact with specific points in the environment. This ventral rubbing is performed as a distinct movement from sandbathing, which in *Meriones* consists almost solely of side-rubbing. The functional aspects of this behavior will be discussed in the section on communication.

#### CARE OF THE BODY SURFACE

Auto-grooming (washing) is performed in the typical Myomorph pattern (BÜRGER, 1959). The smaller heads of gerbils and pocket mice permit simultaneous wiping of the face with the forepaws without the necessity of turning the head to one side and wiping alternately as is the case in the jerboas and kangaroo rats. Aside from this difference, the temporal patterning of the activity is remarkably uniform (EISENBERG, 1963a, 1967).

Sandbathing by *Perognathus* differs somewhat from the pattern shown by the gerbils. All species of *Perognathus* combine ventral rubs with side rubs into an integrated sandbathing movement which apparently serves both to mark the substrate as well as to dress the pelage (EISENBERG, 1963b). *Meriones unguiculatus* and *Gerbillus nanus* also perform sandbathing which consists almost entirely of extending and flexing while lying on the side. The ventral rubbing component is rarely expressed as such by *Gerbillus nanus*, but is expressed as an independent marking movement by *Meriones unguiculatus* and *M. hurrianae*. Sandbathing is generally shown at specific loci on consecutive days; thus implying that sandbathing has the potential for chemical communication in addition to marking behavior. Further discussion of differences in the form of sandbathing behavior are included in the publications by EISENBERG (1963b, 1967).

#### ANTI-PREDATOR BEHAVIORS

Gerbils and pocket mice are relatively small, nocturnal rodents which appear to escape predators by relying on speed and inconspicuousness (Fig. 7). No special anti-predator behaviors have been noted for *Gerbillus* and *Perognathus*. Species of *Meriones* are larger and, to an extent, semi-



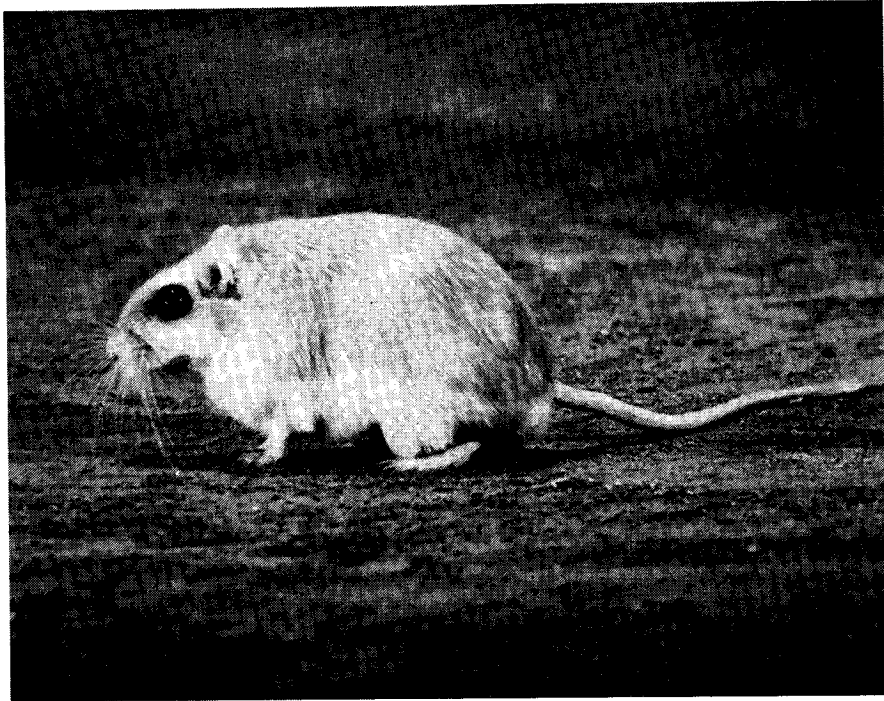


Fig. 7. *Gerbillus gerbillus*. In size, coat color and texture, this species resembles *Perognathus penicillatus* of North America.

diurnal. Foraging during daylight hours certainly exposes them to certain forms of predation shared in common with ground squirrels. Since some species of *Meriones* are often colonial, one would expect convergences in anti-predator behaviors similar to those shown by ground squirrels. The habit of sitting at the burrow entrance in an upright posture and scanning the terrain has been remarked on as convergent toward ground squirrel habits (see ALLEN, 1940, for remarks on *Meriones unguiculatus*).

