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Biology of Desert Rodents

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GREAT BASIN NATURALIST MEMOIRS

Biology of Desert Rodents

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INTRODUCTION

O. J. Reichman[1] and James H. Brown[2]

Studies of desert rodents, especially the heteromyid species of southwestern North America, have a long and illustrious history. These investigations have not only revealed many fascinating aspects of the biology of the rodents themselves, but they have also contributed importantly to our general understanding of such diverse disciplines as functional anatomy, comparative and environmental physiology, population and community ecology, and systematics and evolutionary biology. The great early biologists C. Hart Merriam, Joseph Grinnell, and Lee R. Dice were profoundly influenced by their field experiences with small mammals in the southwestern United States. Subsequently, many leading figures of American mammalogy have contributed to the knowledge of desert rodents. The works of these, and many other scientists, are cited in the papers of this symposium.

Until the last 25 years, most of this work was primarily descriptive and was largely performed by mammalogists interested in taxonomy, classification, and geographic distribution. Important systematic and biogeographic work has continued, and by the late 1950s sufficient basic information was available to allow investigators to delve into the challenging relationships between form, function, distribution, and evolutionary history. The pioneering studies of Schmidt-Nielsen and Bartholomew and his students on physiological adaptations, by Eisenberg on comparative behavior, and by the Websters on functional morphology of the ear have been followed by investigations in such diverse disciplines as cytogenics, community ecology, and sociobiology.

The majority of research on desert rodents has focused on representatives of the Heteromyidae that inhabit arid regions of southwestern North America. Although this symposium has concentrated on heteromyids, it is obvious that vast areas of the globe are covered by deserts and inhabited by other rodents as significant biologically as heteromyids. A glimpse of these is obtained in the paper by Mike Mares, but much more is missing—either because these proceedings were limited in time and publication space, or because so many other desert rodents are poorly known. Even within the North American deserts there are other important groups of rodents (e.g., cricetids and ground squirrels), but we have chosen to concentrate on the heteromyids because of their specialized adaptations to desert environments. Perhaps more is known about the comparative anatomy, physiology, behavior, ecology, and evolution of these rodents than is known about any comparable group of related organisms, with the possible exceptions of Hawaiian *Drosophila*, Galapagos finches, and West Indian *Anolis*. In a very important sense, heteromyids provide an empirical model of the

[1]Division of Biology, Kansas State University, Manhattan, Kansas 66506.
[2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721

patterns and processes involved in the adaptive radiation of a monophyletic group to exploit diverse ecological opportunities within a limited geographic range. This system is being used as a model to answer general questions and to test theoretical predictions about relationships between form and function, the adaptive nature of evolutionary change, and the organization of ecological communities.

In organizing the symposium and arranging for its publication we had two major goals: (1) to present in one place a review and synthesis of much of what has been learned about diverse aspects of desert rodent biology, and (2) to stimulate continued and additional research by calling attention to both unanswered questions and recent advances. If the published versions of the papers generate as much interest, enthusiasm, and critical discussion as did the original symposium, our goals and expectations will have been exceeded.

Condensed versions of these papers were presented at the 62nd Annual Meeting of the American Society of Mammalogists at Snowbird, Utah, on 22 June 1982. We thank J. Mary Taylor, H. Duane Smith, the American Society of Mammalogists Program Committee and Local Committee, the speakers, and an exceptionally attentive and interactive audience for the success of the symposium.

EVOLUTIONARY RELATIONSHIPS OF HETEROMYID RODENTS[1]

John C. Hafner[2] and Mark S. Hafner[3]

ABSTRACT.— The rodent superfamily Geomyoidea is an old, undoubtedly monophyletic lineage having only obscure affinities with other rodent groups. Geomyoid rodents, autochthonous in North America, experienced major evolutionary diversification in the Mio-Pliocene coincident with the development of the Madro-Tertiary Geoflora and the climatic trend toward increasing aridity and coolness. Extant geomyoids are divisible into two groups: (1) the Geomyidae, all members of which are fossorial, and (2) the Heteromyidae, whose members display an adaptive continuum from bipedal, xeric-adapted forms to scansorial, mesic-adapted forms. These moieties, although recognizable on biochemical criteria, become particularly difficult to distinguish when paleontological data are considered. Nevertheless, most lines of evidence indicate that the families Heteromyidae and Geomyidae are distinct, monophyletic lineages.

The extant heteromyids comprise three main lineages (including six genera) that diverged during the Eocene: (1) subfamily Perognathinae (*Chaetodipus* and *Perognathus*); (2) subfamily Dipodomyinae (*Dipodomys* and *Microdipodops*); and (3) subfamily Heteromyinae (*Liomys* and *Heteromys*). Protein differentiation has occurred at heterogeneous rates among these major lineages. Based on available karyotypic data, the main direction of chromosomal evolution in the Heteromyidae appears to be toward increasing chromosome number. Cladistic analysis of morphological characters used in previous studies supports biochemical evidence allying *Microdipodops* with *Dipodomys*. A model is introduced to describe how heterochronic changes in ontogeny may explain the great breadth of morphological diversification within the superfamily. Taxonomic recommendations at the subfamilial, generic, and subgeneric levels are provided.

> The most important point to be emphasized is that "Parallelism, parallelism, more parallelism and still more parallelism" is the evolutionary motto of the rodents in general and of the heteromyids in particular. This extends to all parts of the body. It makes the task of determining interrelationships particularly difficult, and renders exceptionally dangerous any postulates as to what the relationships of a given form may really be, if full evidence does not exist to clear the maze of parallel adaptations for us. This shows the insuperable difficulties awaiting anyone who attempts a classification based on a single character or on a group of characters with a common cause.
>
> Albert Elmer Wood (1935:250)

A trio of monographs on the evolutionary biology of heteromyid rodents appeared in the early 1930s and, subsequently, has hallmarked this specialized area of scientific inquiry. Hatt (1932) and Howell (1932) provided definitive accounts of the morphology of the ricochetal forms, and Wood (1935) synthesized the then available data, gleaned from fossil and recent forms, into a coherent summarization. Interestingly, the last comprehensive statement of the evolutionary relationships within the Heteromyidae was Wood's exhaustive treatment, now aged one-half century. However, during the past 50 years a tremendous volume of literature pertaining to heteromyid evolution has accumulated, justly reflecting the immense interest in these mammals. Some of the questions posed by Wood and the others have been answered to satisfaction, whereas the answers to other queries still elude us and await extrication by future research.

It is the intent of this contribution to present a compendium of the evolution of heteromyid rodents, wherein we attempt to integrate the classic morphological studies of the 1930s with the more recent systematic treatments. As a definitive statement on heteromyid relationships, this effort may appear inchoate in a few years. However, the assimilation of earlier ideas with those of the present, coupled with due introspection, is necessary in any field of science. The study of heteromyid evolution is no exception and

[1]From the symposium "Biology of Desert Rodents," presented at the annual meeting of the American Society of Mammalogists, hosted by Brigham Young University, 20–24 June 1982, at Snowbird, Utah.

[2]Moore Laboratory of Zoology and Department of Biology, Occidental College, Los Angeles, California 90041.

[3]Museum of Zoology and Department of Zoology and Physiology, Louisiana State University, Baton Rouge, Louisiana 70893-3216.

through this reflection of the present to the past we hope to gain a profitable avenue for further investigations.

The evolution of the Heteromyidae (kangaroo rats, pocket mice, and their allies) is closely associated with that of the Geomyidae (pocket gophers) and, consequently, their taxonomic histories are necessarily intertwined. Together these two families form an internally cohesive superfamily (the Geomyoidea) whose members are united by the presence of externally opening, fur-lined cheek pouches (among other features). Geomyoid rodents underwent major phyletic radiation from the Oligocene to Pliocene of North America, in step with the global trend toward a cooler and drier climate (Flint 1971) and the diversification and migration of geofloras (Axelrod 1950, 1958, 1976). Historic biogeographic considerations have been presented elsewhere (e.g., Wood 1935, Reeder 1956, Genoways 1973, Hafner, J. C., 1981a) and will not be repeated here; for general reviews see Stebbins (1981; coevolution of grasses and herbivores), and Cole and Armentrout (1979; Neogene paleogeography). It is interesting to note, however, that heteromyids and geomyids represent two of the three families of living mammals autochthonous in continental North America (the third being Antilocapridae). As a consequence of the similarities in heteromyid and geomyid biogeographic histories and their intimate phyletic relationships, we have found it illuminating to include relevant geomyid information in this review of the Heteromyidae. Indeed, in order to appreciate fully the history of evolutionary diversification within the Heteromyidae, it is necessary first to view this family within the broader framework of the superfamily Geomyoidea.

REVIEW OF GEOMYOID SYSTEMATICS

The taxonomic history of the Geomyoidea began with the description of the "tucan" or "Indian mole" (probably a pocket gopher, *Thomomys*) by Fernandez in 1651. According to Merriam (1895:201), both Fernandez and, later, Kerr (1792, not seen) believed the tucan to be a large, aberrant species of mole (*Sorex mexicanus* Kerr 1792). *Systema Naturae* (Linnaeus 1758) did not mention geomyoids, and it was not until 1848 that Waterhouse recognized the Saccomyina (= modern Geomyoidea) as a distinct group of New World rodents (Waterhouse 1848). In 1872, Gill recognized two closely related families within Waterhouse's Saccomyina, the Geomyidae (= modern Geomyidae) and the Saccomyidae (= modern Heteromyidae). Gill (1872) united these families under the superfamilial nomen, Saccomyoidea. Weber (1904), recognizing that *Saccomys* Cuvier 1823 was a junior synonym of *Heteromys* Desmarest 1817 (see Gray, 1868 for details), first used the superfamily name Geomyoidea.

The phyletic position of the Geomyoidea within the order Rodentia has long been a matter of debate. Coues (1877) considered the geomyoids to be "myomorphs" (*sensu* Brandt, 1855). However, Miller and Gidley (1918) and many recent workers place the geomyoids near, or within, the "sciuromorphs" (e.g., Simpson, 1931, 1945). Most recently, Wood (1965:128) suggested that the muroid and geomyoid rodents may have shared a common ancestor within the primitive, protrogomorphous rodent family Sciuravidae, and he thus placed the Geomyoidea within the suborder Myomorpha (see also Wood 1955, Wahlert 1978).

Rodents of the family Eomyidae represent a third, wholly extinct group of geomyoid rodents present from late Eocene to Plio-Pleistocene in Europe and North America. According to Wilson (1949a, 1949b), who first placed the eomyids within the Geomyoidea, the eomyid skull shows many similarities to both primitive heteromyids and cricetids. Wood (1955) concurs with Wilson in recognizing the Eomyidae as a primitive geomyoid group, perhaps ancestral to the Heteromyidae. However, none of the known eomyid forms appears to be directly ancestral to living geomyids or heteromyids (Wahlert 1978).

The phyletic propinquity of geomyids and heteromyids, and the fact that both groups evolved under similar environmental conditions in western North America, may account for the remarkable level of evolutionary parallelism in the two groups as evidenced in the fossil record. Due, in large part, to the confounding effects of parallelism, the taxonomy of extant geomyids has vacillated between a

single family classification (either the Saccomyidae, Geomyidae, or Heteromyidae; Baird 1858, Carus 1868, Gray 1868, Alston 1876, Shotwell 1967, Lindsay 1972) or a classification composed of two families equivalent to the modern Geomyidae and Heteromyidae (Gill 1872, Coues 1877, Merriam 1895, Wood 1931, 1935, Rensberger 1971, 1973). Recently, M. S. Hafner (1982) used biochemical evidence to demonstrate that the extant genera commonly placed in the separate families do indeed represent inclusive, monophyletic lineages, thus supporting the traditional two-family classification.

Pocket Gophers: Family Geomyidae

For almost a century, Merriam's (1895) monograph on the Geomyidae has stood as the definitive statement on systematic relationships among extant members of the family. Merriam's work has been modified to varying degrees by Hooper (1946), Russell (1968), M. S. Hafner (1982), and Honeycutt and Williams (1982). Living geomyids are represented by five genera (six according to Honeycutt and Williams 1982), and 33 nominal species, all of which are fossorial herbivores.

Within early geomyids (= Geomyinae of Shotwell 1967, and Lindsay 1972), there was a Miocene radiation in western North America of forms that ranged from semi-ricochetal to fossorial in habitus as inferred from both cranial and postcranial structure (Rensberger 1971, Munthe 1975). These forms are assigned to the geomyid subfamilies Entoptychinae and Pleurolicinae, which appear to have been early, independent geomyid side-branches not directly ancestral to later geomyids.

Following the radiation and eventual extinction of the Miocene entoptychines and pleurolicines, there was a Pliocene radiation of geomyine pocket gophers in western North America. Most workers agree that all subsequent geomyids had their roots in this Pliocene radiation. Details are very scarce; however Shotwell (1967) and Lindsay (1972) tentatively derive all living pocket gophers directly from the Mio-Pliocene form *Parapliosaccomys*. The geological time ranges of the genera *Thomomys*, *Geomys*, *Zygogeomys*, and *Pappogeomys* extend from the early Blancan (late Pliocene) to the Recent of both the Great Plains and southwestern United States. *Orthogeomys* (subgenus *Heterogeomys*) is known from the Rancholabrean (late Pleistocene) of Nuevo Leon, Mexico. *Orthogeomys* (subgenera *Orthogeomys* and *Macrogeomys*) are known only from Recent material (Russell 1968).

Kangaroo Rats, Pocket Mice and Their Allies: Family Heteromyidae

The heteromyid rodents constitute a morphologically and ecologically diverse assemblage of geomyids whose fossil history dates back to middle Oligocene of western North America (see review by Wood 1935). Wood arranged the heteromyids into three subfamilies (Perognathinae, Dipodomyinae, and Heteromyinae) and later recognized a fourth subfamily, the Florentiamyinae, based on the early Miocene genus *Florentiamys* (Wood 1936). More recent, suprageneric systematic treatments of fossil heteromyids include the works of Reeder (1956) and Lindsay (1972).

Living heteromyids are traditionally subdivided into five genera and approximately 66 species. In this paper, we will recommend that a sixth genus, *Chaetodipus*, be recognized. Analyses of suprageneric relationships among extant heteromyids include Kelly's (1969) study of bacular and penile variation, Homan and Genoway's (1978) study of hair structure, and M. S. Hafner's (1982) biochemical analysis of intrafamilial relationships. Results of each of these studies, and others, will be incorporated into the following accounts.

KANGAROO RATS: GENUS *Dipodomys*.—The 24 species of kangaroo rats currently recognized are spread throughout much of western North America from south central Canada to central Mexico. Fossil material referable to *Dipodomys* is known from the Barstovian (late Miocene) to the Recent of western North America. The most recent diagnosis of fossil kangaroo rats is provided by Zakrzewski (1981; see included references).

The phyletic position of *Dipodomys* within the Heteromyidae is an area of controversy that will be addressed in the present study. Morphologically, kangaroo rats are truly bizarre, and they show no obvious affinity to

any other heteromyid genus. Although kangaroo rats show a gross overall resemblance to kangaroo mice (*Microdipodops*), Wood (1935) and J. C. Hafner (1978) attributed shared features such as inflated auditory bullae and elongated hind feet to evolutionary convergence. In contrast, Reeder (1956) interpreted the fossil evidence to suggest a true phyletic link between *Dipodomys* and *Microdipodops*, the same conclusion reached by M. S. Hafner (1982) using biochemical evidence. It is hoped that our reanalysis of Wood's (1935) data, as well as new information presented herein, will clarify this issue.

Relative to other heteromyids, kangaroo rats have received considerable attention from systematic biologists. Studies of interspecific relationships based on morphology include the works of Grinnell (1921, 1922), Wood (1935), Burt (1936), Setzer (1949), Lidicker (1960), Kelly (1969), Best and Schnell (1974), and Schnell et al. (1978). Phylogenies resulting from these analyses are far from concordant (see Schnell et al. 1978). Studies of interspecific relationships in *Dipodomys* based on karyology (Stock 1974) and protein electrophoresis (Johnson and Selander 1971) present still different pictures of kangaroo rat relationships. It is not within the scope of this study to reevaluate *Dipodomys* species relationships; we only wish to call attention to the need for a thorough, comprehensive analysis utilizing a broad spectrum of approaches. In view of the complexity of the situation, we suggest that chromosomal banding studies, DNA hybridization, and protein sequencing analyses may provide new insights to this old problem.

SPINY POCKET MICE: GENUS *Heteromys*.—Spiny pocket mice of the genus *Heteromys* are, by far, the least studied of all heteromyids. To date, the genus has no fossil record. According to Hall (1981), *Heteromys* is represented by 10 Recent species ranging from southern Mexico to northwestern South America. Until very recently, Goldman's (1911) revision of *Heteromys* stood as the most recent taxonomic work focusing on interspecific relationships in the genus. Rogers and Schmidly (1982) have reevaluated interspecific relationships in Hall's (1981) *H. desmarestianus* group (exclusive of *H. gaumeri*) using external, cranial, and bacular characters and have recognized only two of five species recognized by Hall. Specific results of their analysis will be discussed in a later section of this paper. A comprehensive study of chromosomal and biochemical variation in the genus is now in progress (D. S. Rogers, pers. comm.). *Heteromys* shows close phyletic ties with spiny pocket mice of the genus *Liomys* (Goldman 1911, Wood 1935, M. S. Hafner 1982), and the two genera are placed together in the subfamily Heteromyinae. The relationship of the Heteromyinae to other heteromyid subfamilies remains obscure.

SPINY POCKET MICE: GENUS *Liomys*.—Five extant species of *Liomys* are currently recognized, ranging from northern Mexico to Panama. The fossil record of the genus extends back to late Pliocene of Kansas (Hibbard 1941). Goldman's (1911) revision of *Liomys* has been substantially updated by Genoways (1973), who subducted 6 of 11 species recognized prior to his analysis. As discussed previously, *Liomys* shows its closest phyletic affinity to *Heteromys*, and the placement of these genera into the subfamily Heteromyinae has never been seriously contested.

KANGAROO MICE: GENUS *Microdipodops*.—There are but two living species of kangaroo mice (*M. megacephalus* and *M. pallidus*), both forms restricted to the arid Great Basin region of western North America. Fragmentary fossil material (referred to *M. megacephalus*) is known from late Pleistocene of Nevada (Miller 1979). The genus was described by Merriam (1891) and subsequently revised by Hall (1941) and J. C. Hafner (1981a). D. J. Hafner et al. (1979) affirmed the specific status of the two living forms using morphological, chromosomal, and biochemical evidence.

The genus *Microdipodops* is certainly the most problematic heteromyid in terms of our understanding of its phylogenetic affinities within the family. Wood (1935:107–117) discussed at length the morphology of *Microdipodops* relative to *Dipodomys* and *Perognathus* (subgenus *Perognathus*). Although he pointed out a close morphological resemblance between *Microdipodops* and *Perognathus* (see also J. C. Hafner 1976, 1978), Wood remained equivocal as to its phyletic placement (see Wood 1935:78). Both Reeder

(1956) and Lindsay (1972) derived *Microdipodops* and *Dipodomys* from the Mio-Pliocene form *Cupidinimus* and, thus, suggest dipodomyine affinities for kangaroo mice. In contrast, J. C. Hafner (1976, 1978) derived *Microdipodops* from perognathine stock while recognizing the possibility that kangaroo mice may represent an independent heteromyid lineage with no close relatives in the extant fauna. M. S. Hafner (1982) assessed the phylogenetic affinities of *Microdipodops* using electrophoretic and immunological evidence and concluded that kangaroo mice are genetically somewhat closer to kangaroo rats than to other living heteromyids. In this study we will reexamine the phyletic position of *Microdipodops* relative to other heteromyids and introduce new evidence relevant to the issue.

POCKET MICE: GENUS *Perognathus*.— The genus *Perognathus*, as defined prior to this study, includes 25 nominal species spanning much of western North America from southern Canada to central Mexico. The genus exhibits an unusually long and complete fossil record extending from Lower Miocene of western North America (Reeder 1956, Lindsay 1972).

In traditional treatments dating from Merriam (1889), *Perognathus* is subdivided into two subgenera, *Perognathus* and *Chaetodipus*. For reasons detailed beyond, we recommend that *Chaetodipus* be elevated to full generic status and, thus, reduce the number of extant *Perognathus* species to a total of nine.

Species groups within the genus *Perognathus* (*sensu lato*) are not clearly delineated using the evidence available at present. Studies of interspecific relationships based on morphology include works by Merriam (1889), Osgood (1900), Wood (1935), and Caire (1976). Systematic treatments based on karyology include studies by Patton (1967a, 1967b) and Williams (1978). Protein variation in the genus (with emphasis on *Chaetodipus*) has been analyzed by Patton et al. (1981). It appears that a complete elucidation of interspecific relationships within *Perognathus* and *Chaetodipus* must await future studies involving finer considerations of chromosomal evolution (banding studies) and molecular change (DNA hybridization; protein sequencing).

COMPARATIVE ANALYSIS OF THE MALE REPRODUCTIVE SYSTEM

A large body of data concerning morphology of the glans penis, baculum, spermatozoa, and accessory glands of the male reproductive system in heteromyids is now available and may be brought to bear on the issue of phyletic relationships within the family. Much of the evidence presented here is previously unpublished; in particular, we wish to call attention to the work of Kelly (1969), which is a particularly thorough analysis of penile and bacular variation in heteromyids. Figure 1 illustrates representative phalli, bacula, and spermatozoa from eight geomyoid taxa. In the interest of brevity, we have omitted detailed descriptions of the various structures in individual species; for this, we refer the reader to the original literature.

Glans Penis

The glans penis has been shown to be a valuable tool in systematic studies of rodents (Hooper 1961, 1962, and included references, Hershkovitz 1966, Lidicker 1968, and others) but the glans penis of heteromyids has received little attention. Noteworthy exceptions include Kelly's (1969) study of penile variation in *Dipodomys*, Genoways' (1973) study of the glans penis in *Heteromys* and *Liomys*, and J. C. Hafner's (1976) analysis of penile variation in *Dipodomys*, *Perognathus*, and *Microdipodops*. Following is a synthesis of the results of these studies, emphasizing salient differences in penile morphology among heteromyids.

Kelly (1969) and Genoways (1973) reported that the glans penes of *Heteromys* and *Liomys* (Fig. 1 C, D) are similar in overall structure and share several characteristics unique among heteromyids. These features (spineless phalli; glans long relative to bacular length; unique urethral lappet morphology) may be viewed as shared-derived characters supporting the union of these genera into the subfamily Heteromyinae. Outgroup comparison with *Thomomys* (Kelly 1969) supports the derived nature of penile characters used to define the Heteromyinae.

Based on outgroup comparison with geomyids, the male phalli of *Dipodomys*, *Micro-*

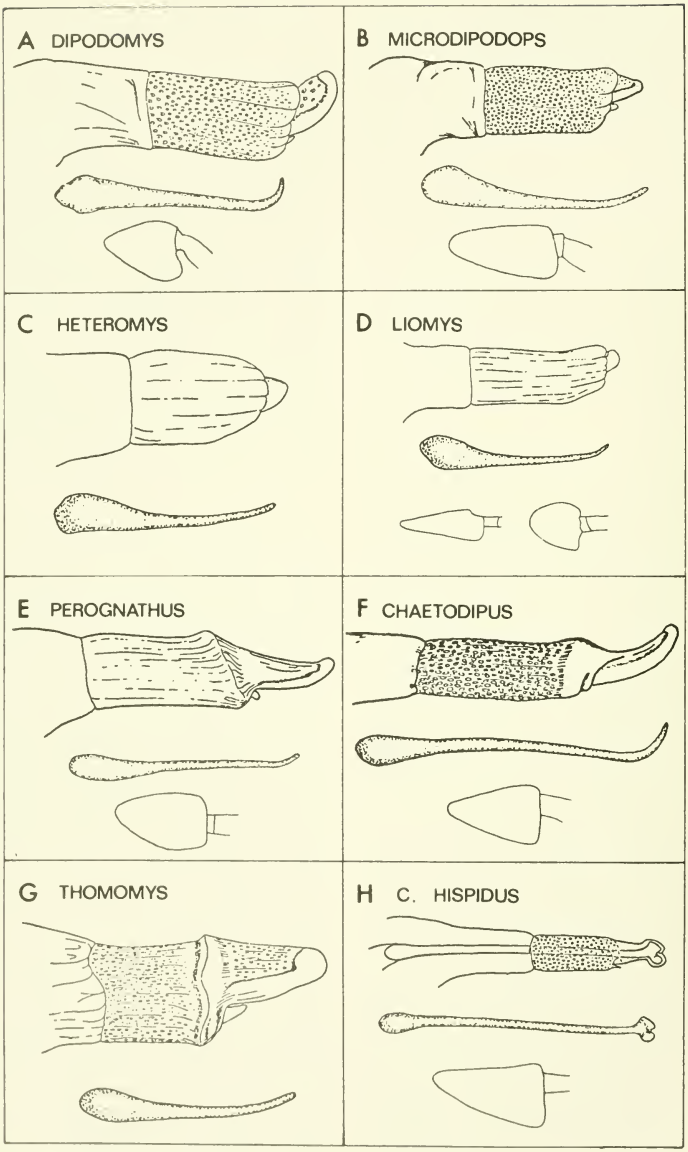

Fig. 1. Representative phalli, bacula, and spermatozoa from seven heteromyid and one geomyid taxa. Phalli and bacula are shown in lateral view. To facilitate comparison, all illustrations are drawn to different scales. Sperm from *Liomys salvini* (right) and *Liomys pictus* (left) are illustrated. Sperm from *Heteromys* and *Thomomys* are as yet undescribed. (Illustrations modified from Kelly, 1969, Genoways, 1973, and J. C. Hafner, 1976).

dipodops, and pocket mice of the subgenus *Perognathus* (Fig. 1 A, B, E) have retained a broad spectrum of primitive geomyoid characters. The phallus of *Thomomys* (Fig. 1 G) most closely resembles that of perognathine pocket mice (Kelly 1969), and in this and other respects (see beyond) members of the subgenus *Perognathus* appear to be extremely conservative morphologically.

The glans penis of *Microdipodops* is similar in most respects to that of *Dipodomys* (Kelly 1969). Importantly, several phallic characters shared between *Microdipodops* and *Dipodomys* (including morphology of urethral lappets and external spines) are unique within the Geomyoidea and, hence, are of phylogenetic signficance. Those features used by J. C. Hafner (1976) to suggest a close relationship between *Microdipodops* and members of the subgenus *Perognathus* (cylindrical, nonelongated phallus; dorsal groove) are now known to be present in the geomyid genus *Thomomys* (Kelly 1969) and are thus regarded as shared-primitive characters. The sharply upturned distal portion of the phallus in *Dipodomys* (Fig. 1 A) clearly distinguishes kangaroo rats from all other heteromyid genera.

The male phallus in pocket mice of the subgenus *Chaetodipus* (Fig. 1 F) is unique among all geomyids examined thus far (Kelly 1969, J. C. Hafner 1976). The chaetodipine penis is long and slender, lacks urethral lappets, and the rim of the terminal crater forms a ventlike urethral opening. The structure of the chaetodipine phallus is, doubtlessly, derived within the Heteromyidae. The terminal portion of the phallus in *Perognathus* (*Chaetodipus*) *hispidus* (Fig. 1 H) is markedly different from that of other chaetodipine species in possessing a distinctly ornate tip.

Os Baculum

Bacular variation in heteromyids has received considerable attention, including studies by Burt (1936, 1960), Schitoskey (1968), Kelly (1969), Genoways (1973), Best and Schnell (1974), and J. C. Hafner (1976). Because of considerable intrageneric variation in bacular morphology, the use of this structure in delineating higher-level heteromyid relationships is very limited.

A combination of three bacular features (bulbous base, stout midregion, sharply upturned distal end) clearly distinguishes *Dipodomys* species from other heteromyids (Fig. 1 A). The bacula of *Microdipodops*, *Heteromys*, *Liomys*, *Thomomys*, *Geomys*, and *Pappogeomys* also have bulbous bases, and this feature appears to be primitive for the Geomyoidea. The bacula of certain pocket mice of the subgenus *Chaetodipus* (Fig. 1 F) have moderately to sharply upturned distal ends (Anderson 1964), a feature which appears to have been derived independently in *Dipodomys* and *Chaetodipus*.

Pocket mice of the subgenus *Chaetodipus* are clearly distinguished from members of the subgenus *Perognathus* using bacular morphology (Burt 1936, J. C. Hafner 1976). The baculum in chaetodipine pocket mice is long relative to body length such that the soft tissue of the penis terminates approximately midway along the length of the baculum. In perognathine pocket mice, the baculum is much shorter and soft tissue extends approximately two-thirds of the length of the baculum. The baculum of *Perognathus* (*Chaetodipus*) *hispidus* (Fig. 1 H) possesses an ornate, trifid tip seen nowhere else in the Geomyoidea.

Spermatozoan Morphology

Genoways (1973) presented a rather detailed study of the spermatozoa of *Liomys* and provided a brief statement as to the relative shape of the sperm head in *Perognathus pernix* (*Heteromys* was not examined). J. C. Hafner (1976) analyzed gross sperm morphology in *Dipodomys*, *Microdipodops*, and additional species of *Perognathus*. The head and neck region (minus the acrosomal tip) of representative heteromyid spermatozoa are illustrated in Figure 1.

The spermatozoa of *Microdipodops* (Fig. 1 B) are characteristically large, with especially long heads. The head is roughly triangular in shape, with rounded vertices. The sperm tail is of medium length relative to other heteromyid species. Species of the subgenus *Perognathus* (Fig. 1 E) possess spermatozoa similar in general morphology to those of *Microdipodops*, except that the head is smaller and the tail shorter. These similarities do

not indicate a close phyletic relationship between *Microdipodops* and *Perognathus* (subgenus *Perognathus*), inasmuch as the sperm of certain species of *Liomys* also share these features (Genoways 1973).

The spermatozoa of chaetodipine pocket mice are easily distinguished from those of all other heteromyids (Fig. 1 F, H). Here, the sperm head resembles a somewhat elongated isosceles triangle with acute (unrounded) vertices. The sperm of *Perognathus* (*Chaetodipus*) *hispidus* is peculiar in some respects because the tail is very long and the neck region is not discernible.

In *Dipodomys*, the spermatozoan head approximates an equilateral triangle (Fig. 1 A) and this feature alone distinguishes kangaroo rat sperm from that of other heteromyids; the apex of the sperm head is rather acute and the tail long.

Accessory Glands of the Male Reproductive Tract

With the exception of Gunther's (1960) description of the male reproductive tract in *Thomomys*, no studies of geomyoid reproductive tract morphology have appeared prior to this analysis. The descriptions below are taken from M. S. Hafner (1979). The male accessory reproductive gland complements of 11 geomyoid genera are listed in Table 1. *Microtus* is included in Table 1 to represent the most common muroid (outgroup) condition, i.e., all gland complements present (Arata 1964).

Loss of glandular complements appears to be much more widespread among geomyid than among heteromyid taxa. Patterns in loss or retention of gland complements agree in general with patterns seen in muroid rodents (Arata 1964); for example, it is not uncommon to find the preputial glands absent in taxa representing either group of rodents (geomyoids or muroids), whereas the bulbourethral glands are present thus far in all muroid and geomyoid taxa examined.

By far the most striking changes in the male reproductive tract of geomyoid rodents involve changes in the morphology of the vesicular glands (seminal vesicles). In the large majority of geomyoids (and in rodents in general), the vesicular glands are elongate, hook- or cane-shaped, translucent structures. In contrast, most specimens examined thus far of the genus *Thomomys* (subgenus *Megascapheus*) have tubular, translucent vesiculars (J. L. Patton, pers. comm.), and all specimens

TABLE 1. Male accessory reproductive gland complements in 14 geomyoid taxa (+ indicates gland complement present). *Microtus* is representative of the typical muroid condition (Arata, 1964). Terminology as per Arata (1964).

Taxa examined	Gland complements[1]							
	v[2]	*vmp*	*vlp*	*ap*	*dp*	*a*	*bu*	*p*
Thomomys bottae	3		+	+	+		+	
Thomomys umbrinus	3		+	+	+		+	
Geomys bursarius	1		+	+	+	+	+	+[3]
Zygogeomys trichopus	1		+		+	+	+	
O. (*Orthogeomys*) *grandis*	1		+	+			+	
O. (*Macrogeomys*) *heterodus*	1		+	+	+	+	+	
Pappogeomys gymnurus	1		+	+	+	+	+	
Heteromys desmarestianus	1		+			+	+	
Liomys pictus	1	+	+	+	+	+	+	
Perognathus spinatus	2	+	+	+	+	+	+	
Perognathus parvus	1	+	+	+	+	+	+	+
Microdipodops megacephalus	1		+	+	+	+	+	+
Dipodomys ordii	1	+	+	+	+	+	+	
Dipodomys merriami	1	+	+	+	+	+	+	
Microtus sp.	1	+	+	+	+	+	+	+

[1]v = vesicular, vmp = ventromedial prostate; vlp = ventrolateral prostate; ap = anterior prostate; dp = dorsal prostate; a = ampullary; bu = bulbourethral; p = preputial

[2]Numbers refer to shape of vesicular gland complement: (1) elongate; (2) round; and (3) short, tubular.