#### COMMUNICATION MECHANISMS

The introductory remarks for the discussion of kangaroo rats and jerboas are applicable to these species as well. Chemical and tactile modes of communication are often combined and visual communication mechanisms seem to be of reduced importance (see also EISENBERG, 1963a, 1967).

Auditory communication involves the same 3 classes of sounds discussed previously for the jerboas and kangaroo rats. Tooth-chattering is shown by all species and drumming with the hind foot is found in many species included in this study; however, it should be noted that not all

Table 5. Some Vocalization Patterns of *Meriones* and *Tatera*.<sup>1</sup>

Species	Sound	Context(s)	Implied Function	Sample (N)	Structure of Sound	Frequencies with Greatest Energy (Hz)	Duration of Pulse (sec.)
<i>Meriones hurrianae</i>	1. Squeal	When defensive	Inhibits attack	3	Harmonic	1700-4600	.53
	2. Cry of abandoned young (Day 3)	When cold	Attracts mother	4	Harmonic repetitive	2000-3000	.15-.20
<i>M. hurrianae</i>	3. Comfort peeping (Day 9)	When female grooms young	?	5	Harmonic repetitive	2250; 5000	.10-.18
<i>Tatera indica</i>	4. Comfort peeping (Day 9)	When female grooms young	?	5	Harmonic repetitive	4000-6000	.08-.11

<sup>1</sup> All recordings analyzed to 20 KHz only.

? = Function incompletely understood.

species of *Perognathus* drum with the hind foot (EISENBERG, 1963a). Drumming with the hind foot in *Meriones* appears to occur when the animals have been startled and also is shown by the male during bouts of sexual activity (KUEHN & ZUCKER, 1968).

Vocalizations for gerbils and pocket mice fall into 4 functional classes of sounds: 1) defensive squeal, 2) low grunts, 3) cry of the abandoned young, and 4) a comfort sound produced by the young when the female grooms them. As was noted for the kangaroo rat, the optimum auditory sensitivity for *Meriones* seems to correspond to the frequencies carrying the greatest energy in the calls of *Meriones* (see FINK & GOEHL, 1968; FINK & SOFOUGLU, 1966) (See Table 5).

Varying degrees of tympanic bulla expansion can be noted in the species of *Gerbillus*, *Meriones*, and *Perognathus*. The significance of bulla expansion in *Meriones* has been discussed by LEGOUIX, PETTER & WISNER (1954). It would appear that the bullar expansion aids in maintaining the sensitivity of the ossicles for low amplitude sounds at the resonant frequencies of the ossicles themselves.

Olfactory communication has been investigated to a limited extent for these species. As noted previously, the genus *Meriones* is characterized by a large gland field on the ventrum, first noted by LATASTE. Ventral marking by the Mongolian gerbil is displayed most strongly by the male and maintenance of the glandular tissue is under the control of testosterone. Castration of males reduces the propensity to mark and the gland atrophies (THIESSEN *et al.*, 1968). The function of such marking behavior by *Meriones* has been investigated by BARAN & GLICKMAN (1970). It was concluded that presence of marked objects in the environment, even when marked by aliens, increases the propensity to mark by an individual placed in an alien environment. It was further suggested that the glandular secretions are not necessarily employed in territorial defense but rather have some other function in communicating and advertizing the presence of an individual.

Sandbathing appears to be a form of indirect communication for *Gerbillus nanus*, *Perognathus parvus*, and *P. californicus* (EISENBERG, 1967). Considerable overlap is shown in the use of the same sandbathing spot by different individuals which provides the possibility for indirect communication or exchange of chemical information without the animals coming into physical contact.

#### AGONISTIC BEHAVIOR

Quadrupedal genera, such as *Meriones*, *Gerbillus*, and *Perognathus*, may adopt bipedal upright postures as part of their threat behavior (EISENBERG, 1963a). Two animals in a bipedal upright can then spar and ward with the forepaws, however, it should be noted that such quadrupedal genera are more prone to show locked fighting behavior than are bipedal

species such as kangaroo rats and jerboas which fight extensively on their hind legs and seldom roll and tumble together during fighting bouts. Furthermore, both kangaroo rats and jerboas fight by leaping into the air and kicking down at the partner, a maneuver which is seldom executed by the quadrupedal genera.