[3]The presence or absence of preputial glands in *Geomys* was difficult to ascertain due to the presence of large amounts of connective tissue and fat in the preputial region.

examined belonging to the subgenus *Chaetodipus* of the genus *Perognathus* have round, smooth, yellow- to gray-colored vesicular glands (pinkish and granular in appearance in fresh specimens). The morphologies of the respective vesicular glands in *Thomomys* and *Chaetodipus* are unique among those described thus far for rodents. This unusual vesicular morphology in the subgenus *Chaetodipus* is particularly striking in that all specimens examined belonging to the subgenus *Perognathus* have more typical rodent vesicular glands. Typical *Perognathus* and *Chaetodipus* male reproductive tracts are contrasted in Figure 2.

Among the heteromyid genera examined (Table 1), *Heteromys* shows an unusually high level of evolutionary loss of glandular complements (4 of 8 glands are absent). In contrast, all glandular complements are present in *Perognathus parvus* (subgenus *Perognathus*). In *Heteromys* and *Microdipodops*, the absence of ventromedial prostates is certainly a derived condition; however, it would be dangerous to link these two genera phylogenetically based solely on the absence of a single gland complement, especially when loss of ventromedial prostates is seen in the outgroup (Geomyidae). Similarly, the presence of preputial glands in *Perognathus parvus* and *Microdipodops* should not be used to infer a special phylogenetic relationship; the genera have merely retained a gland complement normally present in nongeomyoid rodents.

A conservative assessment of the data reviewed above leads to five conclusions:

1. *Liomys* and *Heteromys* show close phylogenetic relatedness based primarily on morphology of the glans penis.
2. *Dipodomys* and *Microdipodops* are also suggested to be phylogenetically allied, again based largely on morphology of the glans penis.
3. Pocket mice of the subgenus *Chaetodipus* show only remote morphological similarities to species of the subgenus *Perognathus*. All aspects of the male reproductive system support this conclusion.
4. Within *Chaetodipus*, *P.* (*Chaetodipus*) *hispidus* is unique with respect to morphology of the glans penis, baculum, and spermatozoa.
5. Species of the pocket mouse subgenus *Perognathus* show extreme morphological conservatism with respect to the male reproductive system.

BIOCHEMICAL VARIATION

Analyses of intrapopulation protein variation in *Microdipodops* (D. J. Hafner et al. 1979) and *Perognathus*, subgenus *Chaetodipus* (Patton et al. 1981), have revealed levels of genetic polymorphism and heterozygosity approximately equivalent to averages summarized for 46 species of mammals by Nevo (1978). In contrast, the average values of polymorphism and heterozygosity measured in populations of *Dipodomys* (Johnson and

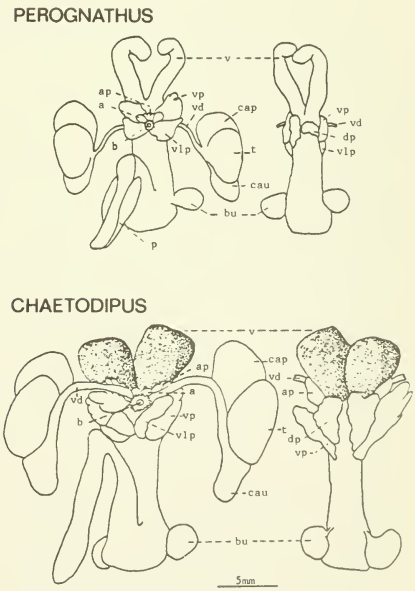

Fig. 2. Ventral (left) and dorsal (right) views of the male reproductive tracts of *Perognathus* (*Perognathus*) *longimembris* and *P.* (*Chaetodipus*) *spinatus*. The urinary bladder (b) has been excised to reveal underlying accessory gland complements. Abbreviations as per Table 1 with following additions: caput epididymis (cap); cauda epididymis (cau); testis (t); vas deferens (vd).

Selander 1971, Patton et al. 1976) are only half as large as those measured in most mammalian populations. Johnson and Selander (1971) suggest that a combination of phylogenetic and ecological factors may explain depressed levels of intrapopulational genetic variation in kangaroo rats relative to other mammals. Indeed, future genetic analyses of kangaroo rat populations may find a causal link between ecological amplitude (niche width) and genetic variation, but a clear connection was not evident in Johnson and Selander's (1971) study.

Interpopulation genetic differentiation in *Dipodomys* and *Perognathus* (*Chaetodipus*) has been shown to be approximately commensurate with values measured between populations of other rodents, and mammals in general (Johnson and Selander 1971, Csuti 1979, Patton et al. 1981). Genetic studies at the intra- and interpopulation level are currently in progress for the genera *Liomys* and *Heteromys* (D. S. Rogers, pers. comm.).

Estimates of interspecific protein differentiation within the three heteromyid genera thus far examined (*Microdipodops*, *Dipodomys*, and *Perognathus*, subgenus *Chaetodipus*) reveal two divergent patterns. First, *Microdipodops megacephalus* and *M. pallidus*, which are sibling species on morphological criteria (D. J. Hafner et al. 1979), are genetically differentiated at the appropriate "sibling species level" as defined by Zimmerman and Nejtek (1977) based on data from 10 species of mammals. Similarly, genetic distances measured between morphologically well-differentiated species of *Dipodomys* (Johnson and Selander 1971) are approximately equivalent to those measured between well-differentiated species in other mammalian taxa (Zimmerman and Nejtek 1977). In *Perognathus*, on the other hand, Sarich (1975), M. S. Hafner (1979, 1982), and Patton et al. (1981) have shown that the genetic distance measured between perognathine and chaetodipine pocket mice is extremely large, in fact larger than that measured between *Liomys* and *Heteromys*. Clearly, the rate of exomorphologic change between *Perognathus* and *Chaetodipus* has lagged far behind that of biochemical change. Moreover, all indications from comparative rate tests suggest that protein evolution has proceeded at the same rate within the perognathine and heteromyine lineages. Thus, due to extreme exomorphological conservatism, *Perognathus* and *Chaetodipus* are, in a sense, "cryptic genera."

Studies of albumin (M. S. Hafner 1982) and transferrin (Sarich 1975) immunology in heteromyids show *Microdipodops* to be extremely conservative with respect to rate of protein change through time. In immunological comparisons with nonheteromyid outgroups, *Microdipodops* shows consistently lower levels of protein change relative to other heteromyids. According to Sarich (pers. comm.), the high degree of protein conservatism seen in *Microdipodops* is unique among taxa thus far examined immunologically belonging to several different mammalian orders. At present, we have no explanation, or even hypotheses, to account for extreme protein conservatism in *Microdipodops*.

KARYOTYPIC EVOLUTION

Chromosomal Variation

Heteromyid and geomyid rodents have attracted a great deal of attention from evolutionary biologists and systematists. Interest in these rodents stems, among other reasons, from the great degree of chromosomal variation across the group. Whereas karyotypic information has been applied commonly to questions at the species level, such information has not been used adequately in assessing evolutionary relationships at higher levels. Further, the fusion paradigm of karyotypic reorganization has been invoked to the near exclusion of other possible mechanisms that alter diploid number (e.g., Thaeler 1968, Davis et al. 1971, Genoways 1973, Selander et al. 1974, Stock 1974, Williams and Genoways 1975, Williams 1978). The Robertsonian fusion model (Robertson 1916), whereby the karyotype is reduced in diploid number through the joining of uniarmed chromosomes to form biarmed elements, has reigned as the predominant view in interpretations of geomyoid chromosomal evolution despite there being no convincing argument to support its occurrence. In geomyoid studies, empiricism has lagged well behind theoretical considerations; and other hypoth-

eses, alternative to the fusion paradigm, have not been seriously considered (see also Imai and Crozier 1980).

Diploid numbers are now known for representatives of all genera and subgenera within the Geomyoidea (Heteromyidae: *Dipodomys*, Cross 1931, Matthey 1952, 1956, Csuti 1971, Dingman et al. 1971, Fashing 1973, Stock 1974; *Microdipodops* D. J. Hafner et al. 1979, J. C. Hafner 1981a; *Chaetodipus*, Patton 1967a, 1969, 1970; *Perognathus*, Patton 1967b, Williams 1978; *Liomys*, Genoways 1973; *Heteromys*, Genoways 1973, A. L. Gardner, pers. comm., D. S. Rogers, pers. comm., M. S. Hafner and J. C. Hafner, unpubl. data; Geomyidae: *Geomys*, Davis et al. 1971, Baker et al. 1973, Selander et al. 1974, Williams and Genoways 1975, Hart 1978, Honeycutt and Schmidly 1979; *Pappogeomys*, Laguarda-Figueras et al. 1971, Berry and Baker 1972, Hart and Patterson 1974, Smolen et al. 1980, Honeycutt and Williams 1982; *Thomomys*, Thaeler 1968, 1972, 1973, 1974a, 1974b, 1976, 1977, 1980, Thaeler and Hinesley 1979; *Thomomys*, subgenus *Megascapheus*, Patton and Dingman 1968, 1970, Patton et al. 1972, Patton 1973, 1980, Patton and Yang 1977, Patton and Feder 1978, J. C. Hafner et al. 1983; *Orthogeomys*, M. S. Hafner 1979, M. S. Hafner and J. C. Hafner, unpubl. data; *Zygogeomys*, M. S. Hafner, 1979, M. S. Hafner and J. C. Hafner, unpubl. data).

Figure 3 summarizes the chromosomal variability for geomyoid species. If Robertsonian chromosomal events (fusion and/or fissions) were chiefly responsible for effecting diploid number change in the six major groups of the Geomyidae, the dots representing karyotypes within a species and species within the major groupings would be expected to be aligned in vertical patterns. It can be seen (Fig. 3A) that this does not appear to be the general case. In the Heteromyidae (Fig. 3B), a similar situation exists. Within the major heteromyid groups, karyotypes are not, for the most part, aligned in vertical arrays. Lacking G- and C-banding information for most groups in the Geomyoidea, it is premature to speculate on the specific mechanisms, or actual mechanics, of chromosomal rearrangement. Moreover, even banding data will not allow us to assess directionality of change, vis-a-vis the fusion/fission controversy.

Directionality in Chromosomal Evolution

Geomyoid karyotypic data do warrant a close evaluation of directionality of chromosome number change within the superfamily, irrespective of the mechanism(s) that may be involved in the change (J. C. Hafner 1981b). The Geomyoidea, with its high degree of diploid number variation and doubtless monophyletic origin, is an appropriate group in which to examine polarity in diploid number change. Are high numbers primitive with a general reductional trend, or are low numbers primitive with an increasing trend? If no general trend is discernible, we must consider the possibility that both trends operate, but in separate geomyoid lineages or at different times in the history of a single lineage.

In this analysis we have considered 12 major taxonomic groups (genera and subgenera listed above). Note that we include both subgenera within the genus *Thomomys* (*Thomomys* and *Megascapheus*, *sensu* Thaeler 1980) as well as the subgenera *Chaetodipus* and *Perognathus* of the genus *Perognathus*. A histogram plot of species numbers versus diploid numbers (including intraspecific chromosomal variation) reveals that the distribution of geomyoid karyotypes is rather trimodal and seems to exhibit a damped oscillatory pattern (Fig. 4). Therefore, the array of diploid numbers can be trisected into chromosomal subgroups or character states: low chromosome numbers (2n = 34–50), medium numbers (about 60), and high diploid numbers (68–88).

Invoking the criterion of character state distribution, we first attempt to assign polarity by using in-group analysis. According to the criterion of in-group analysis, the character state that occurs most frequently within the group under study (the common state) is considered to be the primitive state (Stevens 1980:335–37, Criterion 1A). The low chromosome number character state contains 47 karyotypes, the medium state 44 karyotypes, and the high number state has 27 karyotypes (Fig. 4). Although the evidence may not be strong, the criterion of in-group analysis would lead to the conclusion that lower chromosome numbers (2n = 34–64) are primitive and higher numbers (2n > 64) are derived, which is contradictory to earlier

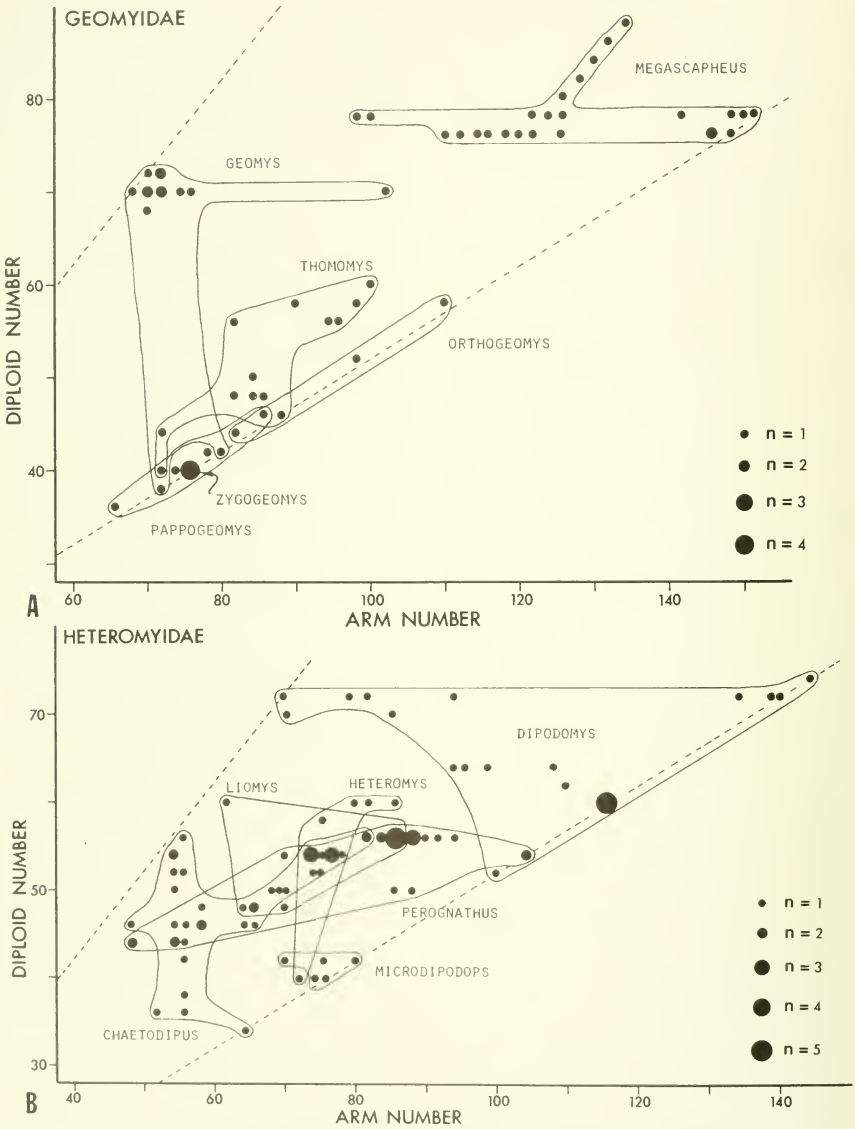

Fig. 3. Chromosomal variation in the Geomyoidea: A, Geomyidae; B, Heteromyidae. See text for data sources. Dashed lines represent the karyotype bounds; n = number of karyotypes. Odd diploid numbers have been omitted for clarity.

published opinions.

To view this in-group analysis at a higher taxonomic level, we next examine the number of major geomyoid groups versus diploid numbers (Fig. 5). Again, the criterion would maintain that the most common character state across the major groupings is primitive. The low chromosome number character state contains 10 of the 12 major geomyoid taxa. In comparison, the medium character state contains 8 of the major taxa and the high chromosome number state contains only three major taxa (*Dipodomys*, *Geomys*, and *Megascapheus*; Fig. 4). The conclusion to be drawn from this refined in-group treatment, once again, is that the lower diploid numbers are primitive and the higher character state derived.

Such evolutionary polarity, assigned by in-group analysis must be confirmed using other criteria. We therefore must consider out-group analysis (see Stevens 1980:337–340, Criterion 1B). Following the out-group method, the character state that is shared with the out-group is taken to be primitive. It has been suggested by some workers that the murids stand as a distant sister group to the Geomyoidea. The range of diploid numbers in the Muridae (Fig. 6A) is almost entirely within the low diploid number character state defined earlier; the mode for the Muridae is 2n = 48. Selecting another out-group for comparison, the Cricetidae, again we see that the vast majority of cricetid karyotypes fall into the low chromosome number character state (mode: 2n = 48; Fig. 6B). Further, out-group comparison with the Sciuridae (Fig. 6C; mode: 2n = 38) and the Aplodontidae (2n = 46; Matthey 1973), two families commonly believed to represent primitive rodents, again corroborates the earlier assigned polarity. Thus, all out-group comparisons indicate that the low character state is primitive.

One other criterion that can be used to determine the polarity of character states is that of correlation among character states (Stevens 1980:345–348, Criterion 5). This argument is based on the assumption that primitive character states frequently occur together. As Stevens (1980) aptly noted, the criterion of correlation should be used in combination with other criteria (e.g., in-group and out-group analyses) as has been done here.

One morphological character whose character state polarity is reasonably well supported is that of sulcation in the upper incisors. It seems that grooved upper incisors is

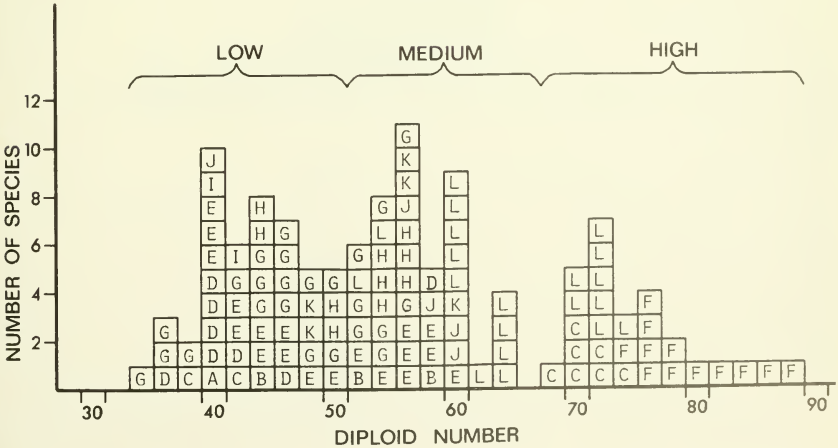

Fig. 4. Frequency distribution of the chromosome numbers in the Geomyoidea. The distribution is trimodal and skewed to the right. Odd diploid numbers have been omitted for clarity. GEOMYIDAE: A, *Zygogeomys*; B, *Orthogeomys*; C, *Geomys*; D, *Pappogeomys*; E, *Thomomys*; F, *Megascapheus*. HETEROMYIDAE: G, *Chaetodipus*; H, *Perognathus*; I, *Microdipodops*; J, *Heteromys*; K, *Liomys*; L, *Dipodomys*.

plesiomorphic for groups within the Geomyoidea, with loss of a sulcus being the derived state (see Merriam 1895, Wood 1935, Russell 1968). Within the Geomyidae, only one extant group totally lacks sulci in the upper incisors. This is the smooth-toothed pocket gophers, which include *Thomomys* and *Megascapheus*. Interestingly, pocket gophers of the subgenus *Megascapheus* have the highest diploid numbers in the superfamily (Fig. 4), and *Megascapheus* is a major taxon that is entirely restricted to the high diploid number character state. Although it cannot be demonstrated that this instance of character state correlation is not due to chance alone, it is nevertheless in accord with the aforementioned polarity and the general trend for increase in chromosome number.

Within the Heteromyidae, kangaroo rats (*Dipodomys*) display a surfeit of derived morphological characters. Kangaroo rats are generally large in body size, have large eyes, long hind feet, expanded auditory bullae, a middorsal sebaceous gland, a long tail, and elaborate pelage markings; doubtless, kangaroo rats are the most morphologically derived members of the Heteromyidae (see beyond). Correlated highly with the derived nature of these characters is the high diploid numbers of *Dipodomys*. Kangaroo rats are distributed chromosomally in the medium and high diploid number character states and exhibit the highest diploid number for the Heteromyidae. This correlation criterion again supports our initially assigned polarity. We shall argue beyond that *Microdipodops*, which exhibits relatively low diploid numbers (2n = 40,42), is much less derived morphologically than is *Dipodomys*.

Further evidence that can be used to support this mode of directionality comes from recent information on *Thomomys bottae* pocket gophers in Colorado (J. C. Hafner et al. 1980, J. C. Hafner et al. 1983). Throughout its extensive range, *T. bottae* is known to have, almost without exception, 76 chromosomes. However, a chromosomal race of *T. bottae* recently discovered in Colorado had 88 chromosomes (the second highest known for the Mammalia); yet allozymically it is nearly identical with the parental 2n = 76 form. Clearly, this anomalous race, characterized by a diploid number of 88, is derived from the common 2n = 76 form. Had the 88 chromosomal race been primitive, one would have expected its level of genic divergence to be equal to or greater than levels of major protein differentiation seen within the 2n =

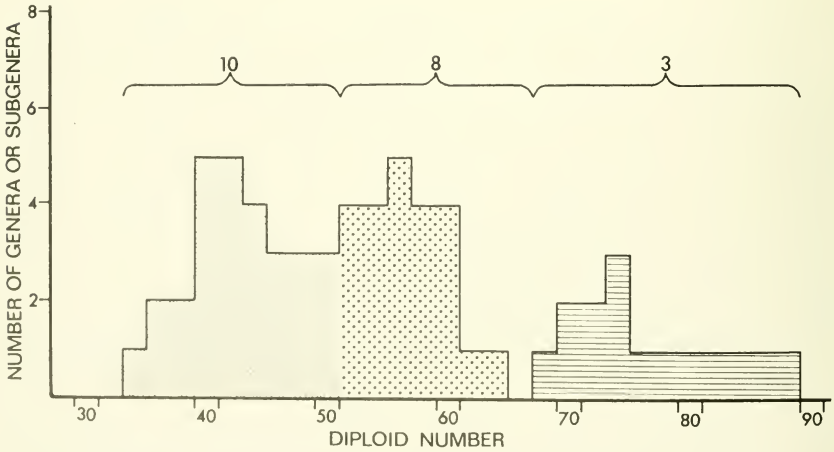

Fig. 5. Number of genera or subgenera versus diploid number. Numbers above brackets indicate number of major taxa represented in the three chromosomal character states.

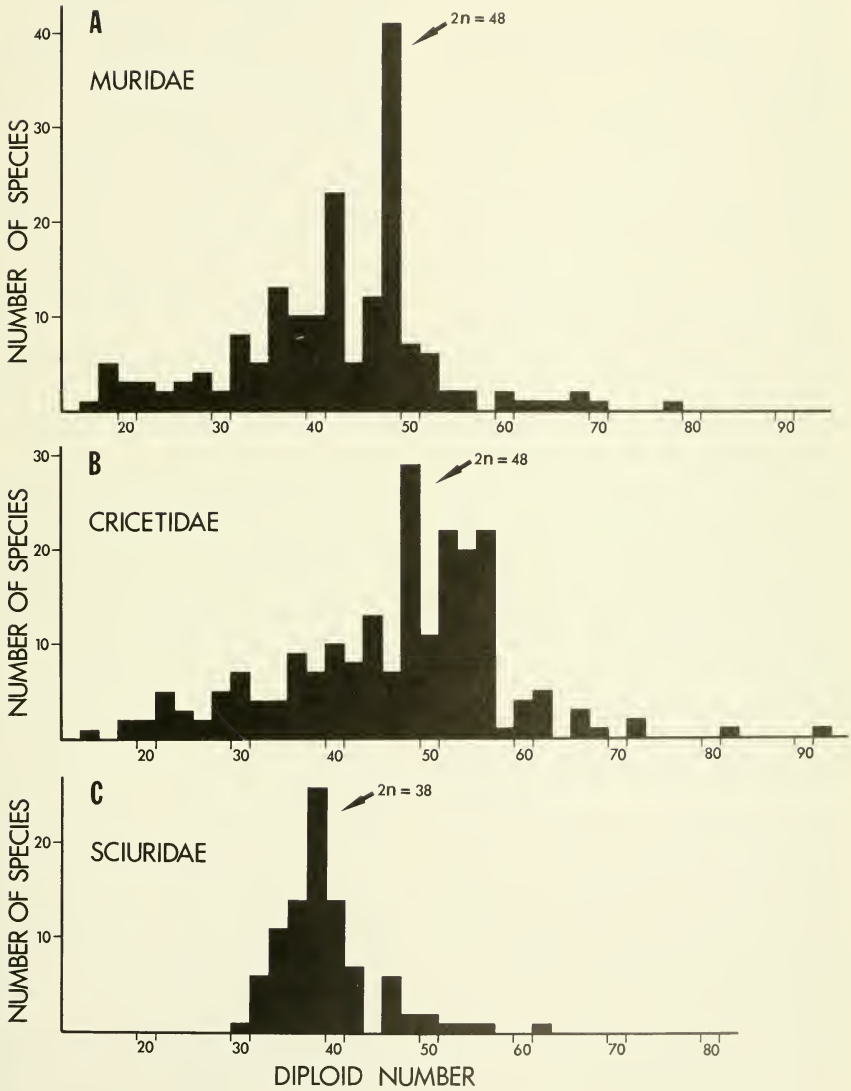

Fig. 6. Frequency distributions of diploid numbers for out-group comparisons: A, Muridae; B, Cricetidae; C, Sciuridae. Data are taken from Hsu and Benirschke (1967–1977) and Matthey (1973). Modal numbers are indicated in the figures.

76 form; this is not the case (see Patton and Yang 1977, J. C. Hafner et al. 1983). Importantly, this study represents the only thoroughly documented (chromosomal, allozymic, morphologic) demonstration of chromosomal directionality in the Geomyoidea.

In view of the foregoing, it seems that there is certainly ample justification for an alternative viewpoint with respect to the direction of chromosomal number change in the Geomyoidea. Several statements in the literature claiming high diploid numbers to be primitive for particular heteromyid groups and for the entire Geomyoidea (e.g., Williams 1978:605) are without support. We fully realize that reductional trends may indeed have occurred in specific geomyoid lineages; however, arguments used to support the diploid number reductional trend are weak and commonly utilize general biogeographical and ecological explanations (e.g., Williams and Genoways 1975). As pointed out by numerous authors, such reasoning is fraught with problems of circularity and is inadmissible in the assignment of polarity to character states. In contrast, ingroup and out-group analyses and correlation among character states support an alternative view that low diploid numbers seem to be primitive for the Geomyoidea, and the overall direction of karyotypic change has been that of increase in chromosome number. We shall not speculate on the mechanism of increased numbers at this time, but will mention that fission may be involved, as well as other mechanisms such as chromosome duplication and addition of euchromatin or heterochromatin to centromeric fragments. A full discussion of karyotypic interconversions within the Geomyoidea must await the time when more karyotypes have been banded and we have a more firm understanding of the complexities of chromosomal evolution.

MORPHOLOGICAL EVOLUTION

Cladistic Analyses of Heteromyid Relationships

A prominent issue in the study of heteromyid relationships is the question of the subfamilial affinity of kangaroo mice. Since Merriam's (1891) description of *Microdipodops* there has been much controversy as to whether kangaroo mice are most closely related to kangaroo rats or pocket mice (for review see J. C. Hafner 1978, M. S. Hafner 1982). Kangaroo rice are phenetically most similar to pocket mice (J. C. Hafner 1978), yet biochemical data indicate that they are somewhat more closely related to kangaroo rats (M. S. Hafner 1982). One might therefore hypothesize that *Microdipodops*, although being a cladistically old group, is patristically primitive and the similarities it shares with pocket mice are actually symplesiomorphous. Thus, it is necessary to perform a cladistic study in which shared-derived characters (hypothesized on the basis of out-group comparisons) are used to unite taxa. Accordingly, herein we evaluate this central issue in heteromyid phylogeny by analyzing the phenetic data of Wood (1935) and J. C. Hafner (1978), using cladistic procedures.

WOOD (1935) REVISITED.— Fifty-three characters were used by Wood (1935) in his treatment of the evolutionary relationships of kangaroo mice. Wood (1935:108) tabulated the character-state distribution for each of these characters across the heteromyid genera and concluded that kangaroo mice were most closely related to pocket mice. It is these tabulated data (Wood 1935:108) that are available for the present cladistic analysis; we have made no effort to reexamine Wood's characters and, for present purposes, accept his selection of characters and his interpretations concerning character homologies. In our analysis of Wood's data, the Heterominae (*Liomys* and *Heteromys*) was chosen for out-group comparison because most authors agree that it is an evolutionarily independent lineage quite removed from *Perognathus*, *Microdipodops*, and *Dipodomys*. Consequently, characters shared with *Liomys* and *Heteromys* (see Wood 1935:108) are hypothesized to be primitive. Ten of Wood's original characters were omitted from the analysis (all three genera shared seven characters with the out-group and three other characters were ambiguous), reducing the total number to 43 characters (Table 2).

The three possible phylogenetic hypotheses, showing the apportionment of the 43 morphological characters, are presented in

TABLE 2. Characters used in our reanalysis of Wood (1935). Ten of the 53 characters listed by Wood (1935:108) have been omitted in the reanalysis (see text).

Character number	Wood's (1935) ordering	Description of feature
1	1	Locomotion ricochetal
2	5	Protoloph of P^4 unites between hypocone and metacone.
3	7	Upper molars do not surround central lakes
4	8	Playa lake in metaloph of P^4 absent
5	9	Check teeth hypsodont
6	10	Occlusal pattern not elongated with crown
7	11	Teeth unrooted or form roots late in life
8	13	Bases of upper molars in orbit
9	14	Zygomatic process of Mx. expanded
10	15	End of palate not behind M^3
11	16	Pits in basioccipital absent
12	17	One pair of pterygoid fossae
13	18	Pterygoid fossae reach endocranium
14	19	Masseter separated from IOF by crest
15	20	Orbit overhung by frontal
16	21	Ethmoid foramen absent
17	22	Incipient postorbital process
18	23	Temporal fossa not distinct
19	24	Alisphenoid canal anterodorsad
20	25	Bulla extends anterad of glenoid
21	27	Squamosal perforated by bulla
22	28	Lacrymal expanded not free of Mx.
23	29	Parietal between squamosal and mastoid
24	31	Paroccipital process not lateroc-audad
25	33	Knob for pulp cavity at lower edge of ascending ramus
26	34	Pit by M_3, no foramen on condyloid
27	35	Cervical vertebrae fused in part
28	36	No median ventral foramen in caudals
29	37	Notch in transverse process of caudals gently curved
30	38	Tail tufted
31	39	Scapula prolonged posteriorly
32	40	End of acromion not expanded
33	41	Short supinator crest
34	42	Deltoid crest ends steeply
35	43	Articulation of trapezium and scapholunar
36	44	Triangular obturator foramen
39	47	Process of pubis at front of obturator foramen
40	49	Cnemial crest ends at gentle slope
41	50	External and internal malleoli do not reach same level
42	51	No astragalo-cuboid contact
43	53	Metatarsal IV not the longest

Figure 7A–C. Six derived characters unite *Perognathus* with *Microdipodops* (Fig. 7A), nine characters unite *Perognathus* with *Dipodomys* (Fig. 7B), and the *Microdipodops-Dipodomys* association is supported by 12 synapomorphies (Fig. 7C). Hence, the tree topology in Figure 7C is most parsimonious and contradicts the conclusion proferred by Wood (1935). It is interesting to note that the murinelike *Perognathus* is lacking an autapomorphic descriptor; we view this to be a problem not in the analysis or with the taxon, per se, but in the nature and breadth of the characters analyzed.

It is possible that the association of *Microdipodops* with *Dipodomys* (Fig. 7C) is incorrect because the analysis does not recognize possible parallelisms associated with the ricochetal mode of locomotion; the apomorphies used to unite the two taxa may be independently derived characters. To evaluate this possibility, we remove all those features in the analysis that are shared with the distantly related bipedal form, *Jaculus* (Fig. 7D–F; see Wood 1935:107–109). It can be seen in this refined analysis, controlling for ricochetal habitus characters (Fig. 7D–F), that there is still stronger support for the *Microdipodops-Dipodomys* phylogenetic hypothesis (Fig. 7F) than the other two possibilities. However, problems exist. If the presumed synapomorphic characters uniting kangaroo mice and kangaroo rats are to be believed, then the others must be misleading. As Wood (1935) himself observed, however, parallelism is the evolutionary motto of heteromyids.

REANALYSIS OF HAFNER (1978).— In an attempt to resolve the *Microdipodops* controversy, J. C. Hafner (1978) compared the two kangaroo mouse species with three species of kangaroo rats and four species of pocket mice (two species each of the subgenera *Perognathus* and *Chaetodipus*), using phenetic clustering and ordination procedures. Hafner (1978) concluded that *Microdipodops* is most closely related, phenetically, to pocket mice and adduced a broad spectrum of phenetic characters with assumed overall genotypic representation. Here we reanalyze Hafner's (1978) data hypothesizing shared-derived characters, using out-group comparison with *Liomys* and *Heteromys* (het-

eromyine data from Genoways 1973). A total of 17 characters was available for cladistic analysis (Table 3) after paring down Hafner's (1978:363–364) data matrix of 40 characters (quantitative characters were omitted from our analysis as well as those characters with indeterminable character-state polarity). Throughout our analysis, we have accepted as a working hypothesis that *Perognathus* and *Chaetodipus* form a clade relative to the other lineages; this assumption is supported by biochemical evidence (e.g., Sarich 1975, M. S. Hafner 1982).

Figure 8 shows the three phylogenetic hypotheses with the 17 characters (Table 3) apportioned among them. The results of this analysis, in accord with our above treatment of Wood's (1935) data, suggest that the most parsimonious phylogenetic hypothesis is that which links *Microdipodops* and *Dipodomys* as a clade independent of the *Perognathus-Chaetodipus* clade (Fig. 8C). However, the analysis is less than robust; the *Perognathus-Chaetodipus* clade lacks an autapomorphic character, and the characters that define the *Microdipodops-Dipodomys* association (Fig. 8C) are dubious (fully haired soles of hind

TABLE 3. Seventeen characters used in the reanalysis of Hafner (1978). Quantitative characters (J. C. Hafner 1978:363–364) and characters whose character-state polarity was indeterminable were omitted in our analysis.

Character number (Hafner 1978)	Description of feature
3	Lacrimals joined
4	Molars nonrooted
7	Morphology of Y chromosome metacentric
9	Urethral lappets absent
12	Sharply upturned morphology of baculum tip
13	Harsh pelage characteristics
15	Middorsal gland present
16	Soles of hind feet (naked, a; fully haired, b)
17	Crested tail present
18	Flank stripes present
21	Locomotion: partially bipedal to fully bipedal
31	White side stripes on tail present
33	Molar wear patterns: enamel limited to anterior and posterior plates
34	Tail greater diameter in middle than at base or tip
35	Absence of median ventral foramina in caudal vertebrae
36	Astragalus-cuboid articulation present
40	White ring at base of tail present

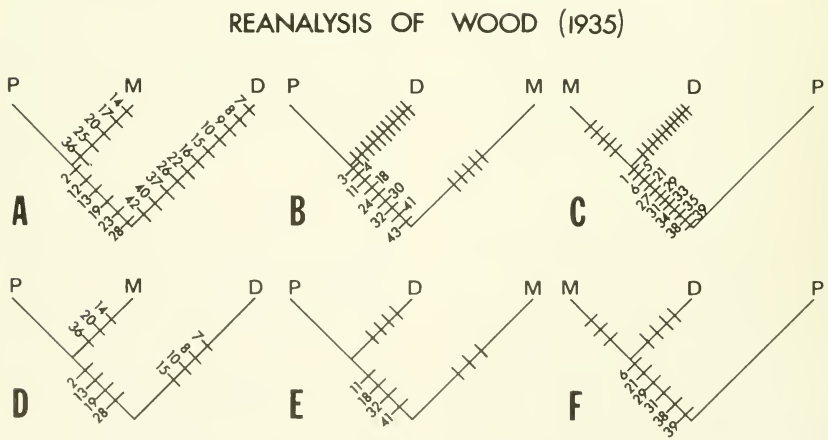

Fig. 7. Cladistic analysis of morphological data presented by Wood (1935) for *Perognathus* (P), *Microdipodops* (M), and *Dipodomys* (D). In A, B, and C, 43 of Wood's original 53 characters (see Table 2) are apportioned on the three possible trees, omitting those characters shared with *Liomys* and *Heteromys*. In D, E, and F, those characters shared with the ricochetal form *Jaculus* (Dipodidae) are also omitted to remove features that are functionally related to bipedality. Note the high number of autapomorphies on the *Dipodomys* branch and the conspicuous absence of autapomorphies on the *Perognathus* branch.

feet and ricochetal mode of locomotion).

CONCLUSIONS ABOUT THE *Microdipodops* CONTROVERSY.— The above cladistic analyses of the data of Wood (1935) and J. C. Hafner (1978) are necessary exercises, yet the results are not unequivocal and provide us with only a preliminary insight to the problems of ascertaining phylogenetic relationships within the Heteromyidae using morphological characters. Both reanalyses demonstrate modest support for the recognition of the *Microdipodops-Dipodomys* clade; thus, they are in agreement with biochemical evidence. However, the treatments are inchoate and there is a need for a detailed phylogenetic analysis wherein character homologies and character-state transformations are determined. As noted by many workers (e.g., Hennig 1966), the crux of any analysis and its attending arguments relies on the characters under study.

Several others points emerge from the above analyses. Importantly, these cladistic treatments tabulate quantitatively the tremendous amount of parallelism in the heteromyids. That the morphology of these rodents is rife with parallelisms is documented convincingly in Figure 7A–C. The analyses also provide a comparative measure of the degree of morphological divergence among the heteromyid genera. In accord with intuition, these results document that *Dipodomys* is the most derived genus in terms of morphology (highest number of autapomorphic features; Figs. 7 and 8), the pocket mice are the least derived, and *Microdipodops* exhibits an intermediate number of derived features.

Evolution of Geomyoid Morphotypes: An Hypothesis

The diversity of morphological forms, or morphotypes, within the superfamily Geomyoidea eclipses that seen within any other mammalian group of comparable size. The evolution of forms as structurally divergent as kangaroo rats, pocket mice, and pocket gophers is commonly believed to be the result of orthoselection; i.e., directional selection acting on ancestral species favoring certain adaptations which are accentuated in descendant species. The origin of each structural novelty is thus explained in terms of its present day functional advantage to the animal. Although it cannot be denied that a conspicuous morphological feature present in a living animal may, and probably does, have an adaptive function today, we agree with Gould and Vrba (1982:13) that "current utility carries no automatic implication about historical origin." As Lewin (1982:1212) points out, "it is folly to infer without caution the historical genesis of a feature from its current utility." Accordingly, we herein introduce a causal hypothesis, devoid of functional explanations, to account for the evolutionary origin of morphological diver-

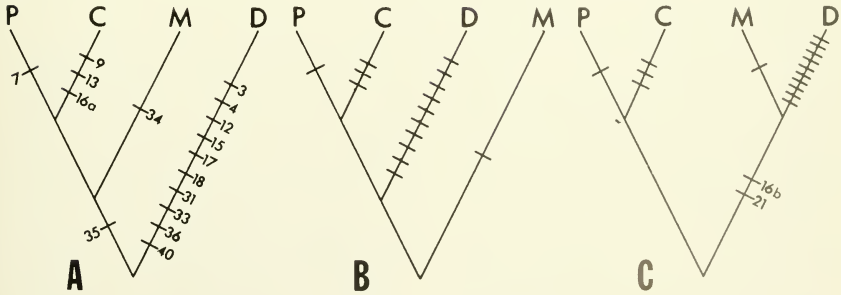

Fig. 8. Cladistic analysis of morphological data presented by J. C. Hafner (1978) for *Perognathus* (P), *Chaetodipus* (C), *Microdipodops* (M), and *Dipodomys* (D). Cladograms A, B, and C reflect the three possible ways that *Microdipodops* and *Dipodomys* may be linked with the *Perognathus-Chaetodipus* assemblage. *Liomys* and *Heteromys* are treated as an outgroup (data from Genoways, 1973). See Table 3 for list of characters.

sification within the Geomyoidea. This hypothesis is expanded and supportive evidence is detailed elsewhere (J. C. Hafner and M. S. Hafner, in manuscript).

Several years ago we observed that the conspicuous morphological features of adult kangaroo rats and kangaroo mice, most notably the large head and eyes, enlarged brain, long hind feet, and delicate, weakly fused skeleton, were traits commonly seen in the juvenile state of other animals. Further examination revealed that kangaroo rats and kangaroo mice possess many of the classical features characteristic of paedomorphic forms. This initial observation, coupled with the subsequent discovery that neonatal pocket gophers look remarkably like mature pocket mice, prompted further investigation culminating in our hypothesis that geomyoid morphological transformations through phylogeny may be the result of evolutionary epigenetics (for recent reviews see Gould 1977, Alberch et al. 1979, Alberch 1980, Løvtrup 1981a, 1981b, Rachootin and Thomson 1981). In other words, regulatory changes in ontogeny may have affected the timing of gene action and rates of morphogenesis and growth and thus have led to morphological phyletic evolution in this group.

Most authors would agree that pocket mice, including *Perognathus*, *Liomys*, and *Heteromys*, exhibit a generalized body plan and probably represent a good approximation of the ancestral geomyoid morphotype (e.g., Eisenberg 1981:90). Our hypothesis suggests that perturbations in developmental "control parameters" in ancestral (pocket-mouse-like) geomyoids, including changes in the time of onset of growth, cessation of development, and rate of growth, could deform the ancestral ontogenetic pathway and effect phylogenetic transmutations in morphology leading to such diverse forms as kangaroo mice, kangaroo rats, and pocket gophers.

According to our hypothesis, paedomorphosis in kangaroo mice and kangaroo rats may have originated via different kinds of developmental perturbations. Both morphology and general life history of kangaroo mice suggest that they are progenetic descendants of pocket-mouse-like ancestors. Progenesis is the process whereby ontogeny is truncated and maturation is accelerated. Gould (1977) argues that the key to understanding the immediate significance of shifts in developmental timing (heterochrony) lies in the theory of *r* and *K* selection (life history strategies). Gould (1977:293) predicts that progenesis will be associated with *r*-strategists, and, indeed, early kangaroo mouse evolution is postulated to have occurred in an obvious *r*-selected environment (ephemeral sand-dune habitats in the Great Basin Desert; J. C. Hafner 1978); kangaroo mice possess many of the classical attributes of an *r*-strategist. It appears that in kangaroo mice there has been progenetic truncation by precocious maturation and that this early maturation is the principal object of selection. That is, there has been a "redirection of selection" (Gould 1977) away from morphology, per se, and toward precocious maturation as a life history strategy; juvenilization may have been entirely incidental.

Both morphology and general life history of kangaroo rats lead us to suggest that paedomorphosis in this group is the result of neoteny. Neoteny is fundamentally different from progenesis and involves retardation in growth rate resulting in juvenilization of the adult animal. According to Gould's (1977) hypothesis, neoteny is a common occurrence and may result from direct selection for juvenile features and/or larger body size in environmental regimes that are more *K*-selected. Indeed, kangaroo rats are all medium to large heteromyids possessing many of the classical features associated with the neotenic syndrome (e.g., long life span, slow development, small litters, enlarged brain; J. C. Hafner and M. S. Hafner, in manuscript). The early evolution of kangaroo rats appears to have been confined to grasslands (Reeder 1956), and several living forms inhabit fairly stable, nondesert environments; those that are strictly desert-dwelling forms tend to buffer an otherwise unstable environment by subsisting on a fairly stable resource (leaves) and/or utilizing large stores of hoarded food during periods of food scarcity.

Lastly, we suggest that pocket gophers may be hypermorphic descendants of a pocket-mouse-like ancestor. Hypermorphosis is a process wherein heterochronic perturbation in ontogeny has led to a length-

ened growth period producing a "peramorphic" (as opposed to paedomorphic; Alberch et al. 1979) organism. The marked similarities between neonatal pocket gophers and adult pocket mice suggest that reproductive maturation in pocket gophers has been retarded relative to exomorphological maturation, allowing for extreme development of somatic features prior to reproduction. Adult pocket gophers possess many of the classical features characteristic of late mammalian ontogeny, most notably a rugose, heavily ossified skeleton that results from prolongation of somatic growth late in life.

In summary, we suggest that many, perhaps most, of the flamboyant morphological modifications seen in heteromyids and geomyids may have *originated* as incidental byproducts of heterochronic shifts in ontogeny. Instead of acting separately on each morphological feature (e.g., large head, long legs, delicate skeleton, etc.), natural selection may have acted at the developmental level favoring the new life history strategy associated with a progenetic, neotenic, or hypermorphic animal. The paedomorphic traits invariably associated with these developmental changes (peramorphic traits in the case of hypermorphosis) may have been "tolerated" by natural selection initially and subsequently modified (adapted) for functional purposes. On the other hand, certain novel traits may provide little or no functional improvement over the ancestral condition, but are maintained (as long as they are not deleterious) because they are developmentally mandated.

TAXONOMIC COMMENTS ON THE HETEROMYIDAE ALLEN AND CHAPMAN 1893

The following is an up-to-date statement on the taxonomy of the Recent Heteromyidae, necessarily reflecting the views and biases of the authors. We use as our point of departure Hall (1981) and included references. In the interest of brevity, those heteromyid species recognized by Hall (1981) are not listed, except where we feel taxonomic comments are warranted. For species groupings within each genus we again refer the reader to Hall (1981), but we hasten to add that species groupings within *Dipodomys*, *Heteromys*, *Perognathus*, and *Chaetodipus* are suspect and in need of thorough reevaluation. Finally, we provide a synonymy for *Chaetodipus*, which we herein evaluate to full generic rank. Our views on supraspecific relationships within the family are summarized in Figure 9.

Subfamily Dipodomyinae Coues 1875

GENUS *Dipodomys* GRAY 1841.— Hall (1981) recognizes 22 species of kangaroo rats, partitioned into six species groups following Setzer (1949; see Schnell et al. 1978, for discussion of interspecific taxonomy in the genus). Best (1978) has used morphologic criteria to suggest that three species recognized by Hall, *D. antiquarius* Huey 1962, *D. paralius* Huey 1951, and *D. penisularis* (Merriam 1907), are conspecific with *D. agilis* Gambel 1848. Biochemical (Johnson and Selander 1971) and morphological (Schmidly and Hendricks 1976) evidence has been used to suggest that *D. compactus* True 1899 (not recognized by Hall 1981) warrants full specific status. Similarly, Patton et al. (1976) have used biochemical evidence to document *specific status for D. californicus* Merriam 1890.

GENUS *Microdipodops* MERRIAM 1891.— Herein, kangaroo mice are placed provisionally in the subfamily Dipodomyinae, based largely on biochemical evidence (M. S. Hafner 1982) and comparative analysis of the male reproductive system (this study). We regard the many morphological similarities between *Microdipodops* and *Perognathus* (Wood 1935, J. C. Hafner 1978) to be shared primitive features. Nevertheless, more detailed analyses at the molecular level are needed to confirm or refute the placement of *Microdipodops* within the Dipodomyinae. Two species of *Microdipodops* are recognized by Hall (1981). Hall's suggestion (1981:560) that *M. megacephalus leucotis* may warrant specific status is not supported by chromosomal or protein evidence (J. C. Hafner 1981a).

Subfamily Heteromyinae Coues 1875

GENUS *Heteromys* DESMAREST 1817.— Hall (1981) recognizes 10 species of *Heteromys* partitioned into two subgenera, *Heteromys* and *Xylomys*. *Heteromys nigricaudatus*

Goodwin 1956 (recognized by Hall 1981) was synonymized under *H. lepturus* Merriam 1902 by Goodwin (1969). Rogers and Schmidly (1982) have analyzed phenetic relationships in Hall's (1981) *desmarestianus* group (exclusive of *H. gaumeri*) and have synonymized *H. longicaudatus* Gray 1868, *H. temporalis* Goldman 1911, and *H. lepturus* under *H. desmarestianus* Gray 1868.

GENUS *Liomys* MERRIAM 1902.— We have reviewed a large body of evidence supporting the phyletic affinity of *Liomys* and *Heteromys*. Hall (1981) follows Genoways (1973) in recognizing five species in the genus *Liomys*. Future biochemical and chromosomal banding studies may serve to identify species groups within the genus.

Subfamily Perognathinae Coues 1875

GENUS *Perognathus* WIED-NEUWIED 1839.— Our elevation of *Chaetodipus* to full generic rank (see beyond) results in the inclusion of only "silky pocket mice" (formerly referred to the subgenus *Perognathus*) within the genus *Perognathus*. Hall (1981) recognizes 10 species of silky pocket mice, including the problematic species *P. formosus* Merriam 1889 (see Osgood 1900). Patton et al. (1981) have shown that *P. formosus* is clearly referable to *Chaetodipus*, thus reducing the number of Recent taxa of *Perognathus* to nine.

GENUS *Chaetodipus* MERRIAM 1889.— *Chaetodipus* is here elevated to full generic status. Following is a synonymy and a rediagnosis of the taxon.

Genus *Chaetodipus* Merriam, *new status*

Chaetodipus Merriam, 1889, N. Amer. Fauna 1:5 (25 October). Type-species: *Perognathus spinatus* Merriam, original designation. Subgenus elevated to generic level.

DIAGNOSIS.— Size medium to large (total length 152–230; Hall 1981). Pelage generally harsh, often with spiny bristles on rump. In those species lacking harsh pelage and rump spines, tail crested distally and longer than head and body. Hair flattened in cross section with distinct trough having well-developed ridges on dorsal surface (Homan and Genoways 1978). Soles of hind feet naked. Interparietal width equal to or greater than interorbital width. Auditory bullae not

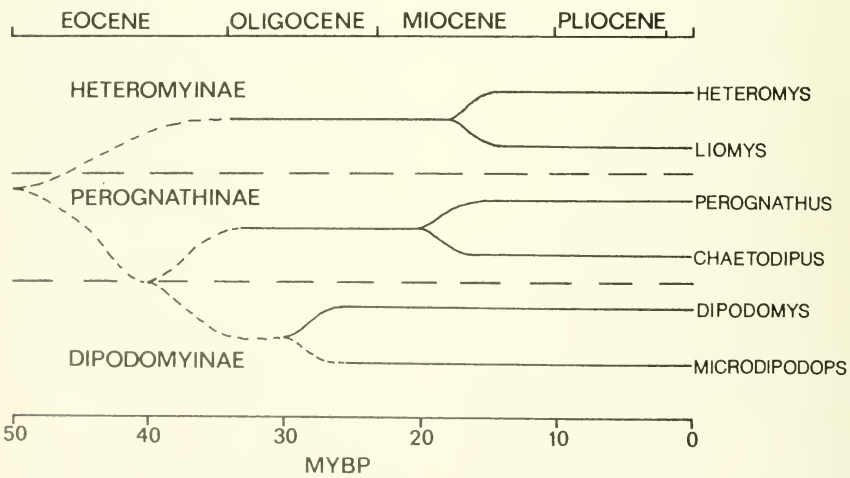

Fig. 9. Phylogeny of the extant Heteromyidae indicating subfamilial groupings. Dashed lines in the dendrogram indicate probable relationships and signal areas where further investigation is needed. The time scale is approximate and is based on fossil evidence (Wood 1935, Lindsay 1972) and immunological and allozymic time calculations (Sarich 1975, M. S. Hafner 1979, 1982).

markedly inflated as in *Perognathus*. Male phallus long and slender, lacking urethral lappets; rim of terminal crater forms ventlike urethral opening. Baculum long relative to body length (Burt, 1936), having a narrow proximal end and sharply upturned distal end (the baculum of *C. hispidus* is unique in possessing an ornate, trifid tip). Head of spermatozoa resembling elongated isosceles triangle with acute, unrounded vertices. Vesicular glands round or bulb shaped, yellow to gray in color (pinkish in fresh specimens).

INCLUDED TAXA.— *Chaetodipus anthonyi, C. arenarius, C. artus, C. baileyi, C. californicus, C. dalquesti, C. fallax, C. formosus, C. goldmani, C. hispidus, C. intermedius, C. lineatus, C. nelsoni, C. penicillatus, C. pernix, C. spinatus. Chaetodipus anthonyi* Osgood 1900 is most likely an island race of *C. fallax* Merriam 1889 (J. L. Patton, pers. comm.). The specific status of *C. lineatus* Dalquest 1951 is dubious (Patton et al. 1981), and further study is necessary to confirm the validity of *C. dalquesti* Roth 1976, which has a karyotype identical to *C. arenarius* Merriam 1894 (J. C. Hafner and M. S. Hafner, unpubl. ms.). According to Patton et al. (1981), no strongly delineated species groupings are apparent within *Chaetodipus*. However, *C. hispidus* is biochemically divergent from other members of the group.

COMMENTS.— Extreme evolutionary conservatism in exomorphology in the genera *Perognathus* and *Chaetodipus* belies their long history of evolutionary independence as documented by fossil (Wood 1935) and biochemical evidence (Sarich 1975, Patton et al. 1981, M. S. Hafner 1982). M. S. Hafner (1982) has shown that the genetic distance between *Perognathus* and *Chaetodipus* exceeds that measured between *Liomys* and *Heteromys* and approaches that measured between *Dipodomys* and *Microdipodops*. Taxonomic consistency within the Heteromyidae demands that the high degree of chromosomal, anatomical, and biochemical differentiation between *Perognathus* and *Chaetodipus* be recognized at the generic level.

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DESERT RODENT ADAPTATION AND COMMUNITY STRUCTURE[1]

Michael A. Mares[2]

ABSTRACT.— Desert rodent communities are compared for evidence of convergent evolution at various levels of organization, including the systemic (physiological, anatomical, etc.), autecological, and synecological. Convergence is quite pronounced at the systemic level, less pronounced at the autecological level, and even less detectable at the synecological level. This is not to imply that community convergence does not occur, but rather that our current abilities to quantify and detect convergence at the community level are rudimentary—and our data base is still far from adequate to the task of rigorously comparing community attributes. Most research on the ecology, behavior, physiology, and community structure of desert rodents has been conducted on North American species inhabiting deserts of the United States. The patterns of species coexistence that have been elucidated in these deserts are often presumed to apply in other deserts of the world. It has become apparent in recent years, however, that the complex North American desert system is unique in many ways, perhaps especially in the biogeographic history of its habitats and faunas, from most of the other deserts of the world. The North American deserts offer an unusually diverse fauna of desert rodents (both alpha and beta diversity are high) which evidences patterns of distribution and coexistence that excite biologists working with the mechanisms of competitive interactions. Similar studies carried out in other deserts might very well lead to a different set of ideas concerning the ways in which desert rodents manage to coexist and how desert communities develop over time. The present paper is an attempt to compare community structure and development as well as patterns of coexistence among the various faunas of desert rodents of the world. Although data are sketchy for many areas, sufficient information is available to allow a preliminary comparison of methods of adaptation and coexistence to be made.

Research on desert rodents began over a century ago in the United States. The earliest studies examining desert rodents were those of Coues (e.g., 1868), Coues and Allen (1877), and C. Hart Merriam and his team of investigators from the old Biological Survey. In addition to the taxonomic investigations of Merriam himself (e.g., Merriam 1889) and those of his subordinates (e.g., Osgood 1900, Goldman 1911, Howell 1938), there were other studies by contemporaries of the survey scientists (e.g., Grinnell 1932, Benson 1933, Blossom 1933, Hall and Dale 1939). After the initial work had formed a rather firm taxonomic foundation, field research entered the stage of natural historical, ecological, and biogeographical studies (e.g., Taylor and Vorhies 1923, Bailey 1931, Benson 1935, Dice and Blossom 1937, Blair 1943, Monson and Kessler 1940, Tappe 1941, Fitch 1948). Although ecological and taxonomic investigations continued during the mid-twentieth century, much research was centered on the physiological adaptations of rodents to arid environments; this research was greatly stimulated by the studies of the Schmidt-Nielsens (see Schmidt-Nielsen 1964, for a review), who showed convincingly that some small mammals were well adapted physiologically to pronounced aridity. Later research has allowed a finer resolution of the mechanisms of physiological adaptation to deserts (e.g., McNab and Morrison 1963, MacMillen 1964a, 1964b, 1972, Hudson 1964a, Chew 1965, Carpenter 1966, Brown 1968, Brown and Bartholomew 1969, Mullen 1971, Abbott 1971, Whitford and Conley 1971, Maxson and Morton 1974, Baudinette 1974).

Within the last 15 years, desert research in the United States has centered on problems dealing with species coexistence. It has long been remarked that the deserts of the United States support a broad diversity of species, but only since the mid-1960s have researchers attempted both to understand the causative agents of this diversity as well as the mechanisms of species coexistence. Earlier

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[2]Stovall Museum, University of Oklahoma, Norman, Oklahoma 73019.

studies of coexistence had examined the possible roles of abiotic factors on species distribution patterns (e.g., Hardy 1945), but later research has focused on the role of interspecific competition as a possible determinant of distributional patterns (see Brown et al. 1979, for a review). Research emphasis over the last decade has centered on the body sizes of coexisting rodent species (e.g., Brown 1973, Brown 1975, Bowers and Brown 1982), the sizes of seeds taken by granivorous rodents (e.g., Brown and Lieberman 1973, Mares and Williams 1977), the distribution of the seed resource in the desert and whether or not clumped seeds are favored by bipedal species (e.g., Reichman and Oberstein 1977, Wondolleck 1978, Price 1978, Hutto 1978, Trombulack and Kenagy 1980), and on the importance of microhabitat selection in maintaining coexistence (e.g., Rosenzweig 1973, 1977, 1979, Rosenzweig et al. 1975, Schroder and Rosenzweig 1975, Lemen and Rosenzweig 1978).

Each of these areas of research is controversial. For example, Lemen (1978) has strongly criticized the proposed seed size–body size relationship, and support for his position can be garnered from Stamp and Ohmart (1978), M'Closkey (1978), and others. Early indications that bipedal rodents are able to travel greater distances more rapidly and at lower energetic costs than quadrupedal species (e.g., Dawson 1976) have been shown to be in error (Thompson et al. 1980), thus casting doubt on the validity of a linchpin in the theory relating locomotor mode (bipedality) to the habit of foraging on widely dispersed seed clumps (see also Frye and Rosenzweig 1980). Evidence for body size differences among coexisting competitors has been challenged by Conner and Simberloff (1979) and Rebar and Conley (in press). Even the basic premise that competition has helped mold desert rodent communities (Brown 1976, Munger and Brown 1981) has been shown to be a hypothesis that is testable only with the greatest difficulty, if it can be unambiguously tested at all (e.g., Rosenzweig 1981).

The many basic studies done in the arid portions of the United States have made this region one of the best studied areas on earth. Since ecologists tend to extrapolate the results of research carried on in one biome to other areas supporting apparently similar ecosystems, it is tempting to believe that as we explain patterns of coexistence or adaptation within the deserts of the United States we will have described these patterns for deserts around the world. As MacArthur (1972:1) noted, "To do science is to search for repeated patterns." In this brief essay I will characterize the patterns of adaptation of desert rodents that have been described largely within the conterminous United States. Realizing full well that "natural selec tion depends for its effectiveness on a series of chances" (Leigh 1971:221), I believe it is important to distinguish between local patterns and those of a global nature. Perhaps all important questions regarding life in deserts can be answered by studying intensively one particular geographic unit—then again, perhaps not. If all deserts are not equal, a very real problem develops in discovering which patterns are truly generalizable.

THE PATTERNS

The first problem that presents itself is that of scale—does one seek patterns at the level of biochemical reactions, organ systems, or communities? The second problem is that of confounding causation. Does bipedality develop, for example, because of intrinsic problems related to integrated locomotor design (e.g., Alexander 1975), or do such seemingly unrelated factors as seed distributions, granivory, predator avoidance, and substrate all play a part in the selection of a particular type of movement? Although it is easy to become overwhelmed by the complexity of desert rodent adaptations, I will limit my analysis to characteristics above the purely biochemical level. This broad brush approach will give an overview of adaptations of desert rodents from the United States and will compare these with rodents from other parts of the world that have also successfully made the transition to desert life. I will in essence be assessing the available literature on desert rodent biology for examples of convergence, "the strongest sort of evidence for the efficacy of selection and for its adaptive orientation of evolution" (Simpson 1953:171).

PHYSIOLOGICAL ADAPTATIONS

Water Balance—North America

Perhaps one of the most widely known traits of small mammals in desert regions is the ability to withstand water deprivation. Schmidt-Nielsen (1964) has provided the most complete summary of the complex adaptations associated with this ability in North American rodents (see also Schmidt-Nielsen 1975, for a discussion of the mechanisms of water conservation in desert rodents). It is clear that withstanding either low free environmental water or high solute loads demands numerous physiological and anatomical specializations. Certainly, the North American Heteromyidae, kangaroo rats and pocket mice, are the most specialized rodents in this regard in the deserts of the United States. Their adaptations include specialized kidneys, elongated renal papillae, long nasal passages for countercurrent heat exchange, and numerous other characteristics that minimize water loss or increase their ability to obtain vegetational water (e.g., Schmidt-Nielsen 1964, Mullen 1971, Kenagy 1973a, Soholt 1975). Similar adaptations, although perhaps not as pronounced, are known to occur in North American cricetines (e.g., Abbott 1971, Andersen 1973), and sciurids (e.g., Hudson 1962, Maxson and Morton 1974). In all these higher taxa, some species are capable of producing fairly concentrated urine, reducing fecal and respiratory water loss, and existing on minimal inputs of free or vegetational water. There is little doubt that the physiological and anatomical adaptations of desert rodents that minimize water loss encompass all the major systems of the organism. For example, Hatton et al. (1972) showed that in desert rodents the cells of that portion of the brain responsible for producing vasopressin (ADH) are multinucleate, a trait that is uncommon in rodents from moist habitats; this trait is very likely related to water retention ability. They examined several species from both New and Old World deserts.

As physiological studies are extended to the arid portions of Mexico, numerous other species will probably be found to be highly adapted for existing in an environment having minimal moisture available for ingestion. Not all rodents inhabiting North American arid areas are desert specialists (e.g., Lee 1963, Andersen 1973, MacMillen and Christopher 1975). Although it is clear that the ability to withstand water deprivation has a strong phylogenetic component (e.g., Hudson and Rummel 1966, Fleming 1977), it can develop readily in species inhabiting nondesertic habitats where water is scarce (e.g., Fisler 1963, MacMillen 1964b).

Water Balance—Other Deserts

Because of the widespread nature of various physiological adaptations among species of the North American fauna, one might expect that similar types of adaptations would develop in other deserts. Despite the complexity of the suite of traits associated with water independence, this does not appear to be a particularly difficult path for evolution to follow. Indeed, water independence has developed among one or more species of rodents from deserts in Australia (e.g., MacMillen and Lee 1969, Baudinette 1972), Asia (Winkelman and Getz 1962), India (e.g., Ghosh 1975), North Africa (e.g., Burns 1956, Kirmiz 1962 for *Jaculus*, but see Ghobrial and Nour 1975), southern Africa (e.g., Christian 1978, 1979), and Peru (Koford 1968). The extensive Monte Desert of Argentina lacks water-independent species, although *Eligmodontia typus*, a cricetine, is well adapted to process high concentrations of sodium chloride (Mares 1977a). Curiously, although Mares (1977b) did encounter a water independent rodent in Argentina (*Calomys musculinus*), it was an inhabitant of the mesic fringes of the desert.

Only a relatively small percentage of the desert rodents of the world has been examined physiologically. Similar adaptations may have developed repeatedly in all deserts of the world. There is some question as to how physiologically specialized the dipodids are (Ghobrial and Nour 1975), but there is little doubt that pronounced adaptations toward aridity have occurred in such disparate families as the Muridae, Dipodidae, Heteromyidae, and Sciuridae. Similar adaptations will probably be found in other families of desert rodents (e.g., Octodontidae, Ctenodactylidae).

The apparent regularity with which physiological adaptations develop is illustrated by their being characteristic not only of granivorous or herbivorous rodents, but of insectivorous-carnivorous rodents (e.g., Whitford and Conley 1971) and small marsupials (e.g., Schmidt-Nielsen and Newsome 1962, MacFarlane 1975, Morton 1980).

Mares (1975a, b, 1976, 1977c) found that not all rodents inhabiting the Monte Desert of Argentina showed pronounced levels of physiological adaptation (see also Meserve 1978). Many species inhabit that region by limiting their activities to relatively mesic microhabitats. In view of the widespread nature of physiological adaptation toward a xeric existence, Mares (1975a, 1976) hypothesized that most of the rodents of the Monte Desert had not reached the region until latest Pliocene, or even Pleistocene, times. Thus, there had not been sufficient time to evolve the complex group of physiological, anatomical, behavioral, and ecological attributes characteristic of desert life.