The propensity to exhibit agonistic behavior is highly variable when species are compared. *Meriones unguiculatus* appears to be extremely tolerant and semi-communal. *M. hurrianae* shows a high male-female tolerance but a lowered threshold for the exhibition of agonistic behavior toward strange conspecifics. *Gerbillus gerbillus* is similar to *M. hurrianae*, whereas *Gerbillus nanus* is highly antagonistic toward conspecifics of either sex, and pair tolerance is low. Contact between a male and female is generally shown only when the female is in estrus (KIRCHSHOFER, 1958; EISENBERG, 1967). Most species of the genus *Perognathus* are similar to *Gerbillus nanus* in being non-contact animals. In general, adults tend to nest alone in burrows and, although they share foraging areas in common, are disinclined for contact except during the female's estrous period (EISENBERG, 1963a).

#### COURTSHIP AND MATING

Mating behavior involves a preliminary period of mutual investigation which may often grade into agonistic behavior (EISENBERG, 1967). If the female is in estrus, the male will begin to follow her and attempt to mount. Mounting and thrusting occur in bouts, often including repeated bouts of mounting with intromission preceding a final mount with an ejaculation. *Gerbillus nanus*, *Perognathus californicus*, and *P. parvus* show a rather similar temporal patterning of mounting leading to a mount with an ejaculation. Although *Meriones unguiculatus* exhibits, in common with *Perognathus* and *Gerbillus*, a multiple mount series prior to ejaculation, the number of mounts with intromission necessary before ejaculation is 3 to 4 times as great (KUEHN & ZUCKER, 1968; EISENBERG, 1967).

#### PARENTAL CARE BEHAVIOR

The basic patterns of maternal care for these rodent species are similar to those described for kangaroo rats and jerboas. The maternal retrieving response is highly developed in all of these species in contradistinction to *Jaculus*.

#### GENERAL SUMMARY

*Gerbillus nanus* resembles the silky pocket mice of the genus *Perognathus* in many respects. It shows strong convergences in morphology, reproduction, water metabolism, and behavior. Their social behavior also

shows similarities since they are sensitive to crowding and the male-female relationship is marked by intolerance except when the female is in estrus. This suggests that a very strong convergence at all behavioral levels exists between the silky pocket mice and *Gerbillus nanus*. It further implies that such similarities in behavior, ecology, and reproduction delineate a special adaptation syndrome exhibited by these 2 forms as they have evolved independently to occupy a similar desert niche.

### *Spacing and Communication*

Before considering the use of space by mammals, it is necessary to clarify the use of several terms. Home range applies to the area traversed by an animal in the normal course of its maintenance activities. Territory refers to either all or part of the home range which is habitually defended by the owner against intruding conspecifics (BURT, 1943). In extremely arid areas the carrying capacity of the environment is vastly reduced; thus, some rodent species may exist at exceedingly low densities (PETTER, 1961). Evidence indicates that spacing mechanisms are operative. Such spacing mechanisms theoretically insure an adequate utilization of the habitat and reduction of competition at the intraspecific level. The possibility that interspecific competition can be important at certain seasons of the year must not be overlooked. Research by MACMILLEN (1964) indicates that interspecific spacing may become critical during the period of minimum rainfall in the south coastal, arid zone of California. In his study, the desert wood rat (*Neotoma lepida*) actively defended prickly pear (*Opuntia*) patches in which it nests. Intrusions by conspecifics and other members of the rodent community are reduced by the defensive behavior shown by the wood rat. The prickly pear is an important reservoir of water for the wood rat and is actively competed for by other rodent species which require succulents for survival.

Most studies of desert rodent populations show the existence of a broad overlap among home ranges when the ranges of males are compared with those of females or other males. The home range of an individual female appears to overlap to a much lesser extent with the range of an adjacent female, especially when the females in question are pregnant. Hence, some form of spacing behavior among females is certainly in effect. REYNOLDS (1960), employing a live-trapping technique, discovered that *Dipodomys merriami* females occupy smaller home ranges than the males and that the female's home range was during the breeding season free from the activities of other females. Although the home ranges of male kangaroo rats overlapped, the center of a male's range seemed to be somewhat isolated. DIXON (1959) studied *Perognathus nelsoni*, employing a trapping, marking, and release method. By setting traps in a permanent grid, he was able to elucidate the spacial distribution of individual animals. He noted that, although the males had larger home ranges than