Although much work remains to be done on the comparative physiology of desert rodents, pronounced convergence and parallelism have occurred in all deserts as the result of similar regimens of natural selection acting on the colonizing stocks of rodents, regardless of their phylogenetic affinities. This convergence (or parallelism, in some cases) extends to many aspects of the behavioral-physiological-anatomical complex involved in osmotic balance. Similarities are seen in the structure of kidneys (e.g., Hudson 1962, Schmidt-Nielsen 1964, MacMillen and Lee 1969, Abdallah and Tawfik 1969, Fleming 1977), in their urine concentrating abilities, in the ability of the animals to withstand dessication or elevated solute loads, in the elongated nasal passages for heat exchange (this characteristic is in need of comparative studies), and in reduced fecal water loss. Only a few studies have been done examining other avenues of water loss in desert rodents and the adaptations that have evolved to minimize these losses. For example, Kooyman (1963) shows that *Dipodomys merriami* produces a very concentrated milk (thus minimizing lactational water loss). Working with native Australian rodents (*Notomys*, *Pseudomys*), Baverstock et al. (1976) found that these species did not produce exceptionally concentrated milk. A later study to examine whether or not these rodents actually reduced the amount of milk produced during lactation (and thereby reduced water loss) was inconclusive (Baverstock and Elhay 1979). What is really needed is a broadscale study designed to examine all avenues of water loss and to compare these across taxa. Emphasis should be placed initially on genera that are known desert specialists (e.g., *Dipodomys*, *Microdipodops*, *Perognathus*, *Gerbillus*, *Gerbillurus*, *Desmodillus*, *Meriones*, *Dipus*, *Jaculus*, *Allactaga*, etc.), rather than on species that inhabit only the climatic peripheries of deserts. Extreme adaptations will be more easily detected than will the fine shadings of "average" adaptations that have been modified to allow persistence only at the environmental peripheries of deserts.

Other Physiological Adaptations

Various secretory glands are known in desert rodents (e.g., *Meriones* from India, Wallace et al. 1973; *Notomys* from Australia, Watts 1975), but their function is not clear. The products of sebaceous glands in *Dipodomys* may function as other than secretions to aid in the care of the pelage (Quay 1953). Whether or not such glands are widespread among other taxa of desert rodents is unknown, but a comparative assessment of these structures could prove useful toward understanding their function. Eisenberg (1963, 1975) discusses possible olfactory communication in desert rodents, an area of research essentially unexplored in mammals, particularly desert rodents.

Several species of desert rodents in the United States are known to undergo facultative torpor: these species include cricetine rodents, heteromyids, and sciurids (e.g., Hudson 1964, 1967, Tucker 1966, Chew et al. 1967, Brown and Bartholomew 1969, Kenagy 1973b, Reichman and Van De Graff 1973, Reichman and Brown 1979). Presumably such a strategy allows a rodent to remain inactive during periods of resource scarcity; however, periodic torpor is not limited to rodents from xeric habitats (e.g., Hill 1977). It has been hypothesized that desert rodents have a lower metabolic rate (irrespective of torpor) than

species from mesic habitats (e.g., McNab and Morrison 1963). Hayward (1965) questioned this idea, suggesting that stored fat reserves of laboratory animals had led to artificially low metabolic rates. McNab (1968), however, showed that lower metabolic rates for species from xeric habitats (i.e., a North American cricetine, *Peromyscus crinitus,* and the naked mole rat of Africa [(*Heterocephalus glaber*), a bathyergid]) characterized individuals whose body fat levels were well within normal limits. Yousef and Johnson (1975) found a correlation between the lower metabolic rate of various North American desert rodent species (representing three families) and reduced thyroxine secretion rate, suggesting a relationship between thyroid activity and metabolic rate; species from xeric areas had significantly lower rates of thyroid activity than species from mesic habitats.

Energy metabolism in North American desert rodents has been examined in both the laboratory (e.g., Dawson 1955, Yousef et al. 1970) and in the field (e.g., Mullen 1971, Soholt 1973, Kenagy 1973b). There are very few comparative studies available on rodents from other deserts (e.g., Dawson 1976, Thompson et al. 1980).

The fact that many similar adaptations are common among species of the three families of rodents inhabiting North American deserts would lead one to speculate that similar traits might be expected in other faunas. All information to date supports the idea that similar physiological strategies toward aridity have evolved independently and repeatedly throughout the world.

ANATOMICAL ADAPTATIONS

North America

Like physiological adaptations, anatomical specializations for desert life are essentially limitless—depending on one's scale, anatomy can be viewed from the cell to the whole organism. Obviously, an organism evolves as an integrated unit. Thus, viewing any structural specialization without regard to its association with function lends a certain artificiality to the analysis. For example, the supraoptic nuclei described above (Hatton et al. 1972) are cellular specializations leading to gross modifications in brain tissue. These structures play a role in ADH secretion and thereby affect osmotic balance. Nevertheless, from the viewpoint of convergent evolution, it is interesting to know whether similar structures have developed and whether or not they function in similar ways. It is also instructive to learn that similar functions are performed by dissimilar structural adaptations.

Bipedality

Quite often, the term "desert rodent" connotes the genus *Dipodomys.* Much research has centered on species of *Dipodomys,* and kangaroo rats are almost synonymous with "desert adaptation." Nevertheless, kangaroo rats are but one of many genera inhabiting North American deserts. It is probably because of the familiarity of many scientists with *Dipodomys* that most desert rodents are assumed to mirror the adaptations characteristic of that single genus.

Dipodomys are saltatorial and bipedal; they are also granivorous. Because of the association between bipedality and granivory in *Dipodomys,* a causal link between these characteristics has been suggested (e.g., Reichman and Oberstein 1977). It is instructive therefore to examine bipedality in some detail.

Several anatomical studies have examined bipedality in desert rodents (e.g., Hatt 1932, Howell 1932, Klingener 1964, Pinkham 1971, Kaup 1976, Berman 1979). The most extensive study was that of Berman (1979), who compared hind limb osteology and myology in a broad spectrum of desert rodents of the world. She noted that bipedal saltation has arisen independently in five families of rodents: four of these (Heteromyidae, Dipodidae, Pedetidae, and Muridae) have their bipedal species essentially restricted to xeric habitats, whereas the Zapodidae are forest species. Small bipedal saltators have also arisen among extant and extinct marsupials. Berman's analyses led her to conclude that there has been a striking convergence in major musculoskeletal modifications of the hind limb of desert rodents. Similarities in structure are so pronounced that unrelated bipedal species were generally grouped more

closely in multivariate space than were bipedal and quadrupedal members of the same families. Her analyses also showed that there were numerous significant differences among desert rodents in the ways in which bipedality had been achieved—different muscles were elongated or shortened, different mechanical advantages had evolved, and different modifications characterized the feet.

Mares (1980) examined the majority of desert rodent genera in a multivariate analysis of morphoecological characteristics. He noted that bipedality in North American deserts is restricted to granivores (although many obligate granivores in North America are quadrupedal), but when all desert rodents are examined, the supposed link between bipedality and seed eating is not found. There are bipedal granivores (e.g., *Dipodomys, Cardiocranius, Stylodipus,* some *Jaculus*), bipedal herbivores feeding on above-ground plant parts (e.g., *Pedetes,* which also feed in below-ground plant parts, *Pygeretmus, Alactagulus,* some *Allactaga*); bipedal herbivores feeding on below-ground plant parts (some *Allactaga,* some *Jaculus*), bipedal herbivores eating all plant parts (e.g., some *Allactaga,* some *Jaculus, Dipus, Paradipus*); bipedal omnivores (some *Allactaga, Notomys*); and bipedal insectivores (*Salpingotus,* the marsupial *Antechinomys*). In Old World deserts, most obligate granivores are quadrupedal (e.g., *Meriones, Gerbillus, Tatera, Phodopus, Brachiones, Sekeetamys,* etc.). [Information on the diets of the various genera can be found in Lobachev and Khamdamova (1972), Naumov and Lobachev (1975), Happold (1975), Prakash (1975), Watts (1977), and Wassif and Soliman (1979).]

Thus, bipedality, when viewed on a global scale, appears to have little relation to diet; bipedal species fill all major trophic categories. Although research limited to North American desert species might be interpreted as supporting a link between diet and locomotion, I find no evidence to support this hypothesis in other deserts.

In addition to elongated hind limbs, bipedal rodents have shortened forelimbs, prompting suggestions that the freeing of the forelimbs for stuffing food into the cheek pouches was the primary selective force leading to bipedality (Bartholomew and Carey 1954). In view of the large number of bipedal rodents that lack cheek pouches (including all pedetids, dipodids, and zapodids), the many quadrupedal species that have internal cheek pouches (e.g., cricetids, sciurids, etc.), and the presence of cheek pouches in fossorial geomyids and quadrupedal *Perognathus, Liomys,* and *Heteromys,* there is little compelling support for this hypothesis.

One hypothesis that has been invoked to explain bipedality (although it has been tied to the pattern of seed distribution) is differential microhabitat utilization. There is some evidence that bipedal species forage in open areas more frequently than they do under shrubs (e.g., Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Rosenzweig 1973, Brown 1975, Price 1978, Wondolleck 1978); this observation appears to hold for Old World desert species as well (e.g., Naumov and Lobachev 1975), although rigorous quantification of this pattern is needed for all deserts, particularly those of the Old World. Nevertheless, if foraging in open areas is correlated with bipedality, then it is inferential evidence that predator avoidance is a primary selective factor of locomotor mode. This is an old idea (e.g., Howell 1932) that has been restated repeatedly (e.g., Eisenberg 1975, Berman 1979, Mares 1980), but appears to have merit. There is little doubt that predation is an important factor in sparse desert habitats—evolutionarily opting to forage in open microhabitats very likely forces rodents into an entirely new adaptive mode, that of bipedality.

Bipedality is also associated with other anatomical adaptations for predator avoidance (although some of these occur in quadrupedal desert species as well). Enlarged bullae (e.g., Howell 1932, Webster 1962, Lay 1972) or elongated pinnae (e.g., Howell 1932, Eisenberg 1975) are probably adaptations for predator detection (e.g., Legiouix and Wisner 1955, Lay 1974). While it might be supposed that the pinnae function in thermoregulation, as is the case in *Lepus* (Hill and Veghte 1976), in fact, the large pinnae of *Allactaga* are not well vascularized and do not function in heat loss (Hill et al. 1974). Bullar hypertrophy is common in desert rodents throughout the world and in other mammals as well

(e.g., Roig 1969, 1972). Fitzwater and Prakash (1969) described *Meriones* in India responding to the wingbeats of avian predators by escaping into burrows.

Finally, desert rodents are generally very pale colored, usually matching the desert soils (e.g., Harrison 1975, Mares 1976, Cloudsley-Thompson 1979). Most authors concur that cryptic coloration is a response to visual predators (cf., Kaufman 1974). Some bipedal species possess a conspicuous black and white tuft on the tip of the tail (almost all bipeds have long tails with a terminal tuft). Tail tufts often regenerate if the tail has been injured (Howell 1932), and it is likely that the tuft itself functions as a rudder that allows the animal to turn abruptly in midair, particularly since the wind resistance of the tuft acts at the end of a long lever arm. The white tail tuft may well act as a flag to confuse or distract predators during their pursuit and/or as a target for predator attack, thus limiting an attack to a tail that may break quite easily and allow the rodent to escape.

An examination of the morphology of desert rodents leads to the conclusion that convergent evolution of structures that reduce the probability of predation is a major evolutionary force.

BEHAVIORAL AND AUTECOLOGICAL ADAPTATIONS

Behavior

Eisenberg (1975) has done the most comprehensive comparative behavioral work with desert rodents. Most are nocturnal; most live in burrows that are plugged during the day. There are many differences among species in aspects of social behavior, but many species in disjunct deserts have remarkably similar behavioral patterns. Unfortunately, little quantitative behavioral research has been done on other than North American species, and even these have been studied primarily in the laboratory. Studies on Old World species include Nel (1975), Daly and Daly (1975a, b), and Agren (1979).

Some workers have examined activity patterns of desert rodents (e.g., Schwab 1966, Jahoda 1973, Kenagy 1973b, 1976, Lockard and Owings 1974, Rosenzweig 1974, French 1975, Lockard 1978). Data from the Old World are in accord with these observations (Naumov and Lobachev 1975). Generally, most desert species are nocturnal (especially bipedal species), although each desert has one or more species of diurnal rodents (usually these are herbivores, Mares 1980).

Autecology

Smith and Jorgensen (1975) and Conley et al. (1977) review reproductive patterns in North American desert rodents, and French et al. (1975) and Wagner (1981) review demographic patterns of desert species throughout the world. Heteromyids generally have small litters, relatively long life spans, low densities, and reproduce during moist and warm times of the year. A complete review of desert rodent reproduction that includes species from each desert has not been produced. In addition to the above reviews, there is some general information available on reproduction for the following areas: Australia (Smith et al. 1972, Crichton 1974, Watts 1979, Aslin and Watts 1980); USSR (Naumov and Lobachev 1975); North Africa (Poulet 1972, 1978, Khammar et al. 1975, Happold 1975, Ghobrial and Nour 1975, Amirat et al. 1977); southern Africa (Nel 1978, Christian 1979, 1980, Butynski 1979); Iran (Lay 1967, Misonne 1975); India (Prakash 1975); Pakistan (Beg et al. 1977); Chile (Fulk 1975).

Although demography has been studied in some detail in North American desert rodents (see above citations), there have been few extensive demographic studies in either South American deserts or in the Old World. Most of these can be located using those citations referring to reproductive patterns (see also Pearson and Ralph, 1978, for Peru).

Synecology

Perhaps the most exciting area of desert ecology today is that dealing with species interactions and community organization. Brown et al. (1979) and Mares (1980) review much of this literature. Research done in North America would suggest that deserts support elevated levels of both species richness and abundance. However, Mares (1979)

has argued that the deserts of the United States support an unusually high diversity of species due to their unique Pleistocene history of refugial formation wherein allopatric speciation processes were amplified. High relative abundance of rodents in U.S. deserts is probably related to the elevated rainfall characterizing much of the North American desert system (e.g., Brown et al. 1979). Much U.S. desert research has been conducted in the Sonoran Desert of southern Arizona, a region that some consider a semidesert due to its relatively high precipitation (e.g., Eisenberg 1975). This preponderance of research in an extremely productive area may have led to a fairly common belief that deserts often support many small mammals. Actually, most deserts seem to support few species of desert rodents at fairly low levels of abundance (e.g., Mares 1976, 1980, Pearson and Ralph 1978, Morton 1979, Brown 1980, Christian 1980), although some areas seem to be equally as rich in species as portions of the U.S. desert system (e.g., Nel 1978).

Just how desert species manage to coexist is the major area of research at the moment, with competition assumed to be a primary selective force leading to observed patterns of microhabitat selection (Rosenzweig 1979), body size differences (Bowers and Brown 1982), or differential utilization of the seed resource (e.g., Reichman and Oberstein 1977). Little comparative work that might shed light on current controversial points has been done in deserts outside the United States, but certainly habitat specificity is a well-known factor characterizing small mammal communities (e.g., Hubert et al. 1977). Nevertheless, Pearson and Ralph (1978:75) found that small mammal species richness in several desert habitats in Peru could be explained by "evolutionary and zoogeographical accident," rather than habitat selection differences.

One reason that controversy surrounds coexistence studies in deserts is that most research to date has been descriptive and inferential. Studies dealing with seed selectivity by rodents have had to contend with the enormous variability in background seed levels and the methodological difficulties of sampling the seed resource (e.g., Brown et al. 1979). Nevertheless, recent trends have focused on manipulative field experiments (particularly the work of Rosenzweig, Brown, Reichman, and their associates, see above citations). Unfortunately, there has been no parallel movement in experimental research in deserts outside of the United States (or even outside the Sonoran Desert). Theory has far outstripped our empirical data base in desert ecology and experimental data are only beginning to be applied to the many hypotheses that currently abound in the literature.

Recent studies dealing with competition between distantly related taxa promise exciting results if they can be replicated in other deserts (e.g., Brown 1976, Brown and Davidson 1977, Davidson et al. 1980). Mares and Rosenzweig (1978) have done comparative work on this topic and found different patterns in North and South American deserts—they offer an evolutionary explanation for different strategies of granivory in distantly related taxa.

Perhaps the area of research that has been most neglected is that of comparative faunal studies. Mares (1975, 1976, 1980), MacMahon (1976), Mares et al. (1977a, b), Mares and Hulse (1977), Pearson and Ralph (1978), and Morton (1979) have attempted to compare quantitatively diverse desert rodent assemblages. Unfortunately, such studies are hampered by a paucity of data for deserts outside of the United States. As data accrue from current desert research, and as statistical and computational techniques are refined, there should be a great deal of information forthcoming on the ways in which desert rodent communities assemble over time.

CLOSING COMMENTS

If one were to go into an unknown desert region, there are many predictions that could be made concerning the small mammal fauna (particularly the rodent fauna) of the area. Beginning at the most basic levels (anatomy and physiology), we could say that at least some rodents inhabiting the area would exhibit the following adaptations: specialized kidneys (with elongated renal papillae and micro- and macroscopic morphological adaptations) able to concentrate the urine and perhaps process high electrolyte loads; a

counter-current heat exchange system in the nasal region; modified brain cells responsible for ADH secretion; lowered metabolic rate; facultative torpor; ability to exist without free water; minimization of water loss through respiratory, excretory, and defecatory pathways; inflated tympanic bullae or elongated pinnae; bipedality (some species)—with foreshortened forelimbs, long tails, concentrations of muscle mass in proximal limb regions, smaller mechanical advantages for hind limb muscles, elongated distal limb segments, toe reduction, terminal tuft of hair on the tail (often colored black and white); sebaceous glands would be present—sand bathing would be common; dorsal coloration would match the background (pale colors predominating) and countershading would be pronounced; species living on sand would have extremely hirsute hind feet; eyes would be placed dorsally; vibrissae would be abundant and long; white flank markings would be common in bipedal species. There are many other physiological and anatomical traits that would very likely characterize the rodents of this unexplored desert.

Above the systemic level, we could predict the possession of numerous autecological traits: nocturnality would predominate (particularly in bipedal species); both diurnal and nocturnal species would inhabit burrows—these would be plugged during hot periods; bipedal species would differentially forage in open microhabitats, and quadrupedal species would favor closed microhabitats; bipedal forms would occur in flat areas having few rocks; reproduction would be associated with the rainy season, with birth taking place after the rains—populations would peak at this time; territoriality would be pronounced; home ranges would be relatively large; survivorship would be high and fecundity low (e.g., French et al. 1975); population levels would generally be low (although they are often quite high in North American deserts).

Clearly, at the levels of organization from population down to cell, there are numerous predictions that could be made regarding the suite of desert adaptations that would characterize our unknown species, and the lists presented are far from exhaustive. As our level of understanding is refined, more and more similarities in adaptive strategies become evident.

At the community level, however, our predictions become more tenuous. Our hypothetical desert would probably possess a bipedal and/or a quadrupedal granivore; a micro-omnivore; a medium (squirrel)-sized diurnal omnivore; a small insectivore; a bipedal or a fossorial medium-sized herbivore eating below-ground plant parts; and a larger herbivore (rabbit size). Species richness would be low (although high species richness would not be surprising, particularly if the biogeographic history indicated a multiple-refugial system). Bipedality could occur in all trophic categories except the completely fossorial niche. Coexisting species might exhibit regular patterns of body size differences, and microhabitat selection might be the primary mechanism maintaining coexistence. Granivorous rodents might show inverse relationships in abundance and diversity to the abundance and diversity of other granivores, such as ants or birds. Ants and rodents might be mutualistic over evolutionary time; thus, a lack of mammalian seed predators could prove detrimental to ant seed predators.

There is some controversy as to whether or not there is convergence at the community level (Schall and Pianka 1978). Certainly community studies based in morphometrics will have a proportion of their overall similarity explained by morphological convergence. However, since morphology often reflects function, there is strong evidence that pronounced convergence exists above the systemic level of organization. It is equally clear, however, that strong community convergence is yet to be demonstrated when only ecological parameters are utilized in the faunal comparisons. This is not to say that such convergent evolution does not exist, but rather that the influence of history on faunal development and our inability to quantify rigorously the many ecological attributes of a fauna (and to produce highly predictive and quantitative theories) have not yet allowed us to assess the presence or absence of community convergence. Our best work is yet to be done. The complexity of the seemingly simple desert ecosystem has not yielded to inferential science—the ability of experimental science to clarify the many remaining enigmas is yet to be tested.

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MORPHOLOGICAL STRUCTURE AND FUNCTION IN DESERT HETEROMYID RODENTS[1]

Joyce C. Nikolai[2] and Dennis M. Bramble[2]

ABSTRACT.— The functional morphology of desert heteromyid rodents (*Perognathus, Dipodomys, Microdipodops*) is reviewed with considerable new information provided. Specific attention is given to the interaction of anatomical structure and the behavioral and ecological patterns of these rodents.

Inflation of the auditory bullae, although apparently related to improved hearing, is also shown to directly impact the structure and function of the feeding apparatus in desert heteromyids. The mechanics of high speed seed pouching behavior in *Dipodomys deserti* as well as the rates of digging activities of various heteromyids are described using data from slow motion films. The biomechanical consequences of cheek pouch loading for body size and locomotor behavior yield theoretical predictive models concerning interspecific differences in foraging behavior, dietary preference, and microhabitat selection.

Structural modifications of the forelimb associated with use of external cheek pouches reduce the mechanical competence of these limbs for shock absorption during fast quadrupedal running. The relative size of various front and hind limb segments are correlated with quadrupedal, tripodal, and bipedal gaits in heteromyid rodents. The interdependence of body balance, gait, and speed are examined in *Dipodomys merriami*. Factors possibly contributing to the origin of bipedalism in rodents are reviewed and discussed.

The heteromyid rodents of North America offer, potentially, a superb opportunity to examine the importance of morphological design as a determinant of behavioral and ecological patterns under natural conditions. This follows from the considerable range of morphologies found within this circumscribed group as well as the impressive breadth of habitats that its living representatives presently occupy. Perhaps more significant is the fact that heteromyids have recently become the focus of numerous investigations aimed at gaining a better understanding of their biology on multiple levels (e.g., physiology, behavior, ecology, community level interactions). Such studies have begun to offer the kinds of information against which carefully framed hypotheses of a functional-morphologic nature might be critically appraised.

Earlier morphologic studies on heteromyids are primarily descriptive but also contain comments on form-function relationships that are, of necessity, relatively superficial and speculative. Excellent works of this type are Howell's (1932) monograph on the myology and osteology of *Dipodomys*, Hatt's (1932) comparative study of vertebral architecture in saltatorial rodents, and Wood's (1935) important survey of the fossil and Recent Heteromyidae. Berman's (1979) recent multivariate statistical analysis of hind limb bone and muscle morphology in bipedal rodents constitutes a very significant extension beyond the older comparative anatomical works.

Recent functional morphologic studies have been more analytical and experimental, but also of more limited scope. Thus, Pinkham (1976) has investigated the gaits and mechanics of quadrupedal and bipedal running in *Liomys* and *Dipodomys* by combining high speed cinematography with force platform recordings. Using similar techniques, but also including cineradiography, Biewener et al. (1981) have studied the mechanical behavior of the major hindlimb tendons in kangaroo rats. Additional information on the ankle mechanics of *Dipodomys* and the physiological properties of its associated musculature has been presented by Williamson and Frederick (1977). Kaup (1975) has also commented on the biomechanical and evolutionary significance of hind limb anatomy in heteromyids.

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[2]Department of Biology, University of Utah, Salt Lake City, Utah 84112.

Of special note are the investigations of the Websters (see below) on the auditory apparatus of heteromyids. Not only have their studies provided a large body of comparative morphologic data, but they also offer one of the few examples wherein specific hypotheses concerning the adaptive value of a major morphological complex have been tested.

In the present paper we briefly review the existing data on the functional morphology of heteromyid rodents and point out significant gaps in our knowledge. Considerable attention is given the forelimbs and cheek pouches, two structures that have received little attention in the past but whose structural organization may place important constraints on the behavior of these animals. Here and elsewhere we have tried to show how functional morphologic analyses can lead to predictive, testable models concerning the natural behavior and ecology of heteromyid rodents.

Limitations of both time and materials have forced us to restrict the present discussion to "desert heteromyids" of the genera *Perognathus, Dipodomys,* and *Microdipodops.* This is done with full knowledge that a better understanding of the functional anatomy and behavior of the modern heteromyines (*Liomys, Heteromys*) would undoubtedly broaden our appreciation of form-function and evolutionary patterns within perognathine and dipodomyine heteromyids and might well alter some of our conclusions.

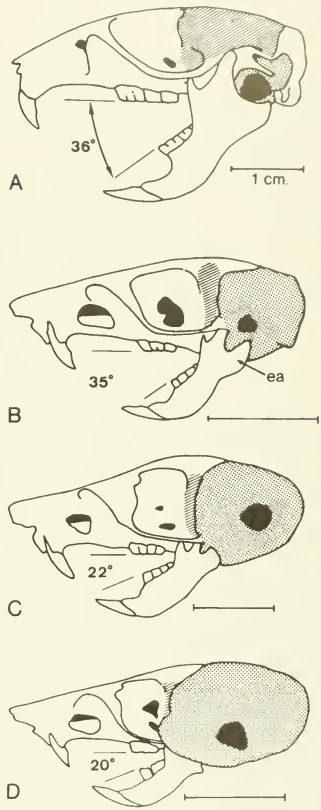

Fig. 1. Influence of auditory specialization on the feeding apparatus of desert heteromyids. A generalized desert rodent, *Neotoma lepida* (A) is compared to *Perognathus formosus* (B), *Dipodomys merriami* (C), and *Microdipodops megacephalus* (D). Inflation of the auditory bulla (stippled) reduces the area of origin of the temporalis musculature (hatched) and also restricts gape by crowding the mandible from behind. The specialized everted angle (ea) of the mandible reduces the impact of bullar inflation in heteromyids. Maximum gape between the cheek teeth (but not incisors) in *Perognathus* (35°) is about equal to that in *Neotoma* (36°), but extreme middle ear hypertrophy has severely reduced gape in *Dipodomys* and *Microdipodops.* All skulls drawn to same length.

SKULL AND NECK MORPHOLOGY

Skull

The most striking cranial feature of desert heteromyids and that which has received the most attention is the enlarged middle ear chambers or auditory bullae. The auditory bullae are moderately inflated in *Perognathus,* but grossly so in both *Dipodomys* and *Microdipodops* (Fig. 1). Relative to overall head size, the middle ear chambers achieve their greatest volume in the latter genus (Webster 1961). Detailed comparative morphologic data on the auditory region of heteromyids have been provided by Webster and Webster (1975, 1977, 1980).

The innovative studies of the Websters and their collaborators have gradually revealed the functional and probable adaptive significance of the modified ears of desert hetero-

myids. Auditory specializations in these rodents, and in certain Old World desert species (Lay 1972), improve the detection of relatively low frequency sound, especially in the 1–3 KHz range. Selective sensitivity to these frequencies has been established on the basis of physiological (Ruppert and Moushegian 1970, Vernon et al. 1971, Webster and Strother 1972, Webster and Webster 1972) and behavioral experiments (Webster and Webster 1972). A suite of structural features appear to be responsible for increased sensitivity to low frequency sound by lowering impedance and, hence, increasing the transmission of such sound from the external to inner ear. Among these features are: (1) a relatively large, compliant tympanic membrane; (2) a small, low-mass, high-leverage ossicular chain; and (3) an enlarged middle ear chamber. The latter feature is apparently a compensatory adjustment that reduces middle ear damping of the large ear drum (Legouix et al. 1954, Webster 1962, Wisner et al. 1954). Experimental reduction of middle ear volume in kangaroo rats significantly reduces sensitivity to low frequency sound (Webster 1961, Webster and Webster 1972, 1980). Certain structural modifications of the inner ear (Webster 1961, Webster and Stack 1968) and related areas of the brain (Webster et al. 1968) may also reflect selective sensitivity to low frequency sound in *Dipodomys*.

How the specialized ears of kangaroo rats might contribute to individual fitness has also been examined. Captive kangaroo rats (*D. merriami*) were tested to see how effectively and by what means they avoided the attacks of owls and rattlesnakes (Webster 1962, Webster and Webster 1971). Animals with unimpaired hearing were usually able to avoid capture by these predators even in total darkness or when blinded. Those with impaired hearing (i.e., artificially reduced middle ear volumes) could also avoid attack, but only when there was sufficient light to see the movements of the predator. Blind kangaroo rats with impaired hearing could not escape predation. A comparison of mortality rates between *Dipodomys* with normal and impaired hearing under field conditions suggests higher mortality among impaired animals, especially during dark of the moon intervals (Webster and Webster 1971). It is presumed that mortality was due chiefly to higher rates of predation upon kangaroo rats whose ability to detect low frequency sound had been reduced. Laboratory recordings indicate that the predatory strikes of both owls and rattlesnakes produce significant sound in the 1–3 KHz range (Webster 1962). In sum, the available data strongly imply that the specialized auditory apparatus of desert heteromyids is indeed adaptive, and that it may confer its greatest advantage on individuals foraging under conditions of dim illumination.

There has been little functional analysis of the feeding mechanism of heteromyid rodents. Most studies have been concerned with dental morphology as it relates to systematics and the identification of fossil materials (Lindsay 1972, Shotwell 1967, Wood 1935). The cheek teeth of modern desert heteromyids are relatively simple and lophodont. In *Dipodomys* the cheek teeth are hypsodont and rootless. Enamel is confined to the ante rior and posterior faces, a condition paralleled in the Geomyidae (Wood 1937). The mandible tends to be small (relative to head size) in all living heteromyids, but is markedly so in *Dipodomys* and *Microdipodops*. The smallness of the mandible causes it to be rather severely underslung. This position, together with the dorsal location of the eyes (Howell 1932), assures that the movements of the hands during feeding and pouching behavior are kept well below eye level.

Inflation of the middle ear has impinged directly on the masticatory apparatus by (1) forcing a reduction of the temporalis musculature and (2) crowding the mandible from behind, thereby placing serious limitations on gape. The latter problem has been partially circumvented by the development of an everted angular process. Reorientation of the angular process delays its contact with the undersurface of the bulla as the jaw is opened (depressed). This permits a wider gape than would otherwise be possible. Even so, middle ear inflation restricts gape in all desert heteromyids, but most especially in *Dipodomys* and *Microdipodops* (Fig. 1). A restriction in gape will limit the size of resistant food items that an animal can effectively gnaw. Exactly how restructuring of the posterior region of

the lower jaw has influenced other biomechanically important descriptors of masticatory function (e.g., force, rate, and direction of mandibular movements; organization of adductor musculature) is unknown at this time.

Another prominent feature of the cranium of desert heteromyids is the strongly projecting, tubular nasal region. The nasal passage is occupied by closely spaced turbinate bones. The length of the nasal passage as well as the diameter of its individual air channels are presumably important to the water conserving, counter-current heat exchanger possessed by *Dipodomys* (Jackson and Schmidt-Nielsen 1964, Schmidt-Nielsen et al. 1970). The relative development of the nasal region in desert heteromyids as regards their ability to detect subsurface accumulations of seeds (Frye and Rosenzweig 1980, Reichman 1979) merits examination.

The interior of the skull of desert heteromyids exhibits at least one obvious specialization. Well-formed bony partitions project medially from the otic capsules into the space between the cerebral and cerebellar lobes of the brain. They are pronounced in *Dipodomys* and *Microdipodops*, but more modestly developed in *Perognathus*. These partitions, which tend to compartmentalize the brain within the cranium, appear to be true tentorial ossifications. As such they cannot be directly related to inflation of the middle ear. Whether or not such structures have any functional connection with the rapid accelerations of the head and brain experienced by bipedal heteromyids invites investigation.

Neck

Hatt (1932) described vertebral modifications that seem to be associated with bipedal saltation in rodents. Among them are: (1) extreme shortening and compaction of the cervical region, (2) pronounced dorsiflexion (= hyperextension) of the neck, and (3) partial or complete fusion of the anterior (excluding atlas) neck vertebrae. These specializations are common to both Old World (Dipodidae, Pedetidae) and New World (Heteromyidae) bipeds, but are most pronounced in *Jaculus*, *Dipus*, and *Dipodomys* (Hatt 1932).

Reorganization of the cervical region appears to accomplish two functions. First, it helps to foreshorten the anterior trunk, which tends to keep the distribution of body mass rearward. This eases the problem of counterbalancing the body over the hind limbs when in the bipedal pose. Secondly, modifications of the neck increase its mechanical strength and stability while the animal is involved in bipedal hopping. Hatt (1932) argued that neck specialization was required to reduce bobbing of the head. This idea has been accepted by many subsequent workers, but has never been experimentally verified. Hatt himself offered no functional analysis in support of his model.

CHEEK POUCHES

Structure, Use and Significance

External, fur-lined cheek pouches are a unique, derived feature of geomyoid rodents. They are not present at birth, but rapidly develop during the early postnatal period from infoldings of the facial skin (Lackey 1967). In the adult, each pouch opens externally via a long slitlike aperture. Internally, the pouch continues rearward to an expanded base that rests over the shoulder blades. Geomyids can voluntarily evert the pouches for cleaning (Vaughan 1966) and perhaps in some cases to help empty their contents. In both geomyids and heteromyids superficial facial musculature is used to control the tension in the skin guarding the entrance to the pouch and a special "pouch muscle," derived (in part) from the trapezius complex, returns the everted pouch to its normal position (Chiasson 1954, Hill 1937, Howell 1932).

Two fairly obvious advantages of cheek pouches are (1) reducing the time required to gather food on the surface, hence reducing exposure to predators and, (2) reducing the locomotor energy expended in foraging, by allowing an animal to collect and store a given amount of food with fewer trips. The latter may be especially important where food resources tend to be widely scattered (Reichman and Oberstein 1977). Another possible advantage of external cheek pouches to desert heteromyids is that of water conservation. Unlike internal cheek pouches (independently evolved in many mammalian

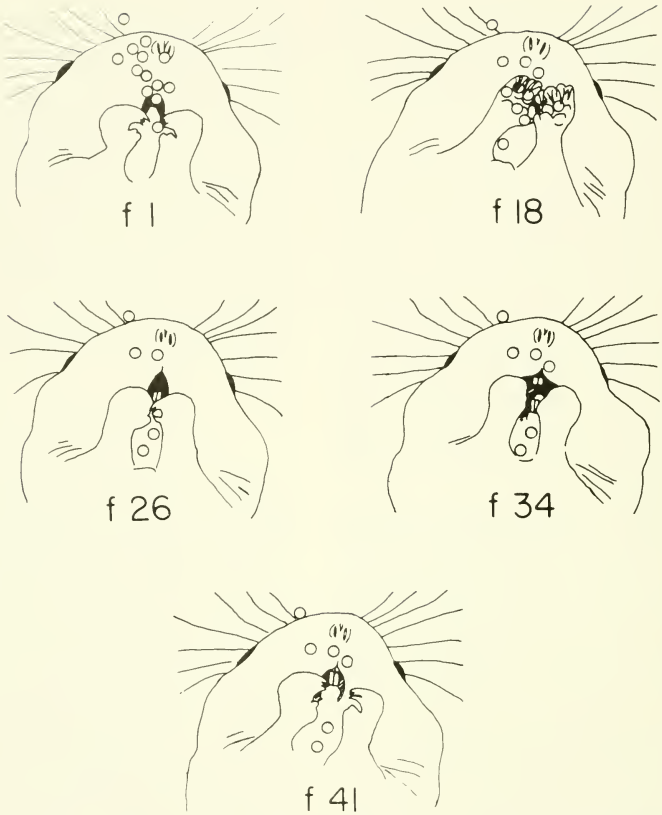

Fig. 2. Seed pouching in *Dipodomys deserti*. Tracings of representative frames of slow motion film (200 fps) of *D. deserti* illustrate one complete pouching cycle. Millet seed and the kangaroo rat were placed on a glass surface and filmed from below using a mirror. See text for details.

groups; Murray 1975), the fur-lined pouches of heteromyids effectively isolate dry food materials from the moist mucous membranes of the oral chamber. This prevents absorption of water by the food—water that would be lost to the environment when the food was later cached in the ground. Given the critical problems of water balance faced by desert heteromyids (see MacMillen, this volume), the savings potentially attributable to the use of external cheek pouches may be significant.

Previous workers have noted the speed with which desert heteromyids are able to collect and pouch seeds. Nonetheless, the speed of food handling has been quantified only for the time required by *Perognathus* and *Dipodomys* to husk relatively large seeds (Rosenzweig and Sterner 1970). Some insight into the much more rapid process of pouching has been gained recently from high speed films made of an adult female *D. deserti* collecting unhusked millet and sunflower seed from a glass plate.

High speed pouching in *D. deserti* is highly stereotyped. Figure 2 illustrates selected stages in a typical pouching cycle. Both forelimbs move in synchrony and each limb serves only the ipsilateral pouch. At the initiation of the cycle the limbs are thrust forward and downward toward the seeds as the

hands are simultaneously pronated and opened (Fig. 2: F1–F18). The hands are next closed on the seeds and then retracted toward the mouth (Fig. 2: F18–F26). During the retraction stage the hands are supinated so that the palms face directly upward by the time the hands are below the pouch openings (Fig. 2: F26). The forearms are next elevated such that the fingers penetrate into the extreme anterior end of the openings (Fig. 2: F34). In the final stage of the pouching maneuver, the food is released and the hands are pulled downward away from the mouth ready to commence the next cycle (Fig. 2: F41).

The cine records reveal two additional aspects of the pouching mechanism. First, the reduced first digit (= thumb) is used in semi-opposable fashion. This small digit is held beside the large palmar tubercle and, hence, opposes the remaining fingers (II–V) when grasping food items. Second, the pouching cycle of the forelimbs is attended by synchronized mandibular movements. Each time the hands are drawn toward the pouches, the mandible is pulled rearward. Opening of the mouth at this time appears to allow the hands to enter the pouches while the pouch entrances are themselves kept tightly closed to prevent the exit of seeds already within them. The backward movement of the lower jaw appears to induce tension in the lips which, during pouching, are pursed behind the incisor teeth. The tension causes the lips to draw inward away from the lateral walls of the pouch, thereby creating small gaps at the extreme front end of the pouch into which the hands are thrust. As the mandible moves forward (= jaw closing), the pouch openings are again closed and the hands withdrawn.

Seed pouching in *D. deserti* is rapid, with a mean pouching rate for millet seed of 9.01 cycles per second. Some cycles are executed in less than 90 milliseconds. Depending on how many seeds are grasped in each hand, pouching rates range between approximately 20 and 60 millet seeds sec^{-1}. Though the conditions under which these values were obtained are admittedly artificial, they indicate the potential speed and efficiency of the pouching mechanism of *Dipodomys* under favorable circumstances. Unfortunately, comparable data are not yet available for *Perognathus* and *Microdipodops*.

Our films also hint at the mechanism by which kangaroo rats distinguish between edible and inedible items during high speed pouching. In no instance were unacceptable items recognized and rejected while in the hands. The films suggest that pouch items are quickly tested for suitability before pouching by being pinched between the pursed lips or, in the case of large items (sunflower seeds), between the lower incisors and the lips. Pinching of the food appears to be another consequence of the coupling of mandibular motion to forelimb movement. Those items judged unacceptable by the "pinch test" are then retrieved from the front end of the pouch and thrown backward beneath the animal.

Mechanical Constraints

Pouch size is important in that it establishes the maximum quantity of food material that a heteromyid can transport. The relationship between pouch size and body size might therefore influence the foraging tactics of desert heteromyid rodents. To examine this issue, Morton et al. (1980) have recently measured mean pouch volume in 13 populations representing 11 species of heteromyids and one species of geomyid (*Thomomys bottae*). Volume was determined by filling the pouches of dead animals to near capacity with material of uniform size and density (unhusked millet seed; 0.71 g cm^{-3}) and then converting the weight of the contents to volume. These authors predicted that pouch volume (V_P) should scale as body mass (Mb) raised to the first power ($Mb^{1.0}$) using the standard allometric expression ($y = ax^b$). They argued that if this relationship existed, larger heteromyids could collect and transport more food relative to actual metabolic need (α $Mb^{0.75}$) than small heteromyids. However, their prediction for the scaling of pouch volume to body size was realized (V_P α $Mb^{1.043}$) only when the sample was limited to small heteromyids (< 30 g) and the much larger pocket gopher (116 g). They found no statistically significant relationship between pouch volume and body size within the genus *Dipodomys*. To explain this finding, Morton

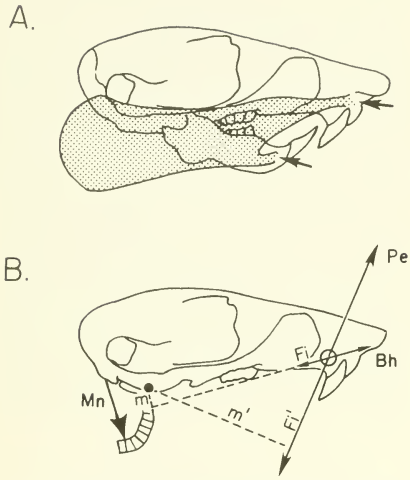

Fig. 3. A, Stylized illustration of anatomical relationship of external cheek pouch to head skeleton in *Dipodomys*. Principal anchorage of pouch (and contents) to skeleton is to rostrum and mandible at points indicated by arrows. B, Simplified diagram of mechanics of head stability under two locomotor conditions. In smooth bipedal hopping, acceleration of the head relative to pouch contents (Bh) is slight and has a largely horizontal trajectory. The opposing inertial reaction force (Fi) of the pouch load is also small and passes close to the fulcrum (dot) at the cranio-cervical joint. Accordingly, the force has a short moment arm (m) about the head-neck joint. The resultant destabilizing torque (= Fi•m) (clockwise) is likewise small and is opposed by a counterclockwise torque supplied by the neck musculature (Mn). A much larger and more vertically oriented inertial reaction force (Fi′) results from the rapid, steep trajectory of the head (Pe) as is occasionally seen during predator escape. This force has a large moment arm (m′) about the fulcrum and therefore generates a much greater destabilizing torque on the head. See text.

et al. (1980) suggest that either relatively large body size, a preferred diet of high caloric seeds, and/or bipedalism may have released kangaroo rats from normal allometric constraints.

Several factors indicate that pouch volume might not increase as the first power of body mass. First, such a relationship implies the maintenance of geometric similarity, a pattern rarely encountered within a phylogenetic series encompassing an appreciable range of body size (Gould 1966). Second, in the analysis of Morton et al. an isometric relationship between pouch volume and body mass was produced only when *Thomomys* was included, an inclusion that seems unwarranted in view of its systematic position, body plan, locomotor mechanics, and foraging behavior. Finally, biomechanical constraints may prohibit the maintenance of geometric similarity between pouch volume and body size in heteromyid rodents.

All desert heteromyids use some form of saltation, quadrupedal (*Perognathus*) or bipedal (*Dipodomys*, *Microdipodops*), when moving fast. Balance and stability are biomechanical problems that may increase with speed, especially if the gait involves rapid changes of direction. Several distinctive structural modifications of the neck in bipedal heteromyids appear to relate to the special problem of head stability (see earlier). The mass of the head will be a critical determinant of any stabilization mechanism. Moreover, the head must enter into any consideration of body balance (particularly in bipeds) since it is among the largest and heaviest structures forward of the point of limb support.

Anatomically, the cheek pouches are anchored to the head skeleton (Fig. 3A). At rest, much of the load provided by the pouch contents rests upon the back. However, during forward acceleration of the body, the load will tend to shift backward due to inertial lag. An appreciable fraction of this inertial force will act on the head. If the mouth is held closed, most of the inertial force acting on the mandible will be relayed to the rostrum of the skull through the masseter muscle. The inertial load from each cheek pouch can, for mechanical purposes, be regarded as concentrated at a single point well out on the rostrum (Fig. 3B).

The same figure illustrates the functional consequences of cheek pouch load under two locomotor conditions. In slow, smooth bipedal hopping, accelerational forces are small and the resultant inertial force is nearly horizontal. The line of action of this force passes close to the cervicocranial joint, thereby yielding only a modest destabilizing torque on the cranium. In the second case, that of escape from a predator, the animal accelerates very rapidly in a more vertical trajectory, similar to that recorded for *Dipodomys merriami* when avoiding the strike of snakes

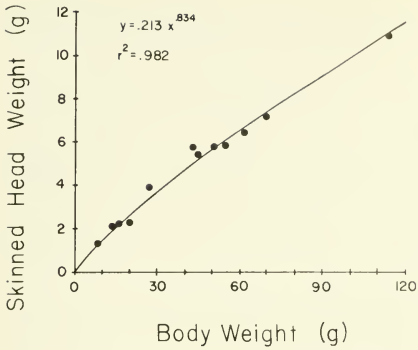

Fig. 4. Relationship of head mass to body mass in desert heteromyids (*Perognathus*, *Dipodomys*, *Microdipodops*). Negative allometry results in relatively heavier heads in smaller species. Restriction of the data set to bipedal forms gives the equation: $Mh = .270 \times Mb^{.776}$; $r^2 = .984$; $P < .001$, where Mh is skinned head mass.

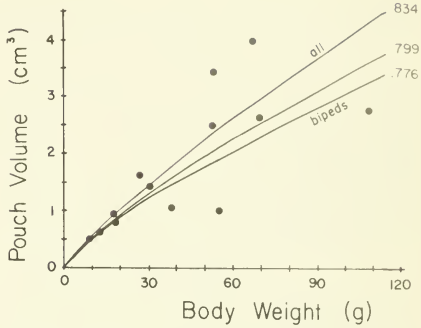

Fig. 5. Allometric relationship between pouch volume and body mass in desert heteromyids. Best least squares regression of standard allometric expression ($y = ax^b$) shows that pouch volume scales with strong negative allometry ($b = .799$) on body mass [$V_P = .085\ Mb^{.799}$; $r^2 = .739$; $P < .001$]. The scaling of pouch volume is fairly closely predicted by the scaling of head mass to body mass in all desert heteromyids (all; $b = .834$) or just in bipedal forms (bipeds; $b = .776$). Taxa are identified in Fig. 6. Data from Morton et al. 1980.

(Webster 1961, Webster and Webster 1972) or for *Microdipodops* when escaping from another animal (O'Farrell and Blaustein 1974). Here the inertial force is much larger and passes further from the fulcrum between head and neck. Consequently, the destabilizing moment is much greater. The same inertial forces will also generate mechanical problems relative to body balance about the point of limb support in the bipedal pose.

Pouch loading can therefore have significant consequences for head stability and body equilibrium in heteromyid rodents, particularly during rapid escape maneuvers. This fact alone might preclude a simple isometric relationship between pouch volume (which is proportional to load) and body size. Because pouch load is coupled to the head, the manner in which head mass changes with body size might well reflect mechanical constraints that, in turn, influence the scaling of pouch size in desert heteromyids. Both head stability and body balance must be controlled even when the pouches are empty. Head mass scales as approximately $Mb^{0.834}$ in desert heteromyids and as $Mb^{0.766}$ when the data are limited to bipedal forms (*Dipodomys*, *Microdipodops*) (Fig. 4). Hence, larger heteromyids have relatively lighter heads than small ones.

If, in desert heteromyids, the scaling of head mass is associated with a constant level of function (i.e., stability and balance) with the pouches unloaded, then continued functional equivalence will require that pouch load and pouch volume scale in the same manner as head mass ($= Mb^{0.83}$) if the density of the pouched material remains constant. The available data show that pouch volume goes as $Mb^{0.799}$ for desert heteromyids (Fig. 5). This is close to the prediction of pouch volume made on the basis of head mass (Fig. 4), and far from the original expectation of isometry ($Mb^{1.00}$; Morton et al. 1980).

Ecological and Behavioral Implications

The present model predicts that head mass and pouch load should scale isometrically with each other, but with negative allometry as regards body weight. The ratio of pouch load to head mass should remain fixed in desert heteromyids regardless of body size. The actual relationship is shown in Figure 6. If the model were correct, all points should fall on the horizontal line indicating isometry. Small heteromyids, in fact, cluster near the expected value except *Perognathus bailey*i. However, the data for *Dipodomys* are scattered widely above and below the reference line. But the model predicts the relationship between *pouch load and head mass*

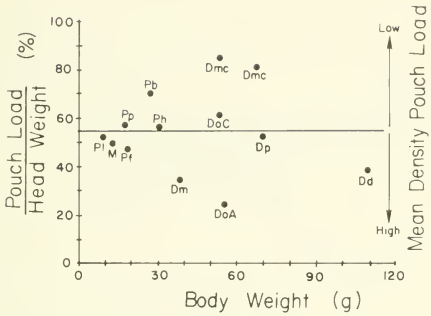

Fig. 6. Maximum pouch load as percent of skinned head mass in desert heteromyids of different body size. Load is based on maximal filling of pouches with unhusked millet seed. Data are derived from Morton et al. (1980). Each point is mean value for sample of that species or population. Maintenance of mechanical similarity among species requires that pouch load scale isometrically with head mass as indicated by horizontal line. Departure of points from this line may reflect natural differences in foraging behavior and dietary preference among the taxa, particularly as regards the average density (mass/volume) of the pouch load. See text for discussion. Taxa are: Dd, *Dipodomys deserti*; Dm, *D. merriami*; Dmc, *D. microps*; DoA, *D. ordii* (Arizona); DoC, *D. ordii* (California); Dp, *D. panamintinus*; M, *Microdipodops megacephalus*; Pb, *Perognathus baileyi*; Pf, *P. formosus*; Ph, *P. hispidus*; Pl, *P. longimembris*; Pp, *P. parvus*.

only. It can predict pouch volume only if the physical properties (size, shape, density) of the food filling the pouches are the same for all species. This requires, in effect, that all desert heteromyids utilize identical food resources, a requirement clearly at odds with the actual foraging patterns of these animals (see Reichman, this volume).

Because the data illustrated in Figure 6 were obtained by filling the pouches with a uniform material (millet seed), the scatter of the points directly reflects interspecific or populational differences in relative pouch volume. Those taxa above the reference line have relatively large pouches; those below, much smaller pouch volumes. To conform to the model, species with larger pouches must, in nature, fill them with lighter materials than those below the reference line. What Figure 6 offers, then, is a graphical indication of qualitative and quantitative differences in pouch contents. It suggests, for example, that *Perognathus baileyi* typically harvests and transports relatively lighter food items than the other *Perognathus* included in the sample. Similarly, the high degree of scatter within the genus *Dipodomys* should reflect considerably greater diversity in foraging behavior as compared to *Perognathus*. The least dense pouch materials are predicted in *D. microps*, an expectation not inconsistent with its tendency toward herbivory (Kenagy 1972, 1973, Csuti 1979). By contrast, the maximum pouch loads of *D. merriami* and *D. deserti* should average 2.48 and 2.24 times denser than those of *D. microps*. Still more intriguing is the apparent disparity between the physical properties of the pouch materials in California and Arizona populations of *Dipodomys ordii*.

Several factors will determine the mean density of the pouch load. Included are the size, shape, and actual density of the individual food particles. Small, round, dense items (certain seeds) should yield the densest pouch loads. Larger or more irregularly shaped items of the same particle density will produce a lower density load. Bulky vegetation (including whole fruiting heads of flowers) will give still lower densities, because it does not pack tightly. Food handling behavior could also affect pouch load. For example, a rodent that husks seeds prior to pouching them is creating a much denser pouch load.

Two additional behavioral-ecological predictions derive from a consideration of biomechanical constraints imposed by pouch loading. The first is that the right and left cheek pouches should be symmetrically loaded. This follows from the fact that mechanical stability of the head will be most easily maintained if the weight is equally distributed, thereby providing for some measure of counterbalancing. Symmetrical pouch loading should be most critical to bipedal forms, less important in quadrupedal saltators (*Perognathus*) and of no consequence to fossorial geomyids.

Next, maximal filling of the pouches in desert heteromyids ought to be on the basis of weight and not volume. As is explained below, maximum pouch load is probably established with regard to predation risk. If the "full pouch" threshold were indeed triggered by weight and not volume, a kangaroo rat harvesting especially dense items might return to its burrow or caching area with the

pouches only partially filled. When gathering very light items, the same animal could conceivably fill its pouches to their volumetric limit without ever reaching the load limit.

The proposed connection between cheek pouch loading and predation again rests with simple biophysical considerations. Suppose a kangaroo rat is sifting the soil for seeds. If suddenly attacked, it will attempt to leap up and away to avoid capture. The rate with which the rodent accelerates away from the attacker is determined by the simple Newtonian relationship, $a = F/m$, where a is acceleration, m is the mass of the animal and F is the propulsive force applied to the ground. If F is the maximum force the rodent is capable of generating, it follows that maximum acceleration, maximum take-off velocity and maximum distance covered by the leap (holding take-off angle constant and ignoring aerodynamic drag) will decline in direct proportion to cheek pouch load. Hence, the acceleration of a loaded heteromyid is given by the expression: $a = F/(Mb + M_P)$, where Mb is the mass of the body and M_P is the additional mass added by the pouch contents.

If heteromyids load their cheek pouches in constant proportion to head mass (as argued above), the potential consequences for predator escape are easily ascertained. Among desert heteromyids the relative loss of acceleration due to maximal cheek pouch loading should scale as $Mb^{0.83}$—i.e., as head to body mass. Small species will therefore be more adversely affected than large ones. All other things being equal, small heteromyids should be at greater risk from predation when transporting a full load in the pouches. If, for example, a 110 g *Dipodomys* and a 10 g *Perognathus* were both carrying pouch loads equaling 50 percent of head mass, the maximum rate of acceleration of the kangaroo rat would be lowered by 4.6 percent and the pocket mouse would suffer a 6.8 percent loss of function.

The ability of heteromyids to accelerate sharply is undoubtedly a key element in their defense against predators. Although vertical leaps and erratic changes of direction have been recorded for *D. merriami* (Webster 1962), during predator escape there is some evidence that *D. microps* run directly to a burrow or bush when suddenly startled (Quinn 1983). Assuming that predation is a major factor in habitat selection, it is possible, therefore, that the relative effect of pouch load could influence their choice of microhabitat. Small species might be expected to forage preferentially in areas of close cover if exposure to predation and the distance to the nearest protection increases with the "openness" of the habitat. Within both *Perognathus* and *Dipodomys* the largest species should be able to successfully operate in the more open habitats since they are less handicapped by pouch load.

Strictly speaking, the model predicts differences in microhabitat availability, not their actual use. On biomechanical grounds large heteromyids are not necessarily excluded from areas of relatively close cover, but small species should be excluded from open areas. The range of microhabitats potentially exploited by heteromyids, with regard to the mechanics of predator escape, ought therefore to expand with increasing body size. This raises an interesting question with respect to *Microdipodops*, which is bipedal but also in the size range of *Perognathus*. At present there are insufficient data to compare the foraging tactics of *Microdipodops* with that of the smallest (but substantially larger) kangaroo rats (e.g., *D. merriami, ordii*). Theoretically, pouch loading should place a kangaroo mouse at greater risk in open habitats than even the smallest *Dipodomys*.

Unfortunately, we do not yet know how acceleration potential actually scales with body size in heteromyids nor how this potential compares with the speed of attack by natural predators. These and other confounding factors might conceivably alter expectations of habitat restriction drawn from simple biomechanical considerations. Still, the present model based on mechanical constraints offers straightforward predictions that are subject to testing.

FORELIMBS

The forelimbs of desert heteromyids have several functional demands placed upon them. Foremost among these are food handling and digging. They are also involved in body support and propulsion in *Perognathus*

at all speeds, but only at comparatively slow rates of travel in *Dipodomys* and *Microdipodops*.

Digging Activities

Nearly all small desert mammals live below ground at least part of the day, where soil acts as a buffer against temperature extremes and desiccation. Below 30 cm of sandy soil, soil temperature remains relatively constant throughout the day, despite fluctuations of 20 C or more at the soil surface (Kenagy 1973, Larcher 1980). Uniform temperatures throughout the year, however, are not achieved except at much greater soil depths. Most desert heteromyids dig elaborate multibranched burrow systems (Anderson and Allred 1964, Culbertson 1946, Quinn 1983, Vorhies and Taylor 1922) where they spend the day. Typically, they emerge above ground to forage only after sunset.

Dipodomys burrows tend to have multiple entrances, which are sometimes plugged during the day (Hawbecker 1940, Tappe 1941, Vorhies and Taylor 1922). They have a maximum depth of 30–75 cm (Anderson and Allred 1964, Culbertson 1946, Vorhies and Taylor 1922). The burrows of *Perognathus* tend to be less branched. Generally they have only one or two entrances and are rather deep, with nest chambers 85–193 cm below the surface (Eisenberg 1963, Kenagy 1973). Little is known about kangaroo mouse (*Microdipodops*) burrow systems, except that those of *M. pallidus* and *M. megacephalus* are short and simple (Eisenberg 1963, O'Farrell and Blaustein 1974), a fact that may minimize the energetic cost of torpor (Kenagy 1973).

The relative digging abilities of heteromyids has been given very little consideration. There is some evidence, however, that species may partition the land available on the basis of soil composition and particle size (Hardy 1945, Hoover 1973). Some species appear to be restricted to soft friable soils, but others are able to use harder, rocky soils. This would suggest that some species may be unable to dig in hard soils. Deynes (1954), however, found that *P. merriami gilvus* and *P. pennicillatus eremicus* were able to dig burrows in heavy clay-loam hard pan, even though they are naturally confined to sandy soils.

Digging Methods

There are three main methods of digging utilized by heteromyid rodents. Very loose soils, such as dry, fine sand are often moved by pulling small piles of soil between the animals' hind feet using both front limbs simultaneously. These motions appear to be very similar to those of the forelimbs during high speed pouching of seeds. When a sufficient pile of soil has accumulated under the body, the hind limbs are used to kick the sand further back. This method of digging is used by *D. merriami* and *D. deserti* during surface foraging and in the initiation of new tunnels.

Soils of intermediate hardness are loosened by scratch digging techniques that employ the front limbs in an alternating pattern. This digging method is employed on the surface when burying seeds and foraging as well as underground when constructing or maintaining tunnel systems (Eisenberg 1963, 1975, Nikolai and Bramble pers. obsers). Soil loosened in this way may be moved with the hind feet by kicking or, when underground, the animal may turn around and push the soil with its forelimbs and chest (Eisenberg 1963). This latter method of transporting soil is invariably used to move soil up a tunnel ramp preparatory to plugging the entrance (Eisenberg 1963, Nikolai and Bramble pers. obsers). The soil is then usually patted into place with rapid alternating hand movements. Slow motion films show the frequency of such movements to be approximately 11.6 cycles per second in *Dipodomys merriami* and 5.5 cps in *Perognathus formosus* when working in damp sand (Table 1).

The third method of digging has been observed only in *Perognathus* on extremely resistant soils. Here the animal uses its incisors

TABLE 1. Digging rates for heteromyids in damp packed sand. See text for details.

Species	BW (g)	Digging (stroke/s)	Patting (stroke/s)
P. longimembris	10.0	4.00	—
P. formosus	21.1	2.55	5.5
D. merriami	42.0	7.58	11.6
D. deserti	115.0	5.27	8.23

to chew through cementlike soils (Deynes 1954). This digging behavior is similar to that seen in the closely related Geomyidae (Hill 1937). It is conceivable that mechanical restrictions on gape (Fig. 1) preclude this type of digging in *Dipodomys* and *Microdipodops*.

Limb Morphology

The forelimbs of *Dipodomys* and *Microdipodops*, like other bipedal rodents, are short compared to the hind limbs (Berman 1979, Howell 1932). Much of the reason for this seems to stem from the strong negative allometry of the hand relative to body size in bipeds as compared to the slight positive allometry in quadrupeds. The humerus is absolutely shorter in bipeds at all body sizes, but its length increases with body size at the same rate as in quadrupedal species (Table 4).

The tiny hands of *Dipodomys* and *Microdipodops* probably reflect specialization for high speed seed handling and pouching. Rapid food handling will, in turn, reduce the time an animal must forage beyond the safety of its burrow. The very high rates at which *D. deserti* pouches seed have already been mentioned. The small hands of the bipedal heteromyids may improve manual dexterity by providing a better fit between hand and small food items. Reduction of the hands may also facilitate high velocity movements of the forearms by reducing the moment of inertia of the distal limb segments. A reduction of mass will permit higher rates of cyclic oscillation without an increase in muscular force (i.e., energy expenditure).

The absolutely higher rates of limb oscillation in *Dipodomys* than in *Perognathus* while digging (Table 1) is somewhat surprising. Normally, maximum limb frequency would be expected to scale negatively on body mass, as does maximum stride frequency while running in quadrupedal mammals (Heglund et al. 1974). The reduced limb mass associated with the relatively smaller hands of *Dipodomys* is, however, unlikely to provide a complete explanation for its more rapid limb movements as compared to pocket mice. We suspect that the faster forelimb movements of *Dipodomys* may also be the product of historical selection for higher rates of food gleening and pouching.

In desert heteromyids each of the four main digits (II–V) bears long, curved but thin claws. The claws are used extensively in burrowing but also appear to serve as winnowing rakes to snag seeds as the hands sift through fine sediment. The reduced first digit has a naillike covering. As suggested above, this finger seems to be semiopposable in *Dipodomys*; from its similar structure, the same function may be expected in *Microdipodops* and *Perognathus*.

The scapula and humerus of the bipedal heteromyids resemble, in several ways, those of highly fossorial mammals. The humerus is relatively short, stout, and wide across the distal epicondyles (Howell 1932). The ratio of epicondylar width to humeral length is about .30–.33 and .33, respectively, in *Dipodomys* and *Microdipodops* as compared to .34–.36 in the pocket gopher, *Thomomys*. The relationship is .23–.29 in *Perognathus*, a value similar to that of generalized quadrupedal rodents (.24–.28) and also close to the figures reported for *Heteromys* (.21) and *Liomys* (.26) (Wood 1935). The wide epicondyles of bipedal heteromyids and other digging mammals are associated with powerful extensor and flexor muscles of the wrist and hand as well as highly developed pronators and supinators of the forearm (Hildebrand 1982). The scapula of all heteromyids and geomyids has a distinct postscapular fossa (Hill 1937, Howell 1932). A similar fossa has been independently evolved in several groups of highly fossorial mammals (e.g., armadillos, badgers, etc.) and is functionally associated with an enlarged teres major muscle (Hildebrand 1982). This structural feature is but one of several that hint that the common ancestor of the Heteromyidae and Geomyidae was more fossorial than the more generalized living geomyoids (*Heteromys, Liomys*) would indicate.

In both heteromyids and geomyids the ability to pronate and supinate the forearm is especially well developed. This ability seems likely to be associated with the maneuvers required (see earlier) to effectively place materials in the cheek pouches. What deserves special notice are the structural specializations that permit such forearm mobility. Unlike most mammals in which pronation and supination involve chiefly long axis rotation of the radius, the movement is accomplished in geomyoid rodents primarily by

long axis rotation of the ulna and radius as a unit. Such exceptional motion of the ulna correlates with an extremely "loose" elbow joint in which the ulna is free to deflect inward and outward. A special check ligament connects the lateral epicondyle of the humerus to the lateral crest of the ulna. It prevents excessive medial deflection of the forearm on the humerus and serves to stabilize the otherwise weak elbow joint when the hand is flexed in the supine position (as in pouching and some digging maneuvers). The ligament cannot, however, strengthen elbow movements when the hand is pronated (palm down), as would be the case in quadrupedal locomotion. This raises the possibility that structural limitations may make bipedalism obligatory for larger desert heteromyids when running at higher speeds. The presence of a specialized elbow mechanism in heteromyids and primitive geomyids (*Thomomys*), together with its absence in selected representatives of other rodent families (i.e., Muridae, Sciuridae, Cricetidae, Zapodidae, Chinchillidae), indicates that the mechanism is derived for rodents but primitive for the Geomyoidea.

HIND LIMBS AND LOCOMOTION

The locomotor repertory of heteromyids can be divided into two major classes: bipedal and quadrupedal. Both bipedal and quadrupedal heteromyids use quadrupedal gaits, such as the walk, half-bound and full-bound during slow progression. These gaits are very similar in their footfall pattern to the gaits used by other quadrupedal rodents (Gambaryan 1974). At higher speeds, however, some heteromyids (*Dipodomys* and *Microdipodops*) employ the bipedal hop, a gait that does not use the front limbs for support. Since much of the thrust of this gait is associated with dorso-ventral oscillation of the vertebral column, the bipedal hop is allied with the gallop as an asymmetrical gait (Badoux 1965, Hatt 1932, Howell 1965).

A question that has plagued researchers for some time is: Why did bipedalism evolve in some heteromyids and not in others? Bipedal locomotion seems certainly to permit greater specialization of the forelimbs for digging and food handling. Several researchers have also suggested that bipedal locomotion is more energetically efficient than quadrupedalism (Dawson 1976, Dawson and Taylor 1973) or that bipedal locomotion is more effective in predator avoidance (Eisenberg 1975).

Based on energetics studies, Dawson (1976) has argued that small bipedal mammals, including heteromyids, are able to move faster using less energy than their quadrupedal counterparts. This suggests that quadrupedal heteromyids (such as *Perognathus*, *Heteromys*, and *Liomys*) might have foraging strategies that do not utilize high-speed running. Several ecological studies have been undertaken to test this idea (Reichman 1981, Thompson 1980, 1982a, 1982b).