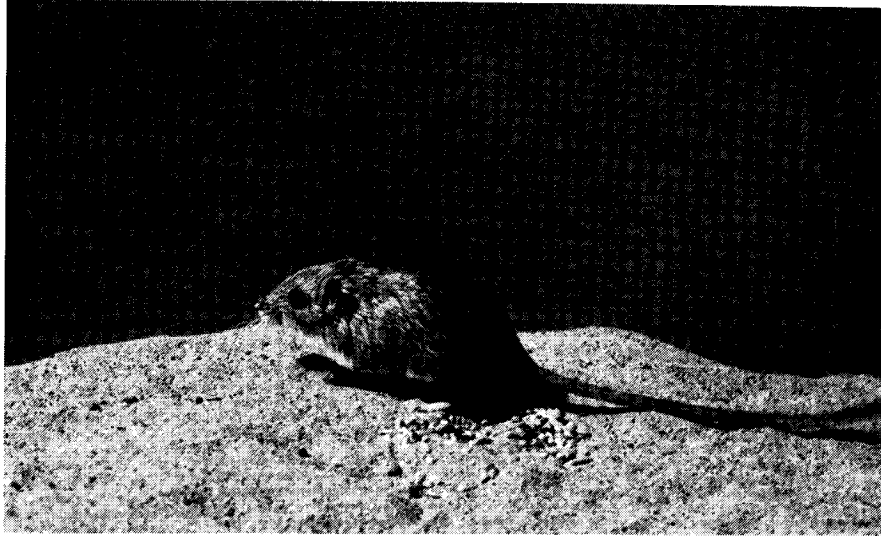
the females and the males' home ranges overlapped, there was almost no overlap among the home ranges of individual females. A detailed trap, mark, and release study by IVERSON (1967) indicated that the burrow system of *Perognathus parvus* appeared to be randomly distributed. The home ranges of males were larger than those of females but broad overlap was shown among home ranges of both males and females, although pregnant females appeared to have less overlapping ranges. IVERSON concluded that each adult animal had a permanent burrow system which was occupied singly and defended. The literature for the heteromyid rodents has been reviewed by IVERSON (1967) and EISENBERG (1963a). By and large, it would appear that *Perognathus* and *Dipodomys* are intolerant of conspecifics in the same burrow system. True territorial defense, then, seems to be restricted to a limited area in the vicinity of and including the burrow but foraging areas are shared. Overlap in home ranges thus makes it possible for animals to communicate with one another at specific points but at the same time defense is shown with respect to the burrow system thus insuring that seed caches are utilized by the owner of the cache itself.

Although active burrow defense and defense of a limited area around the burrow appears to be characteristic of most genera of the family Heteromyidae, many desert rodents appear to occupy burrow systems in the form of mother families. Thus an extended family group can be built up prior to the dispersal of the newly recruited young. Communal burrow occupancy by several families, however, appears to be rare. Pair tolerance within the same burrow system is moderately high in *Allactaga elater* and *Jaculus orientalis* of Asia, as well as *Gerbillus gerbillus* of North Africa, and *Notomys mitchelli* of Australia. Nevertheless, even if pair tolerance is shown, as in the preceding species, some form of communication mechanisms promoting spacing or promoting the exchange of information among members foraging over a common area is necessary. It would appear that chemical communication and auditory communication have become rather important in most desert rodents.

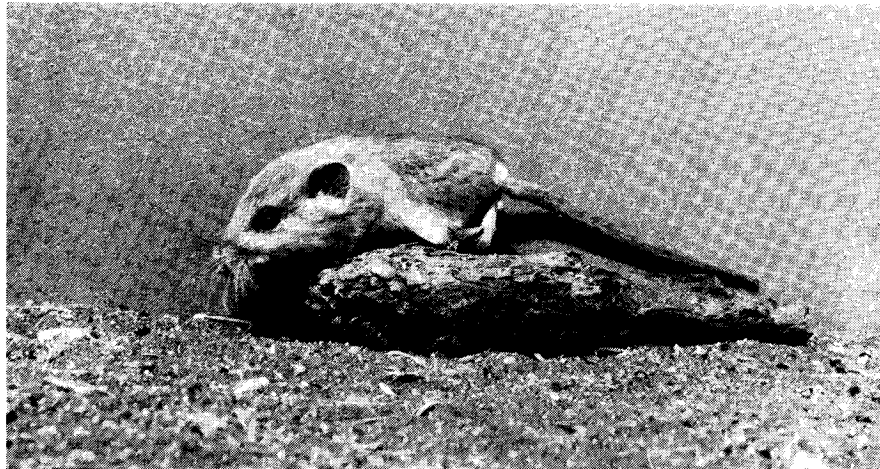
When species of rodents either exist at rather low densities or maintain some form of exclusive use with respect to burrow systems, some form of distance communication becomes mandatory. Visual communication or tactile communication, so useful at close range, may be supplemented by forms of long-range communication. This may involve the deposition of scents which persist for a period of time and thus may be encountered and scented by a wandering conspecific. The production of sounds which have a reasonable range also allows perception by a conspecific at a considerable distance. Let us reconsider these two points. Chemical communication by depositing glandular substances, urine, or feces at specific points in the environment is widely employed by desert rodents as a form of communication (EISENBERG, 1963a, 1967). It has already been pointed out that sandbathing as a mode of dressing the pelage is