A high-speed bipedal gait would be most effectively used by a small desert rodent to avoid predators (avian, mammalian) while moving from its burrow to a protected foraging site or from one site to another. Bipedal hoppers may also be more adept than quadrupeds at avoiding predators in open habitat due to the greater maneuverability and acceleration offered by the bipedal hop. Further, if bipedal hopping is energetically less costly than quadrupedal running, then maximum speed may be greater in bipedal hoppers than in similarly sized quadrupeds. These considerations seem to imply that quadrupedal heteromyids might be forced to confine their foraging to one or two shrubs close to their burrow entrance, but bipedal heteromyids may be free to forage under several more widely scattered shrubs. Thompson (1980, 1982a, 1982b) has compared the foraging behaviors of *D. deserti*, *D. merriami*, and *P. longimembris* (see Table 2), and his results seem to support this hypothesis.

The energetic cost of locomotion in kangaroos increases linearly with speed during quadrupedal (pentapedal) movement, but remains constant or may even decrease slightly during bipedal hopping (Dawson and Taylor 1973). This contrasts sharply with the pattern of quadrupedal mammals wherein the energetic cost continues to increase linearly at all speeds (Taylor et al. 1970). It has been suggested that elastic storage of strain energy in the muscles and tendons of the hind limb and back of kangaroos may be responsible for some of their "energy savings" (Alexander

TABLE 2. Comparison of foraging behaviors of bipedal and quadrupedal heteromyids.

Species	Estimated BW (g)	# Digs and gleans per minute	Average slow foraging speed (km/h)	Average transit speed between shrubs (km/h)	No. shrubs visited/ foraging hr	Maximum recorded speed (km/h)
D. deserti	110	5.00[1]	1.25[1]	6.33[1]	8.7[1]	26.7[1]
D. merriami	36	5.99[1]	.95[1]	3.20[1]	11.3[1]	22.2[2]
P. longimembris	11	.80[1]	.61[1]	1.76[1]	1.8[1]	—

[1](Thompson 1980)
[2](Thompson, ms.)

and Vernon 1975, Dawson and Taylor 1973, Morgan et al. 1978). However, similar studies on small bipedal hoppers, such as kangaroo rats, have yielded conflicting results, with energetic savings indicated in some species (Dawson 1976) and not in others (Thompson et al. 1980, Thompson ms.). Moreover, recent work by Biewener et al. (1981) indicates that storage of elastic energy is not likely in the hind limbs of kangaroo rats due to the relatively thick plantar and achilles tendons.

Unfortunately, all studies of locomotor energetics in bipedal hoppers have utilized treadmills. Recent experiments have shown that the gait of *Dipodomys merriami* is substantially altered during treadmill running (Nikolai ms.). On solid ground, for example, stride length and stride frequency both increase with speed, but on treadmills the stride frequency remains relatively constant over a broad range of speeds. This, in itself, raises serious questions as to the validity of the energetic cost of bipedal locomotion in rodents as established by treadmill tests.

The speed at which gait transitions occur are also higher during treadmill than during overground running (Table 3). *Dipodomys merriami* utilize three distinct gaits on treadmills and on solid ground: (1) quadrupedal half bound, (2) tripodal half bound, and (3) bipedal hop. The tripodal half bound is a transition gait between the slower quadrupedal half bound and the faster bipedal hop, in which only one front limb is used for support during a locomotor cycle (Fig. 7). The use of the tripodal half bound as a transition gait is not completely understood, since by using only one front limb the impact load will be roughly double that where both front limbs are used. In any event, the use of short, relatively weak front limbs as effective shock absorbing devices appears to be limited to slower speeds.

The transition from quadrupedal to bipedal gaits is probably not equivalent to the trot-gallop transition of quadrupedal mammals (see Heglund et al. 1974). Because the half bound and bipedal hop are both asymmetrical gaits, the quadrupedal-bipedal transition speed should always be higher than the trot-gallop transition speed for a quadruped of equal body weight. Nonetheless, bipedal hoppers apparently use the quadrupedal half bound at speeds that a similarly sized quadruped, of normal limb proportions, would trot (Fig. 8). The trot may not be available to bipedal hoppers due to the difficulty of coordinating hind and forelimbs that differ greatly in length.

Impact loading of the forelimbs will increase as the inverse ratio of front limb to hind limb length in running mammals (Gambaryan 1974). When loading of the forelimbs reaches some critical level, bipeds then presumably switch to rear limb support. Therefore, the speed at which the gait changes from quadrupedal to bipedal should be lower in bipedal hoppers with relatively longer hind limbs. Likewise, bipedal hoppers with similar front limb length to hind limb length ratios should have quadrupedal-bipedal transition speeds that conform to a single allometric equation (Fig. 8). *Dipodomys*, which have front limb as a percentage of hind limb ratios of 38.0–43.3, have quadrupedal-bipedal

TABLE 3. Range of speeds for each gait utilized by *D. merriami* on treadmill and on solid ground.

	Range of speeds	
Gait	Treadmill (cm/s)	Solid ground (cm/s)
Quadrupedal half-bound	<115	<68
Tripodal half-bound	67–181	44–109
Bipedal hop	>81	>60

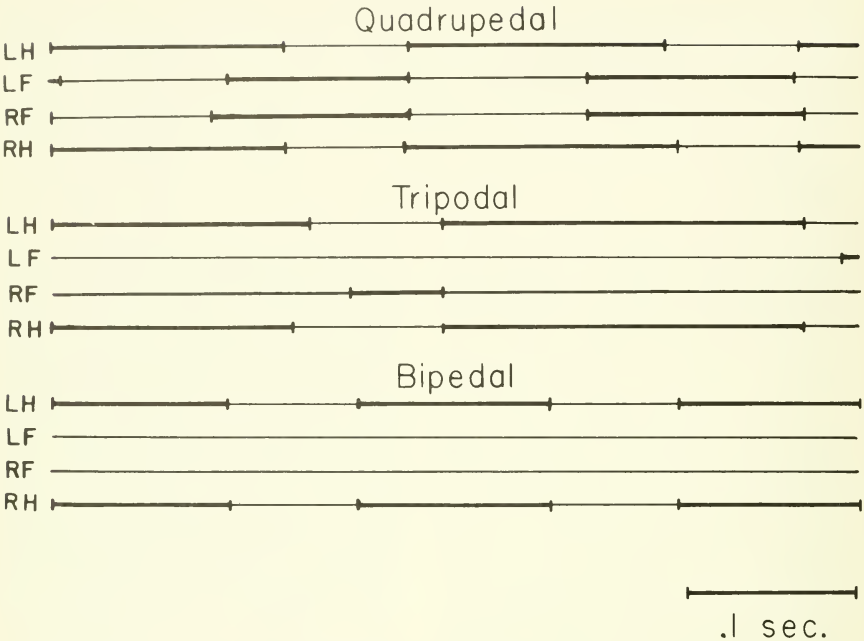

Fig. 7. Gait diagrams for *D. merriami*. Three representative gait diagrams depict the footfall patterns of the quadrupedal bound (top), tripodal half bound (center), and bipedal hop (bottom) at 60 cm/sec. During quadrupedal and tripodal locomotion, front limb support ends at touch-down for the hind limbs. Note that, although speed is the same for all three gaits, stride frequency is highest for the bipedal hop and stride length is greatest for the tripodal half bound.

transition speeds = 3.7 (Body Weight)$^{.178}$. *Pedetes capensis*, which is morphologically very similar to *Dipodomys* (Berman 1979), has a ratio of 35.4 and a quadrupedal-bipedal transition of 4 km/hr (Thompson et al. 1980), which is slightly lower than that predicted by the kangaroo rat equation. Kangaroos have ratios of 43.7–47.7 (Gambaryan 1974) and quadrupedal-bipedal transition speeds of 6.5 km/hr (Dawson and Taylor 1978). This is slightly above the value predicted by the *Dipodomys* equation (Fig. 8). Jerboas of the genus *Allactaga* have front to hind limb ratios of 27.5 (Gambaryan 1974) and therefore should have very low quadrupedal-bipedal transition speeds. The front limb to hind limb ratio of *Perognathus* (55.7–57.7) indicate that it would, in theory, be able to hop bipedally only at very high speeds. The limb proportions of *Microdipodops* (51.2) predict a relatively high quadrupedal-bipedal transition speed, but well below that of a similarly sized *Perognathus*.

The ratio of forelimb length to hind limb length has been used extensively as an index of bipedality (Berman 1979, Howell 1932). It is clear that the hind limbs are elongated in bipedal hoppers and that most of the lengthening occurs in the distal segments (i.e., tibia and foot elements) (Berman 1979, Emerson ms., Howell 1932). However, whether or not the forelimbs are shortened relative to body size is the subject of some controversy (Gambaryan 1974, Howell 1932). Most osteological measures of animal size in common use (i.e., basicranial length, thoracolumbar length, body length) are greatly modified in kangaroo rats, and therefore of dubious value when making comparisons with more generalized rodent species. An exception to this is the length of the basioccipital bone of the skull, which appears to be relatively unmodi-

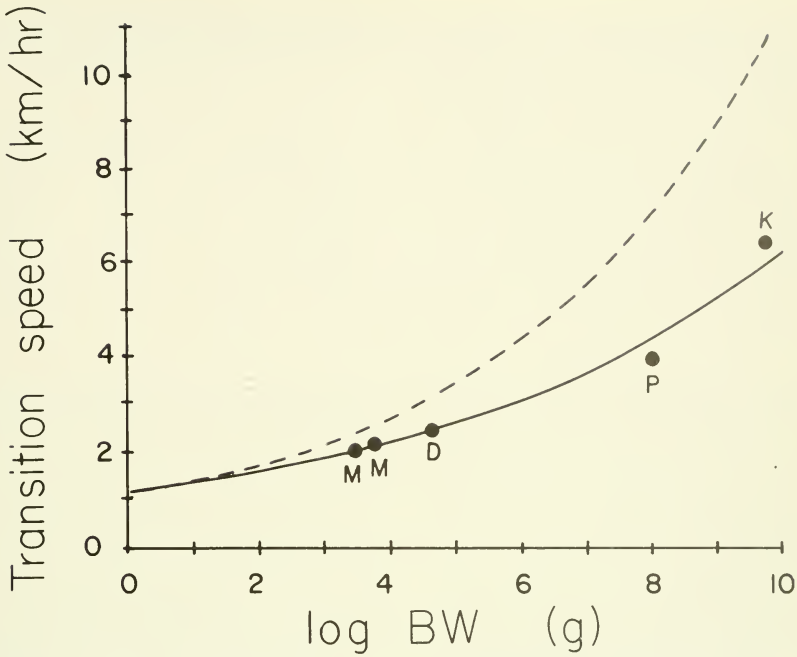

Fig. 8. Gait transition speeds. The trot-gallop transition speed for quadrupeds (dashed line) is 5.5 $Mb^{.24}$ (Heglund et al. 1974). The quadrupedal-bipedal transition speed for kangaroo rats (solid line) is 3.7 $Mb^{.178}$ (Nikolai ms.). The measured quadrupedal-bipedal transition speeds for bipedal hoppers are: (a) Red kangaroo (18 Kg), [K], 6.5 Km/hr (Dawson and Taylor 1973); (b) *Pedetes* sp. (3 Kg), [P], 4.0 Km/hr (Thompson et al. 1980); (c) *D. deserti* (.104 Kg), [D], 2.5 Km/hr (Thompson et al. 1980); (d) *D. merriami* (.0426 Kg), [M], 2.2 Km/hr (Nikolai ms.); (e) *D. merriami* (.032 Kg), [M], 2.0 Km/hr (Thompson et al. 1980). See text for details.

fied in kangaroo rats, as well as in many other mammals (L. Radinsky, pers. comm.). In desert heteromyids basioccipital length scales isometrically with body mass. We have therefore used this as a standard against which limb segment lengths are compared (Table 4).

The hind limbs of *Dipodomys* and *Microdipodops* are greatly elongated, and all three limb segments show strong positive allometry with respect to body size (Table 4). The foot and tibia are much longer in bipedal rodents than in similarly sized quadrupedal rodents, and there is a lesser difference in femur size (see also Berman 1979). It is interesting that as body size increases the relative length of the hind limb increases in bipedal heteromyids (*Dipodomys* and *Microdipodops*). This may have important biomechanical consequences. Since body mass scales as a volume and muscular strength as a cross sectional area (Alexander 1968), the ability of the leg muscles to absorb the shock of impact during bipedal hopping should decrease with increasing body size if geometric similarity is maintained. Increasing the length of the leg, however, will increase the contact time and thus the time course over which impact shock can be absorbed. The ratio of calcaneal length to total foot length also increases with body mass in bipedal hoppers [$= .09 + .514$ Mb, $R^2 = .72$, $P < .02$ for 7 species of *Dipodomys* and *Microdipodops*], thus improving the mechanical advantage of the large ankle extensor muscles.

The vertebral column, pelvic girdle, and hind limb musculature of bipedal heteromyids are considerably modified compared to quadrupedal species (Berman 1979, Hatt 1932, Howell 1932). In general, the long

TABLE 4. Comparison of the allometric equations of limb segment length of bipedal heteromyids and quadrupedal rodents using basioccipital length as a standard unit of relative body size. See text for details. [Bipedal heteromyids: *M. megacephalus* (1), *D. merriami* (2), *D. ordii* (3), *D. microps* (3), *D. spectabilis* (1); Quadrupedal rodents: *P. longimembris* (1), *P. formosus* (3), *P. parvus* (2), *Thomomys* sp. (2), *Peromyscus* sp. (1), *Neotoma* sp. (2), *Eutamias* sp. (1), *Citellus* sp. (1)]. Number of animals in parentheses.

	Bipedal heteromyids	Quadrupedal rodents	ANCOVA	
			Power	Coefficient
Humerus	$2.9\ (B.O.)^{1.17***}$	$4.1\ (B.O.)^{1.31***}$	N.S.	° ° °
Radius	$3.0\ (B.O.)^{.85***}$	$3.7\ (B.O.)^{1.15***}$	N.S.	N.S.
Hand	$1.9\ (B.O.)^{.75***}$	$2.9\ (B.O.)^{1.11***}$	° °	°
Femur	$5.7\ (B.O.)^{1.29***}$	$5.1\ (B.O.)^{1.31***}$	N.S.	°
Tibia	$7.7\ (B.O.)^{1.19***}$	$5.8\ (B.O.)^{1.11***}$	N.S.	° ° °
Foot	$8.6\ (B.O.)^{1.20**}$	$5.1\ (B.O.)^{.84***}$	° °	N.S.

*p < .05
**p < .01
***p < .001

back muscles are greatly enlarged, the pelvic girdle-sacral joint is strengthened, and the cervical and thoracic regions are shortened. The major muscle masses of the hind limbs are concentrated proximally and become highly tendinous distally to reduce the moment of inertia about the hip joint during locomotion.

Experimental studies indicate that at lower bipedal speeds most of the thrust at takeoff is derived from the ankle and hip extensors. The ankle extensor muscles are larger and have greater mechanical advantage in *Dipodomys* and *Microdipodops* than in *Liomys* and *Perognathus* (Berman 1979). As speed increases, the role of the large back muscles, such as the longissimus series, increases with increasing back extension at takeoff. Based on angle measurements, knee extensors also play an increasing role at higher speeds (Biewenier et al. 1981, Pinkham 1976, Williamson and Frederick 1977). The quadruceps and hamstring muscles are probably important in shock absorption during landing. Some elastic storage may come from these muscles; however, this is probably not significant for kangaroo rats (Biewenier et al. 1981).

The tail of *Dipodomys* is elongated, with a rectangular cross section and a terminal tail tuft. It is used as a counter-rotator during bipedal locomotion to counteract the torque applied to the long axis of the body by the limbs. The tail reaches the highest point of its swing cycle just before touchdown. The strong tail depressor muscles (e.g., iliocaudalis, pubocaudalis, flexores caudae) pull the tail down during the contact phase so that the tail is at its lowest point just after take-off (Fig. 9) (Nikolai ms.). The tail elevator musculature is linked to the large back extensor muscles in such a way that when the back is extended the tail is automatically elevated (Howell 1932). Most of the extension of the back occurs during the latter portion of the contact phase of a locomotor cycle; thus, when the tail depressor muscles are relaxed after takeoff, the tail is automatically elevated. Some elastic storage in the dorsal tail tendons seems likely. As the thrust of the hind limb increases with speed, the swing of the tail likewise increases to counteract torques about the center of mass (Fig. 9). During the quadrupedal half bound, the tail is limp and does not oscillate in the same manner as it does during bipedal locomotion (Nikolai, unpubl. data).

Foot length scales approximately isometrically with tail length in kangaroo rats [foot length = $.36\ (\text{tail length})^{.944}$ $R^2 = .923$], but shows strong negative allometry in pocket mice [foot length = $1.29\ (\text{tail length})^{.635}$ $R_2 = .945$]. This implies that kangaroo rats maintain geometric similarity with respect to the tail and foot length, but larger pocket mice have relatively longer tails and shorter feet. This relationship in *Dipodomys* is consistent with the presumed importance of the tail as a counter-rotator during bipedal loco motion. It has been suggested that the tuft of hair on the tip of the tail is effective as a flag to distract predators during high-speed predator avoidance maneuvers. The tuft may also alter the aerodynamic properties of the tail so as to make it more effective as a rudder or counter-rotator during locomotion (Hatt 1932, Howell 1923).

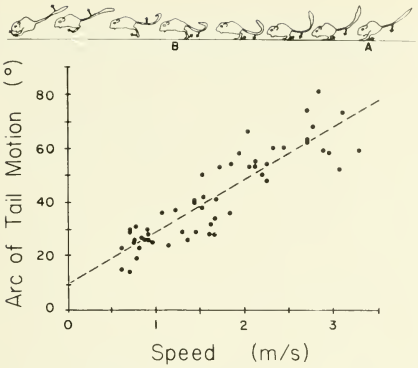

Fig. 9. Use of the tail in *D. merriami*. During bipedal hopping the long axis of the body shows very little rotation about the center of mass. During a locomotor cycle the legs exert a rotating torque on the center of mass (Pinkham 1976, Nikolai, unpubl. data). The rotation of the tail is always in a direction opposite to that of the leg (as indicated by the arrows on the tracings of representative frames from a single locomotor cycle of a *D. merriami* traveling at 100 cm/sec on a treadmill). The tail reaches its highest point just prior to touch-down (A) and reaches its lowest point just after take-off (B). The maximum arc described by the base of the tail increases with increasing speed (dashed line) to counteract the torque applied by the legs. [Degrees rotation = 9.164 + 19.6 (speed in m/s); $R^2 = .80$; $P < .001$; N = 57 for 2 *D. merriami* running on a treadmill] (Nikolai, ms.).

Limited data are available on the relative growth rates of the hind foot, tail, body length, and body mass for several species of desert heteromyids (Butterworth 1961, Chew and Butterworth 1959, Hayden and Gambino 1966, Lackey 1967, Reynolds 1960). However, to date there has been no real attempt to determine how: (1) ontogenetic scaling of body proportions relates to the development of bipedal locomotor ability during growth; or (2) ontogeny might provide a vehicle for morphologic adaptation in the evolution of bipedalism through heterochronic mechanisms (e.g., Alberch et al. 1979). We suspect that a closer examination of these issues might prove especially worthwhile.

Origins of Bipedalism

Why has bipedalism evolved in desert rodents? This is a persistent question for which three main explanations have been advanced: (1) to facilitate escape from predators (Bartholomew and Caswell 1951, Eisenberg 1975, Hatt 1932); (2) to free the forelimbs for efficient food handling (Bartholomew and Carey 1954); and (3) to reduce the energetic cost of locomotion (Dawson 1976, Reichman and Obserstein 1977). As was indicated earlier, recent evidence appears to discredit the latter hypothesis, leaving only predation and food handling as alternative models. The two are, however, strongly interrelated.

Three general features describe bipedal rodents: (1) all inhabit (or forage in) relatively open habitats where the risk of predation is presumably high; (2) all are nocturnal; and (3) all tend to be solitary. The first factor has been much emphasized but may not, in fact, be the most critical. Other rodents, especially sciurids, successfully occupy open environments but none are bipedal. They are, however, mostly diurnal and often exhibit a high degree of sociality (Armitage 1981, Barash 1973, Sherman 1977). The close approach of a predator to such rodents is made difficult by intense illumination and the fact that the detection of predators is a responsibility shared by conspecifics within a living area. Some *Dipodomys* and *Jaculus* respond to novel objects and small predators in their territories by thumping the ground with the hind feet (Eisenberg 1975). Such behavior might conceivably alert nearby conspecifics of potential danger, but true alarm calls have not been reported for any bipedal rodent.

That a predator might more closely approach a solitary rodent at night seems highly probable. If so, its attack will be initiated at closer quarters, thereby demanding a more rapid and forceful response by the prey if capture is to be avoided. *Dipodomys merriami*, for example, appears to have little trouble in jumping away from the strikes of nearby rattlesnakes (Webster 1962, Webster and Webster 1972). Perhaps the most important advantage conferred by bipedalism is the ability to execute a rapid, controlled leap directly from a feeding (or pouching) posture. Virtually all quadrupedal rodents sit semi-erect while feeding or manipulating food with the forelimbs. When forced to flee, such animals must normally drop onto the front limbs before initiating a flat trajectory leap off the rear limbs. The brief time required to do this may be of small consequence to a

diurnal rodent but could easily spell the difference between capture and escape to a solitary, nocturnal animal in open terrain.

Morphological specialization for leaping among vertebrate animals invariably results in elongation of the hind limbs relative to the forelimbs (Berman 1979, Howell 1965). As a consequence, the forelimbs will necessarily incur higher mechanical stresses as they act as shock absorbers to break the fall of the longer, faster bounds generated by the rear legs (Gambaryan 1974). Stress on the forelimbs will be amplified if a high-speed bounding gait incorporates abrupt changes of direction, since the front limbs brake the forward momentum of the body as the turn is executed. Quadrupedal mammals with such gaits (e.g., cursorial lagomorphs, ungulates) exhibit extreme modification of the elbow to increase its resistance to injury. Long axis rotation of the radius and ulna is severely curtailed or eliminated (Hildebrand 1982, Howell 1965). This effectively precludes pronation and supination of the hands, making them nearly useless in feeding. In all bipedal rodents, by contrast, the hands are used extensively in feeding and digging. There has presumably been strong selection for the rapid, efficient use of the forelimbs in order to reduce foraging time. It is in this context that the evolutionary significance of bipedalism becomes clearer. This locomotor strategy seems to offer the only viable means of combining, in a single animal, limb specializations and functions which are otherwise incompatible.

The notion that bipedalism in rodents is directly linked to the occupation of open, arid habitats is seriously contested only by the modern Zapodidae. These rodents favor mesic, well-vegetated environments both in the New and Old worlds. Their possible relationship to the Dipodidae (Eisenberg 1981, Fokin 1978) as well as the presumed bipedal habits of *Zapus* would seem to make the locomotor behavior of these rodents of special value in unraveling the history of bipedalism in desert rodents. However, although *Zapus* is unquestionably capable of rapid, prodigious leaps, there seems to be no solid evidence that it is really capable of sustained, bipedal saltation. Slow motion films of *Zapus princeps* running and leaping on solid ground as well as on a treadmill show that the forelimbs are involved in body support and shock absorption in every stride (Bramble and Nikolai pers. obs.). Further evidence of quadrupedal rather than bipedal bounding is found in the structure of the limbs. The forelimb-hindlimb length ratio of *Zapus* is similar to that of bipedal heteromyids (i.e., *Microdipodops*; Berman 1979), but the forelimb is constructed differently. Forelimb length relative to body size is comparable to that seen in generalized quadrupedal rodents. The hand is large rather than reduced, and there are no obvious specializations favoring pronation and supination of the forearm. We tentatively conclude that true bipedal locomotion probably does not exist in the Zapodidae and that leaping specializations of this group have little to do with the evolutionary pathways leading to bipedal saltation in modern desert rodents.

The development of bipedal saltation as seen in modern heteromyids cannot have been associated with the occupation of desert environments as we know them today. True deserts of North America appear to be of fairly recent origin (i.e., later Pleistocene; Van Devender 1977), whereas heteromyids exhibiting structural modification for bipedal saltation date from at least the later Miocene (Voorhies 1975, Wood 1935). Voorhies' (1975) recent suggestion that bipedalism may have first arisen among primitive dipodomyines living in sandy, floodplain habitats deserves special consideration. Such restricted environments may occur within otherwise typical savannah habitat and may be relatively arid during periods of low rainfall. More importantly, sandy floodplains are frequently characterized by widely scattered vegetation and thus qualify as "open" habitat. If bipedal heteromyids arose under conditions such as these, their distinctive locomotor specializations may have considerably predated other specific adaptations (mostly physiological) to desert life.

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ADAPTIVE PHYSIOLOGY OF HETEROMYID RODENTS[1]

Richard E. MacMillen[2]

ABSTRACT.— Heteromyid rodents are distributed from the New World tropics to the deserts of North America, but their habitation of deserts is relatively recent. Their evolutionary history, though, is associated with progressive aridity, with larger quadrupedal taxa being more mesic (and primitive), and smaller quadrupeds and all bipeds more xeric. The correlation between water regulatory efficiency and body mass is strongly negative in heteromyids; bipedal *Dipodomys* spp. have water regulatory efficiency fixed at an intermediate level independent of mass. Heteromyids generally have basal metabolic rates reduced below the eutherian level, with the greatest reductions occurring in desert species. The use of torpor as an energy-conserving device is cosmopolitan in small (< 40 g) heteromyids, but is inconsequential or lacking in larger ones. Bipedalism, characteristic of *Dipodomys*, confers no direct energetic advantages as revealed in treadmill studies.

Large quadrupedal heteromyids have adaptive physiologies suitable for more mesic habitats, but smaller quadrupeds are suited for xeric existences; these characteristics likely reflect an evolution from a tropical ancestry to rather recent habitation of deserts. Bipedalism occurs only in xeric-adapted forms and has no directly discernible energetic benefit; yet it appears to relieve in some unknown way the energetic constraints of foraging.

The genera and species of the family Heteromyidae are distributed along a pronounced gradient of water availability in the New World ranging from the wet tropics of Central and South America to the driest deserts of North America (Hall 1981). This present-day distribution mimics the paleoclimatological history of the family, starting with a tropical ancestry, followed by an adaptive radiation throughout the Tertiary in response to progressive aridity and seasonality of rainfall, and culminating in the diverse fauna of desert heteromyids with which we are so familiar (Axelrod 1958, Hall 1981, Reeder 1956, Wood 1935). With this in mind, it is my contention that tropical heteromyids may be viewed at least ecologically as ancestral models of early heteromyids, the desert forms as advanced derivatives, and those occupying intermediate habitats as transitional forms. Thus, extant species should provide us with important clues concerning the evolutionary and ecological trajectories of the family at the levels of physiology, morphology, and behavior.

The quadrupedal heteromyid genera (*Heteromys, Liomys, Perognathus*), at least with respect to locomotion, are the more generalized, and the bipedal members (*Dipodomys, Microdipodops*) are the more specialized. In addition, the quadrupedal members span the entire distributional range and nearly the entire size range of the family, but the bipedal forms are confined to semiarid and arid habitats, and (with the exception of the small-in-size *Microdipodops*) occupy the upper portion of the size spectrum (Hall 1981). By inspection (Hall 1981), there is a strong positive correlation within the quadrupedal heteromyids between body size and moistness of the habitat, suggesting that reductions in body mass may confer a selective advantage upon quadrupedal heteromyids living in more arid habitats; on the other hand, the arid-adapted bipeds are commonly relatively large and show no apparent relationship between the body mass of individual species and habitat aridity, suggesting a linkage between bipedality and aridity independent of body mass.

Herein, I explore certain aspects of water and energy regulatory physiology of heteromyid rodents, paying particular attention to patterns related to habitat, body mass, and/or locomotor mode.

[1]From the symposium "Biology of Desert Rodents," presented at the annual meeting of the American Society of Mammalogists, hosted by Brigham Young University, 20–24 June 1982, at Snowbird, Utah.

[2]Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717.

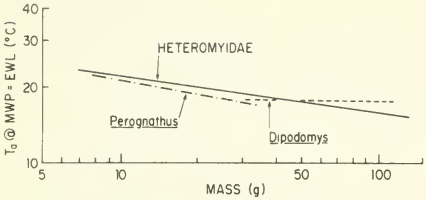

Fig. 1. The double logarithmic relationships between water regulatory efficiency (T_a @ MWP = EWL) and body mass in 5 genera and 13 species of heteromyid rodents. Regression lines are provided for all species (solid line) and *Perognathus* spp. (dot-dash line), and both have significant slopes (*F* test, $P < .05$). The horizontal line (dashed) represents the average value for all *Dipodomys*, which did not have a significant regression. The regression lines are fit to all the values for each species; the regression equations are T_a @ (MWP = EWL) = $29.682g^{-0.137}$ in all 13 heteromyid species, and T_a @ (MWP = EWL) = $31.078g^{-0.166}$ in *Perognathus* spp.; the mean value for *Dipodomys* spp. is 18.1 ± SD 0.6 C. The heteromyid species employed span the geographic, climatological, and body mass ranges of the family and include *Dipodomys deserti, D. merriami, D. ordii, D. panamintinus, Heteromys desmarestianus, Liomys irroratus, L. salvini, Microdipodops megacephalus, Perognathus baileyi, P. fallax, P. flavus, P. hispidus,* and *P. longimembris*. After MacMillen and Hinds (in press).

WATER REGULATORY EFFICIENCY

Numerous accounts in the literature attest to the relatively great powers of water conservation in heteromyid rodents, and indicate that the arid-adapted forms (*Dipodomys, Microdipodops, Perognathus*) are conservative often to the point of exogenous water independence (MacMillen 1972, Schmidt-Nielsen et al. 1948; pers. obs.), and the more mesic adapted forms (*Heteromys, Liomys*) are less conservative in their water economies and require dietary augmentation of exogenous water (Hudson and Rummel 1966, Fleming 1977). I (MacMillen 1983) have argued that the conservative nature of heteromyid water economy, regardless of habitat, is likely linked to the family's dietary specialism, granivory: this is because rodents in particular depend upon a common resource packet to meet nutrient, energy, and water needs, and those that use the driest packets (seeds) are the most conservative in their water economies.

With the supposition that heteromyids are relatively conservative in their water economies, and that, at least for the quadrupedal species, body mass might be positively correlated with moistness of the habitat and negatively correlated with economical water regulation, MacMillen and Hinds (1983) undertook an examination of water regulatory efficiency in extant heteromyids that included both quadrupedal and bipedal members across the entire taxonomic, distributional, and size ranges of the family. This examination was based on a model that predicted that water regulatory efficiency is negatively related to body mass and positively related to ambient temperature. Our criterion of water regulatory efficiency is that ambient temperature (T_a) at which the major avenue of water input (metabolic water production, MWP) just balances the major avenue of water output (evaporative water loss, EWL). Thus, the model predicts that those species achieving water balance (MWP=EWL) at the highest T_as are the most efficient in water regulation, being able to subsist exclusively on air-dry seeds to meet both energy and water needs while active on the surface even under warm conditions. A test of the model in which we evaluated simultaneously MWP and EWL from T_a = 5–35 C in 117 individuals, 13 species and 5 genera of heteromyids, confirms our predictions for the family in general (Fig. 1). However, when the two most speciose genera (*Perognathus, Dipodomys*) are treated separately, *Perognathus* spp. conform even more strongly (possess a steeper slope) to the model, but in *Dipodomys* spp. water regulatory efficiency is fixed at an intermediate level independent of body mass (Fig. 1). This intergeneric break in patterns of water regulatory efficiency coincides with a break in body mass (ca 35g) and a break in locomotor mode, points whose relevances will be discussed later in this paper.

BASAL METABOLIC RATE

It has long been known that the basal metabolic rates (BMR) of mammals are logarithmically correlated with body mass (Kleiber 1932). This scaling of BMR with body mass in mammals was statistically refined by Brody (1945) and Kleiber (1961) to provide indistinguishable regression equations for predicting BMR for mammals of any known mass: BMR (cm^3 O_2/g.h) = 3.8 $W(g)^{-0.27}$

(Brody 1945) or $M = 3.5W^{-0.25}$ (Kleiber 1961; see MacMillen and Nelson 1969 for conversion of equations from animal-specific to mass-specific values). Rodents, too, conform in general to these allometric expectations (Morrison 1948), but Dawson (1955) was the first to suggest that heteromyid rodents may have BMR reduced below the expected levels. Hudson and Rummel (1966) confirmed this suggestion for the subtropical species *Liomys salvani* (=*L. salvini*?) and *L. irroratus*; more recently McNab (1979) has shown through a search of the literature and his own measurements that, of the heteromyid species for which measurements were available (12 species, all 5 genera), only a tropical *Heteromys* (*H. anomalus*) possessed a BMR at or exceeding the Kleiber prediction—all others were reduced. Furthermore, McNab's (1979) analysis revealed the BMRs of *Perognathus* spp. were not only reduced, but also were independent of body mass; it is interesting to note that the four *Perognathus* measurements were from four different laboratories.

Our studies of water-regulatory efficiency as described above and in MacMillen and Hinds (1983) provide a rich data base from a single laboratory for comparing mass-related aspects of water and energy metabolism both within the family Heteromyidae, and with eutherian mammals in general. We are preparing a major synthesis of heteromyid metabolic allometry (Hinds and MacMillen, in preparation), and so the following summarize only briefly the most pertinent information related to BMR.

Because our criterion of water regulatory efficiency required that our animals be oxidizing food of known composition at the time of measurement of oxygen consumption (V_{O_2}), our animals were not postabsorptive when measured in thermal neutrality, and hence did not conform strictly to the requirements for BMR. The animals were oxidizing millet (81.4 percent carbohydrate, 5.1 percent lipid, 13.5 percent protein), which should elevate metabolic rate due to the specific dynamic action (SDA) of food utilization by about 9 percent above basal levels (Brody 1945). In spite of the possible influence of SDA on metabolic rate of our specimens, it is apparent that the basal metabolic rate of the heteromyids we tested is depressed below the values predicted by either the Brody (1945) or Kleiber (1961) relationships (Fig. 2).

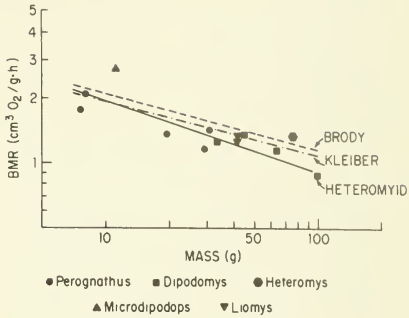

Fig. 2. The double logarithmic relationship between mass-specific basal metabolic rate and body mass in heteromyid rodents, using the same species as indicated in Figure 1. The dashed line is the allometric expectation for eutherian mammals from Brody (1945); the dot-dash line is the expectation for eutherians from Kleiber (1961). The solid line is fit to the data for heteromyids by the regression equation $BMR = 3.69\ W(g)^{-0.28}$ (S_{yx} = .010, S_b = .028, r^2 = 0.504). The geometric symbols represent different genera as indicated on the figure. The BMR values employed in this analysis are the two lowest measures of $\dot{V}_{O_2}$ for each individual at that T_a in thermal neutrality for which the mean $\dot{V}_{O_2}$ of that species was lowest (after Hinds and MacMillen, in preparation; data collection as in MacMillen and Hinds, in press).

Correcting for SDA would yield even greater depressions. The slope of the regression line relating BMR to mass of heteromyids (–0.28) is statistically indistinguishable from that of Brody (–0.27) and Kleiber (–0.25). Using the raw data of Brody (1945), a direct comparison can be made of elevation between his and the heteromyid data sets, which shows that, at the mean body mass (ca 30g) of the heteromyids employed, heteromyid BMR is significantly ($P < .05$) reduced by 11 percent of that predicted for eutherian mammals in general (following method of comparing elevations by Snedecor 1956 and Zar 1974). Of the 13 heteromyid species included in Figure 2, 5 (*Dipodomys deserti, D. merriami, Perognathus baileyi, P. fallax, P. longimembris*) are from severe desert scrub habitats, and their BMR collectively is reduced by 24 percent below that predicted for eutherians.

Lastly, the 5 *Perognathus* spp. conform strongly to the relationship between BMR and body mass, with no indication of the mass-independent relationship reported by McNab (1979) on data emanating from several laboratories. Since two of the four *Perognathus* species included in McNab's (1979) analysis were also employed in ours (*P. longimembris, P. hispidus*) the discrepancy is likely due to interlaboratory differences in measuring BMR rather than to interspecific deviations in metabolism. This attests to the importance of using only data collected from a single laboratory when undertaking metabolic comparisons at lower taxonomic levels.

Thus, it is concluded that heteromyid rodents have reduced BMR (and metabolic rates in general) and that the reductions are not only recognizable at the taxonomic level, but are most pronounced in those members living under more arid conditions.

BIPEDAL LOCOMOTION

The fact that heteromyids are divided in locomotor habits into quadrupedal and bipedal forms, and that the latter are confined to semiarid and arid habitats within the family distribution, suggests the presence of advantages inherent in bipedalism that favor an arid existence. Howell (1933) observed that *Dipodomys* occurred predominantly in open terrain, where bipedality conferred a combination of fast, erratic movements and balance that enhanced predator escape to the extent "that no mammal can catch this rodent in fair chase, but only in stealth." Also favoring the hypothesis that bipedality in *Dipodomys* aids primarily in predator escape and avoidance were Bartholomew and Caswell (1951), who stated "the entire economy of the animal is set up for efficient evasion of danger in areas relatively devoid of cover, which emphasizes that survival in this species has been dependent upon a series of mutually supporting adaptations of which its locomotor equipment is the most obvious."

Recently, investigators have measured the actual costs of locomotion through indirect calorimetry of mammals running on treadmills. These studies have concentrated on quadrupedal running and show considerable uniformity in the scaling of energetic costs to body mass (Taylor et al. 1970). The first suggestion that bipedal hopping might confer unusual energetic benefits was by Dawson and Taylor (1973), who reported that red kangaroos, while hopping, effectively had energetic costs that were independent of running speed, i.e., a bipedal plateau. Shortly thereafter Fedak et al. (1974) reported data suggesting that for small animals (< 1000g) the cost of transport for bipeds (exclusively birds) is less than that for quadrupeds (exclusively mammals). This contention was reversed by Fedak and Seeherman (1979) and Paladino and King (1979), who demonstrated independently, using a more extensive data set including quadrupedal mammals and lizards and bipedal birds and mammals, that there is no difference in the scaling of energy requirements for locomotion between bipeds and quadrupeds, but only differences between clumsy and graceful runners. But these latter studies, as opposed to Dawson and Taylor's (1973) with the kangaroo, employed animals that were either two-legged bipeds (primates and birds) or four-legged quadrupeds (other mammals and lizards), and not mammals that at slower running speeds are pentapedal (kangaroos) or quadrupedal (for example, heteromyids), but then become bipedal at faster speeds.

Dawson (1976) and Baudinette et al. (1976) measured the energetic costs of locomotion in two species of Australian murid hopping mice (*Notomys cervinus* and *N. alexis*, respectively) that are ecological and physiological equivalents to bipedal heteromyids (MacMillen and Lee 1969, 1970). Both species had similar patterns relating oxygen consumption (V_{O_2}) to running speed with a positive linear relationship at slower speeds (< 2.0 km/h) and a plateau at higher speeds (> 2.0 km/h). Dawson (1976) reports intermittent use of both quadrupedal running and bipedal hopping at plateau speeds, but Baudinette et al. (1976) report only quadrupedal running. In addition, Dawson (1976) suggests that the plateau in *N. cervinus* is aerobic and therefore represents a real energetic savings related to elastic energy storage compared to that during strictly quadrupedal running. Baudinette et al. (1976) are less committal and imply that the plateau may be either an aerobic one dependent upon elastic storage,

or it may be purely anaerobic, occurring at the level of maximal aerobic capacity. Clearly this plateau can represent an energy-conserving mechanism only if aerobic.

My recent treadmill studies of the metabolic cost of locomotion in small bipedal and quadrupedal mammals have concentrated on heteromyid rodents. Initial results that compare running and hopping costs of four species of small bipeds (0.03 to 3.0 kg; Rodents: Heteromyidae: *Dipodomys merriami*, *D. deserti*; Pedetidae: *Pedetes capensis*; Marsupialia: Macropodidae: *Bettongia penicillata*) show no aerobic bipedal plateau while hopping at any of the speeds tested. Further, a plateau could be induced in poorly trained individuals that ran in an oscillatory manner, but this disappeared when they were trained to run smoothly (Thompson et al. 1980).

To confirm further the presence or absence of a bipedal plateau in *Dipodomys* spp., simultaneous measurements of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were made in *D. ordii* while running on a treadmill, and of blood lactate immediately after running. The results are reported in Figure 3. At low running speeds (<3.0 km/h) $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, and blood lactate are positively and linearly related to speed. At higher running speeds (> 3.0 km/h) $\dot{V}_{O_2}$ plateaus distinctly, $\dot{V}_{CO_2}$ continues to increase linearly but with a shallower slope, and blood lactate continues to increase sharply, but with the possibility of a plateau at 4.0 and 5.0 km/h.

At running speeds above 4.0 km/h there is a distinct decline in the willingness of individuals to run, with typically less than one-half of the individuals that readily ran at lower speeds willing to run at the higher speeds sufficiently long (2–3 min) to reach steady state. It is unlikely that this unwillingness to run at higher speeds for even short periods of time was due to hyperthermia. As Wunder (1974) has noted, no inhibition of running in *D. ordii* accompanied moderate hyperthermia while running at lower speeds (≤1.8 km/h), but did for prolonged periods of time (10–15 min). The transition from quadrupedal to bipedal running occurs between 3.0 and 4.0 km/h, with most of the $\dot{V}_{O_2}$ plateau coincident with bipedal locomotion.

I am convinced, however, that the $\dot{V}_{O_2}$ plateau depicted in Figure 3 is anaerobic, and therefore cannot be construed as an

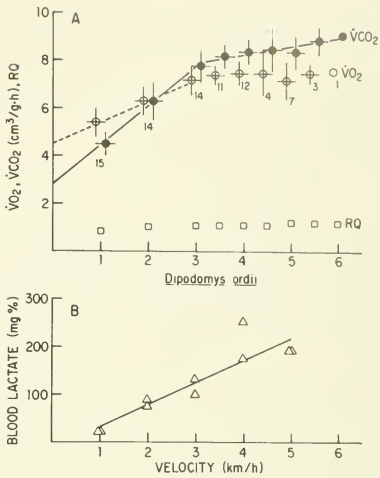

Fig. 3.A. The relation between oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) and velocity in *Dipodomys ordii* running on a treadmill at $T_a = 20$ C. The treadmill was enclosed in a Plexiglas chamber through which air was pulled at a rate of 4.1 L/min. $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ were measured with an Applied Electrochemistry S-3A oxygen analyzer and an Infrared Industries carbon dioxide analyzer. All measurements were corrected to STPD. The dashed line is fit to the $\dot{V}_{O_2}$ data between 1 and 3 km/h by linear regression analysis and is described by the equation $cm^3/g{\cdot}h = 0.91(km/h) + 4.46$ ($S_{yx} = 0.58$, $S_b = 0.60$, $r^2 = 0.64$); the line has a significant positive slope (F test, $P < .05$). The solid line is fit to the $\dot{V}_{CO_2}$ data between 1 and 3 km/h, and between 3 and 6 km/h. Both have significant slopes, and are described by the equations $cm^3/g{\cdot}h = 1.65(km/h) + 2.88$ ($S_{yx} = 0.67$, $S_b = 0.43$, $r^2 = 0.81$) and $cm^3/g{\cdot}h = 0.36(km/h) + 6.83$ ($S_{yx} = 0.58$, $S_b = 0.89$, $r^2 = 0.21$). The numbers represent the number of measurements obtained at each speed from a total of 13 individuals. Solid circles represent mean $\dot{V}_{CO_2}$ measurements, hollow circles represent mean $\dot{V}_{O_2}$ measurements, vertical lines represent the interval $\bar{X} \pm 1$ SD, and hollow squares represent mean RQ values ($\dot{V}_{CO_2}/\dot{V}_{O_2}$).

B. The relation between blood lactate and velocity in *D. ordii* running on a treadmill at $T_a = 20$ C. Each animal was allowed to run at one speed for 2–5 min during measures of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$, and these measurements are included in the data depicted in Fig. 3A. It was then immediately removed, a blood sample was taken from the orbital sinus within 30 sec of removal, and the whole blood placed in perchlorate solution. Lactate concentration was determined using a Boehringer-Mannheim lactate test kit. Each hollow triangle represents one value from a different individual, with a total of ten values (individuals). The solid line is fit to the data by regression analysis and is described by the equation $mg\% = 46.234(km/h) - 13.638$ ($r^2 = 0.825$); the slope is significant (F test, $P < .05$).

energy-conserving mechanism. The mean $\dot{V}_{O_2}$ between 3.0 and 6.0 km/h (7.34 ± SD 0.57 cm^3/g.h; N=52) falls within the 95 percent confidence intervals predicted for maximal aerobic capacity ($\dot{V}_{O_2}$ max) in a small mammal ($\bar{X}$ body mass = 52.7 g) from Lechner's (1978) allometric relationship:

$$\dot{V}_{O_2}\,\text{max} = 0.499\ W^{.678}$$

($\dot{V}_{O_2}$ is in cm^3/min, and W is mass in g).

The mean $\dot{V}_{O_2}$ for *D. ordii* between 3.0 and 6.0 km/h, however, falls below the 95 percent confidence intervals for $\dot{V}_{O_2}$ max as predicted by Taylor et al. (1980):

$$\dot{V}_{O_2}\,\text{max} = 1.92\ W_{.809}$$

($\dot{V}_{O_2}$ is in cm^3/sec, and W is mass in kg).

Lechner's (1978) relationship included $\dot{V}_{O_2}$ max induced by cold, helium-oxygen mixtures or running, in 14 small mammals species (< 2.6 kg), 11 of which were rodents. Taylor et al. (1980) confined their measurements to treadmill running, with the majority of their mammals large (> 2.6 kg) or very large; of the 21 species for which measurements are reported, only 4 are rodents while 11 are ungulates. It is difficult to resolve the discrepancies between these two relationships, as their data bases differ taxonomically, methodologically, and by body mass. Our protocol is most similar to that of Lechner (1978) in terms of taxonomy and body mass, and resembles that of Taylor et al. (1980) methodologically.

Additional confirmation that the $\dot{V}_{O_2}$ plateau reported above for *D. ordii* is anaerobic comes from the analysis of blood lactate following running at the highest speeds tested. The mean of four values for *D. ordii* after running 2–3 min at 4.0 and 5.0 km/h is 201.9 ± SD 34.8 mg percent. This mean, and three of the four values fall within the 95 percent confidence intervals around the mean (190.7 ± SD 9.1 mg percent) of blood lactate levels of 9 mammalian species running on treadmills at $\dot{V}_{O_2}$ max, as reported by Seeherman et al. 1981. The fourth value lies above the confidence intervals. Thus, it is apparent from the perspectives of $\dot{V}_{O_2}$ and blood lactate levels that the bipedal plateau we observed in *D. ordii* is anaerobic. Finally, Biewener et al. (1981) have examined with the use of force plates and X-ray cinematography bipedal hopping in *Dipodomys spectabilis* and conclude that elastic storage of energy in this kangaroo rat is much less than in kangaroos.

The adaptive significance of bipedality in heteromyids has yet to be demonstrated with rigorous laboratory and field tests. The most plausible current explanation is the original one proposed by Howell (1933) and Bartholomew and Caswell (1951) that bipedality aids in predator avoidance and escape. I believe it is additionally possible that bipedality confers other locomotor advantages not readily translatable into energetic currency, such as enhancing acceleration and burst speeds. These ideas have yet to be tested.

USE OF TORPOR

Torpor (or natural hypothermia), in which body temperature and energy metabolism are reduced well below normothermic levels, either on a circadian basis or for longer periods, is well documented in virtually all heteromyids whose mean body masses are typically less than 40 g (i.e., all *Perognathus* spp., *Microdipodops pallidus*, and *M. megacephalus*, pers. obs., Bartholomew and Cade 1957, Bartholomew and MacMillen 1961, Cade 1964, Tucker 1965, Wang and Hudson 1970, Wolff and Bateman 1978). In larger quadrupedal heteromyids (i.e., *Heteromys*, *Liomys*) torpor has not been observed (pers. obs., Fleming 1977, Hudson and Rummel 1966). Torpor appears to be a weakly developed capacity in *Dipodomys*, having been documented in *D. merriami* (Dawson 1955, Carpenter 1966, Yousef and Dill 1971), *D. panamintinus* (Dawson 1955) and observed in *D. deserti* (pers. obs.). In all instances torpor in *Dipodomys* spp. was induced by starvation and/or cold stress, and frequently resulted in death during torpor or after arousal. In the few *Dipodomys* spp. in which torpor has been documented it appears to be best (but still weakly) developed, as a circadian phenomenon, in the smallest species, *D. merriami* (≥ 35 g). I have seen no convincing evidence that torpor in *Dipodomys* spp. is an ecologically meaningful phenomenon.

Among *Perognathus* spp., there appear to be two prevailing patterns in the use of torpor: (1) those that employ it as an emergency

energy-conserving mechanism for short periods of time (one to several days) to avoid temporarily inhospitable surface conditions (*P. californicus*, Tucker 1962; *P. flavus*, Wolff and Batemann 1978); and (2) those that are or nearly are obligate hibernators, and abandon surface activity for several months each winter (*P. longimembris*, Kenagy 1973; *P. parvus*, Meehan 1976). The determinants of one pattern or the other are unknown, but they are not taxonomic because both patterns occur in each subgenus. In *Microdipodops* spp., torpor appears to be employed on a short-term basis, as both species can be trapped all year, even during winter on subfreezing nights, except for those occasions when the substrate is frozen (Brown and Bartholomew 1969, Hall 1946; pers. obs.). In both *Perognathus* and *Microdipodops*, as in *Dipodomys*, the periodicity of torpor seems to be based on a circadian schedule with individuals initially torpid during the usual daylight hours and normothermic at night (Brown and Bartholomew 1969, Carpenter 1966, French 1977, Meehan 1976, Tucker 1962). If conditions that foster the use of torpor prevail, whether it be in obligate hibernators or short-termers, circadian bouts of torpor may extend into those of greater duration, some lasting several days (Brown and Bartholomew 1969, French 1977, Meehan 1976). Whether torpor be circadian or of longer duration, or whether the use of torpor bouts be confined to short periods of inhospitable surface conditions or to a complete winter season, its adaptive significance to these granivores is linked primarily to energy conservation, enabling its practitioners to subsist for short or longer periods in underground burrows on a finite energy store in the form of seed hoards at a fraction of the energetic cost they would expend if continually normothermic (Brown and Bartholomew 1969, Kenagy 1973, Meehan 1976, Tucker 1966).

For torpor to serve efficiently as an energy-conserving mechanism in heteromyids, its use must be accompanied by precision of control. Such precision has been demonstrated in *Microdipodops pallidus* by Brown and Bartholomew (1969), who have shown that periodicity and duration of torpor bouts is related to ambient temperature and food supply in such a way that individuals invariably maintain body weight and accumulate seeds, even at very low temperatures and on seed rations reduced considerably below the normothermic requirement. An additional example of precision of energetic control while using torpor is seen in *Perognathus parvus* (Meehan 1976). This species is an obligate hibernator, and in Great Basin habitats in California is dormant in burrows typically from November through March, employing periodic bouts of torpor that may last as long as eight days interrupted by only brief (< one day) periods of arousal. In the laboratory during winter months *P. parvus* establishes large seed hoards (i.e., an energy surplus) and, while maintained at ambient temperatures equivalent to winter burrow temperatures (ca 5 C), spontaneously enters torpor; torpor bouts are initially circadian followed by progressive increases in duration until, commonly, individuals are torpid for five or more days at a time. Meehan's data under simulated winter conditions indicate that individuals are torpid, with body temperature (T_b) approximating T_a, 90 percent of the time, and expend only 16 percent of the energy that would be expended if normothermic in an insulated nest in the burrow; this energy savings would obviously be increased severalfold if compared with the cost of nightly foraging on the surface.

The magnitude of energetic savings while torpid is demonstrated in Figure 4, which shows that at $T_a = 2$ C (approximating winter burrow temperatures) the metabolic cost for torpid mice is 3 percent of that for resting nontorpid animals. The extraordinary precision of thermoregulatory control while torpid is also demonstrated in Figure 4: at T_as between 2 and –2 C (and at a T_b barely above freezing) *P. parvus* is capable of activating the heat production machinery sufficient to maintain T_b at or slightly above 2 C. Thus, with tissues approaching freezing, these animals are capable of maintaining a constant body temperature at very low metabolic cost, thereby avoiding prohibitively costly normothermia and at the same time ensuring continuing survival throughout a winter season of underground dormancy.

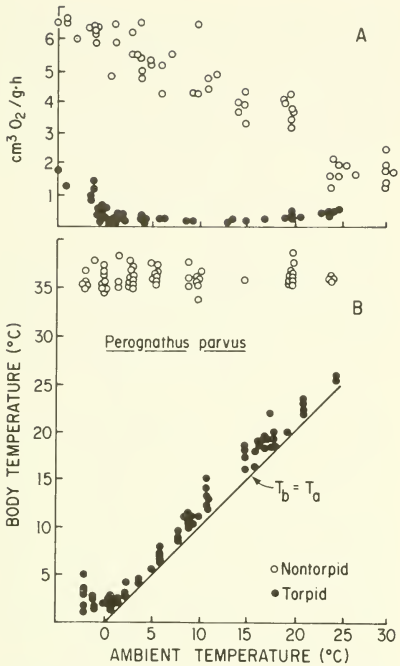

Fig. 4.A. The relation between oxygen consumption and ambient temperature in normothermic (hollow circles) and torpid (solid circles) *Perognathus parvus*. Normothermic values based on 59 measurements from 14 individuals; torpid values on 48 measurements from 12 individuals. After Meehan (1976).

B. The relation between body temperature (T_b) and ambient temperature (T_a) in normothermic (hollow circles) and torpid (solid circles) *P. parvus*. Normothermic values on 62 measurements from 19 individuals; torpid values on 78 values from 25 individuals. The solid line indicates where $T_b = T_a$. After Meehan (1976).

Discussion and Conclusions

As stated in the introduction, it is believed that close attention to extant heteromyids distributed over the geographic (i.e., climatic), size, and locomotor ranges of the family should reveal not only specifics about the daily lives of present-day populations and species, but also about the development of biological patterns over evolutionary time. With this in mind, the patterns of heteromyid physiology described above will be explored and an attempt will be made to place them in an evolutionary perspective with the following scenario.

Heteromyids arose in the early Tertiary New-World tropics (Reeder 1956, Wood 1935) as rather large (≥ 70 g) quadrupedal granivores/frugivores whose cheek pouches enhanced foraging success for a single resource packet (seeds and/or fruits) that provided virtually all nutritional needs. These ancestral heteromyids would have possessed powers of water regulation consistent with the amount of preformed + oxidative water yielded from the food, and equivalent to that predicted for a quadrupedal heteromyid of that mass as depicted in Figure 1. At the time of their origin they likely possessed a BMR close to that typical of eutherian mammals, as in *Heteromys* and *Liomys* (Fig. 2).

From the heteromyid origin throughout the remaining Tertiary, the geographic region of heteromyid evolution (southwestern North America) was subjected to progressive aridity and seasonality of rainfall (Axelrod 1958); this was most pronounced in areas occupied by today's deserts (i.e., around 30° N latitude) and less pronounced with proximity to the equator. The progression of aridity and seasonality of rainfall would have resulted in shorter growing seasons, reduced primary production, and vegetational emphasis on seasonal seed production (rather than fruit) as a reproductive strategy. I envision the heteromyid responses to these climatic and biotic changes to include tracking the increases in aridity and accompanying temporal and volumetric reductions in seed production with reductions in body mass; such reductions in mass would promote increases in water-regulatory efficiency consistent with water yield (MWP) from a dry foodstuff (as seen in Fig. 1) and decreases in absolute energy needs per individual. Concomitant with this would have been reductions in BMR (and overall energy metabolism) comparable to those observed in Figure 2, thereby even further decreasing absolute energy needs in habitats with more limited seed production. The trade-off for decreases in body mass in these still quadrupedal forms would have been an increase in mass-related locomotor costs (Taylor et al. 1970), offset at this stage by reductions in BMR and continuing enhancement in foraging efficiency promoted by the use of cheek pouches. According to my scenario, species that are physiologically (and

ecologically) ancestral and transitional would have persisted through the present in habitats of appropriate rainfall and seed production patterns, most typically in tropical and subtropical settings.

The next sequence of events followed continuing reductions in mass of quadrupedal heteromyids down to about 35–40 g, at which some critical event(s) occurred, resulting in the locomotor dichotomy between quadrupedality and bipedality (and the eventual origins and adaptive radiations of *Perognathus* and *Dipodomys*). During the development of this dichotomy, water regulatory efficiency became fixed at an intermediate level and independent of mass in *Dipodomys*; in *Perognathus*, as in other quadrupedal heteromyids, water regulatory efficiency continued to increase concomitant with further reductions in body mass as the prevailing pattern of increasing aridity continued. Also, it is suspected that the capacity for torpor was developed just prior to the dichotomy in locomotion, and at some critical, relatively small mass (ca 40 g) at which the costs of quadrupedal foraging during periods of excessive energy demand (low temperatures and/or reduced seed availability) exceeded the benefits. Torpor would represent a physiological alternative to relieve either temporarily or for longer periods the energetic trade-off in the inefficiency of locomotion inherent with smaller mass: during energetically stressful periods or seasons for surface activity, the energetic savings of torpor in the burrow might more readily promote positive energy balance. An alternative explanation for the evolution of torpor in smaller heteromyids as a trade-off for locomotor inefficiency might simply be the inability of individuals of small mass (and a high surface:volume ratio) to increase heat production sufficiently to offset heat loss during extreme cold, resulting in hypothermia. This alternative would be independent of food-finding ability. The evidence that torpor was developed in heteromyids at or prior to the locomotor dichotomy is that it occurs in both *Perognathus* and *Dipodomys* (see earlier); it is a finely tuned energy-conserving device in the former (Fig. 3), but is only latently present in the latter and is likely a relictual capacity.

Both *Perognathus* and *Dipodomys* were present in upper Tertiary times (Lindsay 1972, Shotwell 1967, Reeder 1956, Wood 1935), long before the formation of true deserts in southwestern North America (Axelrod 1950). Voorhies (1974, 1975) has described as fossils a *Perognathus* sp. and a bipedal kangaroo rat (*Eodipodomys celtiservator*) preserved in their burrows in early Pliocene deposits in northeastern Nebraska. Preserved with them were seed hoards indicative of their granivorous habits, and their habitat was interpreted to be a riverine area traversing a grassland with a mild, equable climate. Shotwell (1967) describes fossil *Dipodomys* spp. and *Perognathus* spp. from the middle Pliocene of Oregon with no reference to probable habitat, and Lindsay (1972) reports the presence of *Perognathus* spp. in middle Miocene deposits in what is now the Mojave Desert of California, again with no reference to probable habitat. It is apparent that *Perognathus* and *Dipodomys* were geographically wide-spread throughout much of southwestern North America in upper Tertiary times, and inhabited areas predominantly grassland and semiarid in nature (Reeder 1956).

The formation of true deserts resulted from the late Pliocene-Pleistocene uplift of the Sierra Nevada-Cascade axis, together with the transverse and peninsular ranges of California and Baja California and the ensuing rainshadow effect (Axelrod 1950, 1958). *Perognathus* and *Dipodomys*, representing lineages that for many millions of years had been subjected to progressive aridity, likely were preadapted to a desert existence, and occupied this still more arid, new environment without much further modification.

Bipedalism, as exhibited by *Dipodomys* species, would by my scenario have developed in semiarid, open habitats, likely grasslands, as an aid in traversing the expanses between foraging sites. It represents an adaptation that could then readily be exploited in desert habitats. Although there is no evidence that bipedal locomotion in *Dipodomys* confers a direct energetic advantage (Fig. 4), I think there can be no question that it provides some as yet undefined relief (i.e., foraging advantage) from energetic constraints that would be imposed on a quad-

ruped of the same mass and habitat. The evidences for this statement are these: (1) in spite of relatively large mass and large absolute energy requirements while living in habitats of limited seed production, torpor is seldom if ever used; (2) a fixed, intermediate level of water regulatory efficiency restricts seed usage to those higher in carbohydrate composition and therefore higher in MWP (MacMillen and Hinds, 1983); and (3) cheek pouch volume (i.e., food-carrying capacity) in granivorous *Dipodomys* spp. is independent of body mass, but it is strongly and positively correlated with body mass in quadrupedal heteromyids (Morton et al. 1980). Thus, accompanying bipedality in *Dipodomys* are several characteristics that can be construed as energetically liberal, at least in comparison with their quadrupedal cousins, whom they typically exceed in biomass when sympatric (pers. obs.). Yet to be demonstrated are the direct advantages of bipedality in heteromyids; among these is the likelihood of enhancing predator avoidance and escape, but others should not be dismissed without trial.

Another mystery among heteromyids, at least to me, is *Microdipodops*, which inhabits exclusively Great Basin deserts. Their habitats are not only arid but of high elevation, and, therefore, have markedly truncated growing seasons. They are mysterious because virtually nothing is known of their origins, or whether they are more closely related to *Perognathus* or *Dipodomys*. Authorities align them more closely with one or the other (Hafner 1978, Lindsay 1972), not particularly close to either (Reeder 1956), or change their minds (Wood 1931, 1935). This lack of agreement is due largely to the absence of a fossil record. It is due in part, too, to the bipedal mode of locomotion in *Microdipodops* and the assumption that this implies close relatedness to *Dipodomys*. Nevertheless, Wood (1935) emphasizes that bipedalism has arisen several times independently in heteromyids, including extinct lineages only remotely related to extant genera; I see no reason to doubt an independent origin of bipedalism in *Microdipodops*. *Microdipodops* are also mysterious from a physiological point of view. To me they represent an enigmatic compromise that combines the water and energy regulatory virtues of *Perognathus* and *Dipodomys*: they are small in size with low absolute energy requirements and efficient water regulatory capacities; they utilize torpor most propitiously; and they are bipedal. They are deserving of more attention.

The family Heteromyidae is a rather diverse group of rodents with respect to their adaptive physiology. Yet, when interpreted in light of locomotor and size differences within the family, together with paleoclimatological histories, discernible patterns emerge that are consistent both evolutionarily and ecologically.

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BEHAVIOR OF DESERT HETEROMYIDS[1]

O. J. Reichman[2]

ABSTRACT.— Activity patterns of desert heteromyids are characteristic of many nocturnal rodents, with a peak of activity near dusk and a second prior to dawn. Seasonal activity varies with environmental conditions, going from activity throughout the winter in larger species to extended periods of torpor by smaller pocket mice. The rodents forage primarily for seeds, with pocket mice tending to feed under shrubs and on relatively low-density seed patches and kangaroo rats frequently foraging in the open for relatively high-density seed patches. The animals are usually solitary, with aggression exhibited between and within species. Burrow construction can be simple to extensive. Communication occurs visually, with odor (especially at sand bathing sites), and with sound (drumming). Reproductive behaviors are characterized by brief courtships and copulation. Subsequent maternal behavior includes nursing, grooming, and other forms of general maintenance. Individuals spend considerable time autogrooming, presumably to enhance temperature regulation and reduce parasite attack. Although many of the behavioral patterns seen in heteromyids are similar to other rodents, locomotory and auditory specializations appear to yield behaviors characteristic of the group of rodents.

Observational and anecdotal information pertinent to heteromyid behavior is present in the literature beginning around the turn of the century. Although these early pieces of information are valuable in themselves, they offer no coherent view of behaviors across geographic or taxonomic boundaries. The landmark work of Eisenberg (1963) provided a turning point, and much of the work on heteromyid behavior since that time has used heteromyids as tools to answer questions of a more general and conceptual nature.

Although heteromyids suffer from many of the same problems other mammals do for behavioral studies (e.g., nocturnal activity and subterranean burrows and nests), they do offer some distinctive benefits. For example, all heteromyids possess external fur-lined cheek pouches that are used during foraging for gathering seeds. Thus, whereas most animals eat their food as they collect it, heteromyids have separate collecting and ingesting behaviors. Also, some heteromyids (kangaroo rats and kangaroo mice) exhibit a distinctive saltatorial bipedal locomotion important for foraging and/or predator avoidance behaviors. The deserts inhabited by heteromyids tend to be relatively open, allowing observation of these types of activities under special conditions (e.g., with light-amplifying devices). The rodents also are ammenable to laboratory manipulation and observation, although breeding these rodents in the laboratory is difficult. In addition, the seeds the rodents eat are particulate and thus relatively easy to quantify and analyze in studies of diet choice and foraging. With these distinctive features in mind, I will discuss heteromyid activity patterns, foraging, spacing, territoriality and aggression, reproduction, antipredator behavior, burrow construction, sensory abilities, and personal care. When I mention heteromyids in the context of some specific behavior, it is not to imply that all heteromyids exhibit that behavior. Readers should note the citations and recognize that the generalizations actually refer to the specific animals studied by the authors cited.

ACTIVITY

Activity patterns are usually inferred from the number of individuals in a population active during specific times of a diel or annual cycle. This should probably be considered a population phenomenon and I will concentrate on what aspects of the environment might generate those patterns and briefly discuss torpor and its use.

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[2]Division of Biology, Kansas State University, Manhattan, Kansas 66506.