also a means of marking and that discrete sandbathing loci may be used repeatedly by the same individual and shared in common by neighbors (EISENBERG, 1963b). Auditory communication has been little studied in desert rodents but the presence of the inflated mastoid bulla coupled with an extreme sensitivity to low amplitude sounds suggests that such a mechanism may function in the perception of intraspecific signals as well as in the perception of predators. The audible calling produced by the grasshopper mouse, *Onychomys* (HILDEBRAND, 1961), may serve both as a spacing mechanism and as a means of indicating the location of a given individual. This desert mouse tends to live in a dispersed pattern of social organization and, although a series of burrows may be discretely localized in a specific area, such as a small arroyo, 2 adult individuals are seldom trapped at a given burrow site. It would seem that the evening cries of the grasshopper mouse might well be functional in indicating position of such spaced individuals. A similar function has been proposed for the low intensity squeal of the kangaroo rat, *Dipodomys spectabilis* (GIBBS, 1955), and it has been suggested that cries produced by *Jaculus* are employed in intraspecific communication over distance (PETTER, 1961).

Species such as *Perognathus parvus*, which typically exhibit solitary occupancy of a burrow system as adults, very often exhibit marked aggressive behavior when placed together in the artificial confinement of a small cage. Adults of such species will generally fight, often wounding each other severely. Aggressive behavior may be high between a male and a female when the female is not in estrus. Compatible groups may be formed through captive breeding, if littermates are allowed to remain together; however, if littermates of *Perognathus parvus* are separated at approximately 2 months of age for several days and then allowed to re-encounter, they will generally behave aggressively toward one another (EISENBERG, 1967). Such low tolerances for extended proximity in captivity are generally shown by rodents which typically exhibit individual burrow defense as adults in the wild. The testing of social tolerance in captivity will often correlate with distribution patterns exhibited in the field (EISENBERG, 1967). For example, the arid-adapted subfamily Gerbillinae, based on captive studies, would appear to show a range of social types. *Gerbillus nanus* is relatively solitary whereas *Tatera indica* may exhibit a communal structure based on an extended family group. Within the family Dipodidae, *Jaculus orientalis* and *Allactaga elater* show a pair tolerance, however, the female may exhibit a tendency to nest alone at the time of parturition. The desert-adapted family Heteromyidae appears to exhibit an enduring trend toward pair intolerance and individual defense of their burrow systems. By contrast the desert-adapted species of the North American, cricetine genus *Peromyscus* show a range in their social tendencies. *Peromyscus crinitus* is intolerant, whereas the equally xeric-adapted *P. eremicus* exhibits a high pair tolerance (EISENBERG, 1968).



*Fig. 8. Perognathus formosus.* This species of pocket mouse is adapted to pebble deserts and is often found on soils of low reflectance. In size and habits it resembles several smaller species of the Old World murid genus *Gerbillus*.



*Fig. 9. Microdipodops pallidus.* This species is the smallest bipedally saltating heteromyid. The relatively large head reflects the enlarged tympanic bullae. In external morphology *Microdipodops* strongly resembles the Asiatic dipodid, *Salpingotus*. The gerbilline genus *Pachyuromys* shows a similar bullar expansion and in common with *Microdipodops* accumulates fat reservoirs in its tail.



The ultimate conclusion, then, is that adaptation to desert habitats with dispersed food supplies is not necessarily in and of itself conducive to selection for a solitary existence as an adult. Equally important selective forces include other aspects of the species' ecology including its mode of assembly of foodstuffs, its shelter construction, its mode of reproductive behavior, and parental care. Although food caching within the burrow system or in its vicinity is strongly correlated with burrow defense and a solitary way of life within the Heteromyidae, it is not the case that individual burrow defense is always a concomitant of caching. It would appear that the Heteromyidae have retained a phylogenetically ancient trait because of some fundamental adaptive advantage accruing from its individual defense of cached food (EISENBERG, 1963a). Nevertheless, those species of desert rodents which do show individual patterns of burrow defense (such as *Perognathus* and *Dipodomys*) also show forms of chemical and auditory communication which tie the members of a given 'community' into an information exchange system (LEYHAUSEN, 1965). The study of such communication systems offers much promise for the future.

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