In general, heteromyids respond to predictable daily and seasonal cyclical patterns in their environments as well as specific predictable weather phenomena. Heteromyids are primarily nocturnal (Kenagy 1973a, Lockard 1978, Reichman and Van De Graaff 1973), although diurnal activity is occasionally noted. Relatively high winds or precipitation can decrease or halt normal nocturnal activity (Kenagy 1973a, Lockard 1978). On two occasions I have noted, after an evening thunderstorm, that all wet individuals in traps were juveniles and all the adults were dry, suggesting that adults did not come out to forage until after evening rains. There is conflicting evidence for moonlight avoidance in heteromyids. Kenagy (1976a) and Schroder (1979) noted no moonlight avoidance in kangaroo rats, but Kaufman and Kaufman (1982) and Lockard and Owing (1974) suggest they do avoid moonlight. It should be noted that these studies were in different areas on different species. Evidence presented by Lockard (1978) may provide an explanation of the disparity in the other reports. He suggests that *Dipodomys spectabilis* may avoid moonlight, presumably because of increased susceptibility to predation, during times of the year when food is abundant, but be forced into periods of moonlight activity when resources are scarce. Rosenzweig (1974) presents a conceptual explanation for this phenomenon.

Various aspects of heteromyid activity relate to temperature and rainfall (French 1975, Kenagy 1973a, 1976a). Reichman and Brown (1979) elaborate on these aspects of activity and note, along with Brown and Bartholomew (1969), that the amount of food is also important in determining above-ground activity. When temperature or food availability is low (usually in the winter; French 1976), small heteromyids will tend to go into or stay in torpor for extended periods of time (perhaps up to 5 months; Reichman and Van De Graaff 1973). Apparently, larger heteromyids (approximately 18g +) rarely use torpor (Bartholomew and MacMillen 1961, Eisenberg 1963, French 1976, Kenagy 1973a, O'Farrell 1974, 1980). Whereas small homeotherms are probably more affected by cold temperatures than large ones, the larger species may be more affected by heat. Reichman and Van De Graaff (1973) noted that during one extremely hot summer, activity of individual kangaroo rats was reduced but pocket mice remained active.

Two miscellaneous features of heteromyid activity need to be mentioned. Schmidley and Packard (1967) noted that four species of pocket mice could swim by treading water for approximately one minute before becoming exhausted, floating, eventually losing coordination, and drowning. Stock (1972) found that nine species of kangaroo rats were "good" swimmers in artificial ponds and aquaria. Finally, Kenagy and Enright (1980) show that the activity of *D. merriami* in the laboratory was depressed for five days prior to a large earthquake, especially in the premidnight phase. This reduced activity abruptly disappeared the night after the earthquake.

FORAGING

Desert heteromyids are primarily granivorous (Bradley and Mauer 1971, Brown et al. 1979, Reichman 1975, 1978), although they may seasonally ingest large quantities of green vegetation and insects. One study suggests that as individual kangaroo rats encounter water stress by eating too many high-protein mesquite seeds, they switch to eating the herbaceous seed pods (Schmidt Nielson et al. 1948). Many species of heteromyids can apparently go without drinking free water for long periods of time, supporting themselves on metabolic water from food items (see MacMillen, this volume). Eisenberg (1963) noted that young heteromyids eat solid food from the time their incisors erupt.

There are important exceptions to the specialized granivory exhibited by heteromyids. Kenagy (1972, 1973b) detailed the use of saltbush leaves (*Atriplex*) by *Dipodomys microps*. Individuals of this species use their chisel-shaped teeth to strip away the salt-laden epidermis of the *Atriplex* leaves before ingesting them. Csuti (1979) noted a similar behavior and suggested that it was innate because individuals from areas without saltbush developed the behavior as juveniles as quickly as those from areas where saltbush was prevalent, but *Dipodomys ordii* never learned the leaf-stripping behavior. Reichman (1975,

1978) and Tappe (1941) noted the high use of insects seasonally, and Vorhies and Taylor (1922) report an observation of a kangaroo rat chasing and catching a moth. Kenagy and Hoyt (1980) report the reingestion of feces by *D. microps* and show that the animals differentially ingest those fecal pellets that are relatively low in inorganic ions and relatively high in nitrogen and moisture.

The diets of heteromyids apparently affect other behaviors. For example, several authors have noted the relationship between the ingestion of green vegetation and subsequent reproduction (Kenagy and Bartholomew 1981, Reichman and Van De Graaff 1975, Van De Graaff and Balda 1973). There also is apparently a relationship between the ingestion of ants by heteromyids and subsequent infection by alimentary canal helminths, although the effect of this infection on individuals is unclear (Garner et al. 1976).

One of the most striking aspects of the foraging behavior of desert heteromyids is the short length of time they actually spend above ground searching for food. Schreiber (1973) reports total foraging times of up to five hours per night for *P. parvus*, although most other reports are for significantly shorter periods. Kenagy (1973) reports total times averaging one hour, which includes time spent in the burrow on return trips. The short amount of time spent foraging is less striking when it is recognized that seeds are a relatively rich resource that can occur in high-density patches (Reichman and Oberstein 1977). A parameter that is perhaps more significant ecologically than simple total foraging time is the time spent at each foraging stop (time in a patch) and the time (and distance) between patches. Bowers (1982) noted that in a three-species community the smallest pocket mice exhibited the shortest times within and between patches, and kangaroo rats had the longest times for both. An intermediate-sized pocket mouse was also intermediate in these two time parameters. Thompson (1984) also found that the relatively larger bipeds spend more time stopped, and travel longer distances between stops, than the smaller quadrupeds.

Another distinctive feature of desert heteromyid foraging is the bipedal hopping of the kangaroo rats (Bartholomew and Caswell 1951) and kangaroo mice. This contrasts with the quadrupedal locomotion of the pocket mice (Bartholomew and Cary 1954). Significantly, almost no overlap in body size occurs between the quadrupedal pocket mice and bipedal kangaroo rats, although kangaroo mice are small and the quadrupedal *P. hispidis* approaches the size of some of the smallest kangaroo rats. Currently some question over the adaptive significance of these different locomotory techniques exists; this will be discussed later by Price and Brown (this volume).

There are indications that some desert heteromyids climb occasionally or extensively. Kenagy (1972) details the climbing of *D. microps* in saltbushes to obtain leaves, and Rosenzweig and Winakur (1969) suggest that there may be a vertical component to heteromyid foraging. I have observed large *D. spectabalis* climbing in *Ephedra* to harvest flowers, but did not find heteromyids climbing in bushes in an earlier study (Reichman 1979).

There seems to be an inverse relationship between the size of a heteromyid species and the distance it travels while foraging during a night (Bowers 1982, Thompson 1982a,b, and in review). This is true for both average distance between stops and total distance through the night. Thompson (1982a, 1984) reports average distances between foraging stops of 7.52 m, 5.02 m, and 2.65 m for *D. deserti*, *D. merriami*, and *P. longimembris*, respectively. I have observed individual *D. merriami* moving up to 45 m before stopping to forage, and other authors have observed similar distances (Bowers 1982, Thompson 1982a,b). Schroder (1979) found that adult *D. spectabilis* spent less than 22 percent of their time more than 6 m from their burrows, but that they average 68 m per foraging trip, and total 350 m per night in foraging travels. Kenagy (1973a) reported a maximum running speed for a kangaroo rat being chased as 32 kph, and I have calculated speeds of 16 kph in the field for individual *D. merriami* foraging freely (i.e., not being chased). Average foraging speeds are probably significantly less, as Thompson (1984) reports mean speeds in transit of 6.28, 3.27, and 1.76 kph for *D. deserti*, *D. merriami*, and *P. longimembris*, respectively.

Once an animal begins to forage, a number of senses apparently play roles in detecting seeds. Generally, heteromyids seem to be very aware of their surroundings, perhaps using vision to orient and note changes in their local environment (Hall 1946), although Reichman and Oberstein (1977) did not find visual cues to be important in laboratory studies of foraging. Once general areas for foraging are located and entered, olfaction probably becomes important for seed detection. Reichman and Oberstein (1977) found that kangaroo rats in a laboratory experiment were able to detect seeds to a depth of up to 20 cm, and the authors present a regression equation for the relationship between seed detection by captive kangaroo rats and the depth/size of a buried packet of seeds. Lockard and Lockard (1971) and Reynolds (1958) present information from the field dealing with the accuracy of underground seed detection, and Johnson and Jorgensen (1981) suggest that soil moisture is important for seed detection by olfaction. Reichman (1981) discusses the nature of olfaction as a cue for foraging heteromyids.

In an intriguing study, Lawhon and Hafner (1981) show that tactile cues may be the final sense used to judge the nature of a food item. They found differences between species in tactile abilities, and found that individuals most often misjudged nonedible food items that resembled edible items in shape or texture, regardless of weight or overall dimensions. The tactile input discussed by Lawhon and Hafner (1981) comes from actual touching with the forepaws, and is probably important and effective for an animal with its eyes on top of its head. Eisenberg (1963) reported another use of tactile senses involving the long vibrissae of the rodents. He noted that even rapidly running or hopping rodents leave trails in the sand from their dragging vibrissae, and he suggested that this assists the animals in maintaining their balance while running.

Once heteromyids find a seed or patch of seeds, they excavate in a manner typical of rodents, using the forepaws for the initial excavation and moving the soil to the rear, where it is kicked out by the hind legs (Eisenberg 1963). Eisenberg alludes to the tactile cues discussed by Lawhon and Hafner (1981) as he describes how the rodents then sift the soil they have excavated for seeds. Kenagy (1972) and Csuti (1979) describe other food acquisition behaviors associated with vegetation.

Once a food item is secured, a heteromyid can either eat the item immediately or put it in its cheek pouches for transport and storage. This separates the gathering and eating process and has important implications for foraging. From my observation, a heteromyid rarely eats an item at the collection site, but, rather, pouches it and returns to the burrow. Presumably, the burrow provides a more equable environment in which to sort seeds than does the surface, which is hotter (or colder in winter), drier, and rich in predators. Reichman (1977) has shown that although heteromyids do not apparently gather food into their pouches in the exact proportions available, a more diverse sample of seeds is found in the pouches than ingested, suggesting that the rodents do gather items they do not subsequently ingest. Animals without cheek pouches would usually eat a food item as it was obtained. Morton et al. (1980) show that cheek pouch volume scales positively with body mass in grams (volume of cheek pouches in $cm^3 = 0.065\ mass^{0.887}$). They also suggest that a heteromyid could fulfill its total daily requirement with one full load of seeds from its pouches. This, plus the observation that animals rarely are captured with full pouches (Reichman 1978), presents a puzzling question as to why individuals would return to their burrows before filling their pouches. Nickolai and Bramble (this volume) offer an interesting explanation.

The husking of seeds is highly variable between species and individuals, although Rosenzweig and Sterner (1970) suggest that relative husking rates are a phenomenon that might promote coexistence between sympatric heteromyid species. The authors show that larger species husk more rapidly than smaller species, but that the smaller species are more efficient per gram of body weight. Rosenzweig and Sterner (1970) used relatively large domestic seeds and it is not known how this relationship would extrapolate to smaller, native seed species.

There are several additional foraging behaviors exhibited by desert heteromyids. Vorhies and Taylor (1922) suggest that individual

heteromyids might rob the seeds stores of other individuals. Tappe (1941) and Clark and Comanor (1973) found that heteromyids occasionally dig into ant mounds, presumably to secure seeds. Heteromyids also eat many insects (Reichman 1975, 1978), and I have found cheek pouches full of headless ants. These ants may have been "husked" to minimize the probability that the consumer would be bitten. One peculiar behavior noted by Benson (1935) was that of a *D. deserti* kicking sand over a novel food item placed near a burrow by Benson.

One of the most intriguing aspects of heteromyid behavior is the caching of seeds. Voorhies (1974) has found cached seeds associated with fossil pocket mouse burrows that are nearly 10 million years old, so it is an ancient behavior, perhaps associated with the development of cheek pouches. Relatively little is known about caching by pocket mice (Blair 1937) or small kangaroo rats, but most of the large kangaroo rat species are known for their elaborate burrows in which they store large quantities of seeds (Culbertson 1946, Hawbrecker 1940, Reynolds 1958, Shaw 1934, Tappe 1941, Vorhies and Taylor 1922). Some species store on the surface as well as below ground (*D. heermani*, Tappe 1941; *D. ingens*, Shaw 1934), but most store seeds below ground. The piles are usually sorted by species, even if they have been gathered from mixed-species patches, and some of the quantities are huge. Vorhies and Taylor (1922) report caches of from 5 to 5750 gms for *D. spectibalis*, Shaw (1934) found caches of from 1 to 8¼ quarts, and Tappe (1941) found dozens of caches.

Eisenberg (1963) discusses caching by several species in the laboratory and found a possible tendency for females to cache more than males. Lawhon and Hafner (1981) show that pocket mice cache more of the seeds available than kangaroo rats, and that hoarding is greater in the fall and spring than in the winter. Although little is known about the underground regimes of cache management and use, Kenagy (1973) noted that kangaroo rats are quite active underground during the 23 hours a day they are not above ground foraging. Studies I have recently begun with D. T. Wicklow reveal that approximately 20 species of fungi can be found in the cheek pouches and cache environments of these rodents, and that some of these fungi could have important implication for cache management behaviors.

The benefits of caching could include long-term storage for periods of low production, enhancing nutritional and/or moisture conditions of the seeds, and protection of seeds from robbing by other granivores.

Several aspects of heteromyid foraging behavior, as mediated through anatomy and physiology, have been implicated in the community structure of the rodents (see Price and Brown, this volume). Although much controversy remains, most investigators agree that the bipedal/quadrupedal relationships, cheek pouches and seed storage, microhabitat choice and use, and seed patch density selection are important behavioral components that impinge on community structure. Reichman (1981) has suggested that the bipedal/quadrupedal difference could help promote coexistence between kangaroo rats and pocket mice, but this has recently been brought into question by Thompson et al. (1980), who have shown that bipedal locomotion is no more energetically efficient than quadrupedal locomotion for similar-sized individuals. Seed size selection behaviors have been suggested as means of coexistence (Brown 1975, Mares and Williams 1977), but other authors have questioned the sufficiency of this explanation (Lemen 1978, Smigel and Rosenzweig 1974). Numerous studies have suggested habitat selection as a means of coexistence among sympatric heteromyids (Lemon and Rosenzweig 1978, M'Closkey 1980, 1981, O'Dowd and Hay 1980, Rosenzweig 1973, Rosenzweig and Sterner 1970, Rosenzweig and Winakur 1969, Stamp and Ohmart 1978, Thompson 1982a, b) and other authors state that patch density selection is important (Hutto 1978, Price 1978, Trombulak and Kenagy 1980, Wondolleck 1978, but see Frye and Rosenzweig 1980) and related to both seed size selection and habitat selection through seed distribution (Reichman 1981, Reichman 1983, Reichman and Oberstein 1977). It is intuitive that all these behaviors could be, and probably are, important components of community phenomena noted in the heteromyids (Bowers and Brown 1982).

Further research is mandatory before a coherent picture of the relative importance of these behaviors, and the communities and localities where they are important, is established. In addition, other behaviors, such as predator avoidance, may be important in determining desert heteromyid rodent community structure.

Predator Avoidance Behavior

Heteromyids live in an environment rich in potential predators (Hall and Kelson 1959). Vorhies and Taylor (1922) list numerous predators on *D. spectabilis* and note that, of 592 owl pellets they examined, 230 contained kangaroo rat remains. One means of avoiding predators is color crypticity, and Benson (1933) shows that many rodents in the southwestern United States include substrate color matching in their repertoire of predator avoidance schemes.

Heteromyids seem to have a general awareness of their surroundings and are very sensitive to peculiar sounds and sights. Eisenberg (1963) notes that novel items in their cage elicit attention, and occasionally displacement behaviors such as digging. Hall (1946) states that heteromyids are drawn at night to newly disturbed areas (e.g., a boot heel dragged in the soil surface), and many investigators are familiar with kangaroo rats burying traps under a pile of dirt. Some heteromyids are known to plug their burrows at night (Chapman and Packard 1974; Compton and Hedge 1943), and this may partially be a response to potential predation.

As discussed in the section under activity patterns, heteromyids seem to avoid environmental conditions, such as bad weather or bright moonlight, that might hamper their ability to detect predators or make them more obvious to predators. Apparently, both hearing and sight are important components of predator detection. Webster (1962) and Webster and Webster (1971, 1972, 1980) have documented the extremely accurate hearing of kangaroo rats, especially for low-frequency sounds, and they suggest that this has developed in response to predator detection. Desert conditions may be poor for sound transmission (hot and dry), and this would place pressure on the animals to develop exceptional hearing. Another indication of the excellent hearing in heteromyids is enlarged auditory bullae, most notable in the kangaroo rats. Not only is their hearing good, but kangaroo rats have also developed especially acute reception at those frequencies of sound made by a rattlesnake's rattle and an owl's wing (Webster 1962). In other studies, Webster and Webster (1971, 1972, 1980) have shown that kangaroo rats can effectively detect predators with either vision or hearing, but if both senses are eliminated the rats usually succumb to predators.

Bartholomew and Caswell (1951), Thompson (1982a), and Hay and Fuller (1981) suggest that the bipedal locomotion and ricochetal bounding of kangaroo rats might be primarily an adaptation to predator avoidance. Certainly the irregular hopping would be distracting to a predator, and Eisenberg (1975) notes that kangaroo rats immediately hop away when a rattlesnake is nearby. Hay and Fuller (1981) found that heteromyids are more selective in their diet choice when they forage in the open than when they forage in the presumed relative safety of a shrub, and the authors suggest that this selectivity may be due to predator pressures in the open. The opposite prediction, that of low selectivity in the open, could be made if predator pressures are high in the open areas. In this explanation, heteromyids would move rapidly through the open areas, gathering seeds indiscriminantly into their pouches, making the critical diet choices later in the relative safety of their burrows (Reichman 1977, 1981).

Spacing, Territories, and Aggression

For the most part, heteromyids are solitary animals (Blair 1937, 1943, Dixon 1959, Scheffer 1938), living singly in their burrows (Eisenberg 1963 and Martin 1977 describe them as "asocial"). Monson and Kessler (1940) found only 3 of 44 burrows with more than one individual *D. spectabalis,* and Monson (1943) found 41 of 53 mounds to be singly occupied. Several of the dual occupancy burrows had two adults, but most were females and their offspring. Some species are noted

for having more than one burrow, and Chapman and Packard (1974) report that male *D. merriami* average 6–7 burrows and females have approximately 5 burrows each. Current observations in the field by several investigators suggest that this may be more common than is generally thought. Individuals occupying more than one nest may explain why in some areas a large percentage of burrows appear to be unoccupied. Schroder and Geluso (1975) found 42 of 121 *D. spectabilis* mounds unoccupied. All mounds combined showed a uniform spatial distribution, whether occupied or not.

Data on the home range size of heteromyids are scattered throughout the literature, but one feature that seems to emerge is that home ranges are not directly related to the average body size for a species. Small pocket mice frequently exhibit home ranges near the size of larger species (Chew and Butterworth 1964), and Schroder (1979) reported a smaller home range for *D. spectabilis* than *D. merriami*. There are reports that males have larger home ranges than females (Maza et al. 1973) and that the home ranges of male and female kangaroo rats overlap extensively (O'Farrell 1980). Holdenreid (1957) and Flake and Jorgensen (1969) report no difference in dispersal rates between males and females in a population, although it is primarily the juveniles that disperse. Recent work by Tom Jones (see Munger, Bowers, and Jones, this volume) suggests that individual kangaroo rats do not move far from their natal burrow.

Although areas around a home burrow are not as aggressively defended as are territories of other mammals (Eisenberg 1981), heteromyids apparently do show some degree of territoriality, as manifested by aggression and possibly by scent marking, although the latter proposition is unproven. Eisenberg (1963) describes various types of marking, including a perineal drag, and suggests these are for territorial identification. Borchett et al. (1976), Griswold et al. (1977), Laine and Griswold (1976), and Randall (1981a, b) present details of sand bathing by kangaroo rats and suggest that the odors produced may connote information about the species, sex, and possibly reproductive condition of the depositor. Quay (1953) notes the sexual and seasonal characteristics of the dorsal gland in five species of kangaroo rats, and discusses its possible role of scent marking.

Another behavior that may be related to territorial pronouncements is drumming with the hind feet. It is relatively easy to get an adult *D. spectabalis* to respond with drumming by tapping lightly on their mound. Eisenberg (1963) noted drumming in *Dipodomys, Perognathus,* and *Microdipodops* species in relation to aggression, and teeth chattering in the same context. Kenagy (1976b) observed drumming in the field during a contest between male kangaroo rats, eventually leading to copulation between one of the males and a female.

Overt aggression between individual heteromyids may be rare, or simply rarely seen. Eisenberg (1963) provides extensive information of the types of aggressive interactions generated in a laboratory setting, and excellent descriptions of the modes of attack and associated behaviors such as scratches and growls. The general trend in Eisenberg's laboratory study, and those of Hoover et al. (1977) and Blaustein and Risser (1974, 1976) is for large individuals of one species to eventually win over smaller individuals of another species, although the effort involved varied greatly. Congdon (1974) notes a similar relationship in the field, and Vorhies and Taylor (1922) describe fights in the laboratory between *D. spectabalis* and *D. merriami* that are "savage and to the death." I have videotapes of a kangaroo rat pouncing on a pocket mouse at a rich pile of seeds. Conversely, I have watched two separate *D. merriami* chase adult *D. spectabalis* away from a foraging area. Aggression can be related to the sex and reproductive condition of the participants (Eisenberg 1963), and Kenagy (1976b) provides an excellent description of aggression observed in the field between two males courting a female.

Upon occasion, heteromyids will have aggressive bouts with nonheteromyids. I have observed kangaroo rats chase off *Peromyscus* individuals at artificially placed seed piles, and Shaw (1934) notes similar events. McCue and Caufield (1979) report a grasshopper mouse attacking and dismantling a kangaroo rat in daylight hours.

REPRODUCTION AND PARENTAL CARE

Desert heteromyids generally have one or two litters a year. Females are usually in estrus for specific periods, but males may be scrotal the entire year (Bradley and Mauer 1971, Reichman and Van De Graaff 1973). Juvenile female kangaroo rats develop swollen vaginas at about six weeks and can conceive at 12 weeks (Eisenberg 1963).

Observation of courtship and reproduction are rare from the field, although Engstrom and Dowler (1981) and Kenagy (1976b) provide interesting field observations. Daly et al. (1980) note that *D. agilis* and *D. merriami* in reproductive condition prefer traps that contain conspecific odors, whereas nonreproductive individuals show no preferences between odorized and odor-neutral traps. The preferences appear to be independent of the sex of the donor and the recipient. Laboratory studies suggest that near the onset of estrus males become more tolerant of and interested in females (Eisenberg 1963, Martin 1977). Prior to that, males and females can be very aggressive toward each other (Butterworth 1961), or live in the same arena without aggression (Eisenberg and Isaac 1963). Eisenberg (1963) reports that, as the time for copulation nears, a male and a female may share a common nest box for one night, after which they return to their own nest boxes and a peaceful coexistence.

A number of studies describe the copulatory behavior of various heteromyids (Behrends 1981, Dewsbury 1972, Eisenberg and Isaac 1963, Hayden et al. 1966), and Eisenberg (1963) describes an elaborate protocol for reproductive behavior in the heteromyid species he studied in the laboratory. Basically, there is some mutual attention in the few minutes prior to copulation. Subsequently, the male mounts the female from the rear while she exhibits lordosis. After several seconds to several minutes of thrusting and presumably ejaculating, the male dismounts and shows little interest in the female. In some cases, one or the other of the sexes may rush the other, inciting another copulatory bout. Hayden et al. (1966) reported that some pairs fall on their sides during copulation and continue to copulate in this position.

The gestation period is relatively short (18–30 days; Butterworth 1961, Day et al. 1956, Holdenreid 1957) and is almost always accompanied by nest building on the part of the female (Eisenberg 1963). Eisenberg (1963) reports that most births occur during the day and, though mothers will eat any dead neonates, no aggressive behavior is subsequently demonstrated toward their surviving offspring. The young are born in a relatively precocial state (Eisenberg 1963). At the time of birth, the female may stand or lie on her side, assisting the process with her teeth and forepaws (Butterworth 1964, Eisenberg 1963). Subsequent to parturition, the female ingests the placenta. Van De Graaff (1973) notes that the bone formation in the extremities of kangaroo rats is greater than for similarly aged pocket mouse embryos and juveniles, which still have major limb components made of cartilage. Eisenberg (1963) notes that muscular coordination seems to develop in the young from anterior to posterior.

Parental care is carried out entirely by the female. She crouches to nurse the young, and she will move them about the nest by carrying them in her teeth with a grasp behind the neck (Eisenberg 1963, Tappe 1941). The female may plug the entrance to the nest chamber when she is not in the nest (Eisenberg 1963). As weaning approaches, the female will begin to ignore her young, eventually even shoving them away as they try to nurse. As the siblings begin to leave the nest, dominance hierarchies are already being established (Eisenberg 1963). LeVick (1982) does not find any ultrasonic communication between mothers and their offspring in *D. ordii*, but both he and Eisenberg (1963) report a broad range of audible sounds from infants aged 2–14 days. Fourteen days corresponds to the time the young begin to eat solid foods and move from the nest (LeVick 1982).

BURROW CONSTRUCTION

An inverse relationship appears to exist between the size of a heteromyid species and the amount of information on its burrows that has been published. This could be because a similar relationship exists between the complexity of the burrows and the size of

the species. Generally, pocket mice have relatively simple burrows and the largest kangaroo rats are known for their large, conspicuous, and complex mounds and burrow systems.

Blair (1937) reports that the burrow of *P. hispidis* is rather short and simple, with only one entrance and one nest chamber. Scheffer (1938) notes that the burrows of *P. parvus* are also simple, but may include a hairpin turn directly under the opening, and run to a depth of 76 inches. Chapman and Packard (1974) found that female *P. merriami* have more complex burrows than males, and that the adults frequently plug unused burrow openings. Eisenberg (1963) found *Microdipodops* burrows in loose sandy soil, and other authors have noted the soil texture where burrows are constructed (Anderson and Allred 1964, Compton and Hedge 1943, Deynes 1954, Tappe 1941, Vorhies and Taylor 1922). In desert areas burrows are usually obvious around the base of shrubs where loose, windblown soil accumulates, providing a good location for burrow construction. Kenagy (1973a) gives information of the construction of the burrows of *P. longimembris*, *D. merriami*, and *D. microps* in the field, and Eisenberg (1963) gives details for several species in the laboratory, including descriptions of the actual digging behaviors.

The most extensive information about burrow construction is available for the large species of kangaroo rats, including *D. spectabalis* (Best 1972, Holdenreid 1957, Monson 1943, Monson and Kessler 1940, Vorhies and Taylor 1922), *D. venustus* (Hawbreker 1940), *D. heermani* (Tappe 1941), *D. ingens* (Shaw 1946), and *D. nitratoides* (Culbertson 1946, Fitch 1948). Generally these large species have mounds that are approximately two or three meters in diameter and rise from one-half meter to one meter above the ground. Through the mound and down into the ground pass numerous runways. Connected to the runways are various nests and large, flask-shaped caches where seeds are stored. Some of the caches are walled off, but most remain open. The mounds are constructed by the rat kicking dirt with its hind legs up on top of the existing structure. Through time, the area surrounding the burrows is slightly lowered by the excavation, and the mound is built higher. Best (1972) notes that it takes from 23 to 30 months to build what would be considered a mature mound. Mounds that are left vacant begin to deteriorate noticably within a month and are almost completely gone within a year.

SENSORY ABILITIES

Although not much is known about the sensory abilities of heteromyids, some intriguing work has been carried out with the hearing ability of kangaroo rats. Heffner and Masterson (1980), Webster (1962), and Webster and Webster (1971, 1972, 1980) have noted the impressive hearing ability of kangaroo rats across a broad range of frequencies (1–60 KHz). Heffner and Masterson (1981) also note that kangaroo rats are particularly good at locating the origin of a sound, and Webster (1962) details the hearing of kangaroo rats in relation to sounds made by predators. I have noted while watching kangaroo rats in the field that they are startled only by certain kinds of noises. All loud noises get their attention, but metallic clicks seem less disturbing than scratching noises made by a boot in the dirt.

Pocket mice and kangaroo rats can apparently smell seeds in the soil, even to great depths (Lockard and Lockard 1971). Reichman and Oberstein (1977) show the relationship between the ability of a kangaroo rat to detect a seed patch and the size/depth of the seeds and Reichman (1981) discusses olfaction and seed detection ability. Although it is difficult to determine whether rodents cannot smell an item or simply choose not to seek it, it does appear that kangaroo rats have better olfactory ability than do pocket mice. Daly et al. (1980) noted that certain rodents, including kangaroo rats, responded to odorized traps, preferring them if the respondents were in reproductive condition.

I know of no studies on the vision of heteromyids, but it is pertinent to note that their eyes are on top of their rounded heads, making vision ventrally and forward somewhat restricted.

PERSONAL CARE

Personal care seems to be accomplished by two major behaviors. One is associated with

autogrooming and washing, and another with the care of the dorsal gland possessed by many heteromyid species. Eisenberg (1963) details the grooming sequences of various heteromyid species. Grooming frequently occurs shortly after awakening, and includes scratching with the teeth and claws, combing the fur and cheek pouches, and washing with saliva. The animals also apparently bite off any ectoparasites they can locate and reach (Vorhies and Taylor 1922, found fleas of the genera *Ctenophthalium* and *Trombicula* on bannertailed kangaroo rats).

The presence of a dorsal gland on many kangaroo rats has been noted for some time, and Quay (1953) has investigated its structure. Kangaroo rats with active glands apparently groom the secretions over their bodies regularly (Griswold et al. 1977, Borchett et al. 1976, Randall 1981a, b). Although some of the secretion on the hair may assist in reducing evaporative water loss (Quay 1965) or serve as insulation (Randall 1981a, b), too much is apparently detrimental and is groomed off, usually by sandbathing (Randall 1981a, b).

SUMMARY

In many ways the behavior of desert heteromyids is similar to what is known about other nocturnal rodents. At the level of precision available from the current data, it appears that their basic ways of securing food, courting and reproducing, and protecting themselves from the environment and predators are much like those of other rodent families (Eisenberg 1981). A few anatomical and physiological specializations, however, give the desert heteromyids some distinctive behavioral capacities. Certainly one is the bipedal locomotion used by kangaroo rats and kangaroo mice. This is rare for small mammals, and it apparently is not an especially efficient means of locomotion for a small (i.e., low mass) animal (Biewener et al. 1981). Perhaps bipedality simply provides a means of rapid locomotion for moving through the open to forage or avoid predators.

A second feature, possessed by all heteromyids, is cheek pouches. Pouches, used for the temporary storage of seeds while foraging, grossly alter the manner in which a rodent would forage. The pouches make gathering food and eating food two different events ecologically and allow the possessor to quickly gather food while foraging before returning to the relatively safe burrow where appropriate dietary decisions can be made. Pouches also allow the animals to gather large quantities of seeds when they are available. The surplus seeds can then be stored and used at a later date when resources are perhaps less abundant, thus leading to elaborate caching behaviors. Even the use of a food resource such as seeds is adaptive in a desert setting, as seeds are rich in energy and nutrients and thus require less time spent in the hostile above-ground environment, and seeds persist in the soil through time.

A final specialization is in degree, not kind. Heteromyids, and especially kangaroo rats, have exceptionally good hearing, which apparently serves them well in the desert where sound may travel poorly. What is particularly striking about their hearing is its apparent fine tuning for the sounds made by two major predators on the animals, rattlesnakes and owls.

Several areas of heteromyid behavior remain poorly understood or controversial. Although much is known about foraging behavior, several important groups of heteromyids (e.g., the kangaroo mice and the large kangaroo rat species) are underrepresented in the literature. The ways in which differences in foraging affect heteromyid rodent community structure are currently being hotly debated, as are body size relationships within the family. Almost nothing is known about the effects of predation on rodent behavior and community structure, even though most would agree that it is important. As techniques for behavioral observation expand, we can expect more of the important pieces to the heteromyid puzzle to be fitted in.

We tend to think of the desert as being an especially harsh environment, and for humans it is. As this chapter, and others in this symposium, have shown, however, the desert can be much more hospitable to an animal that is adapted to its extremes. It seems safe to assume that most of the behaviors exhibited by desert heteromyids are in some general or specific way tied to the physical environment in which they flourish.

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DESERT RODENT POPULATIONS: FACTORS AFFECTING ABUNDANCE, DISTRIBUTION, AND GENETIC STRUCTURE[1]

James C. Munger[2], Michael A. Bowers[2], and W. Thomas Jones[3]

Abstract.— Literature concerning North American nocturnal desert rodents is reviewed to delimit current knowledge of the importance of various factors to abundance, distribution, and genetic structure. In addition, strategies for further study are suggested. *Abundance*: That increased rodent abundance often follows flushes of annual plant growth that follow favorable rains is well established. The ultimate reason for this pattern has not been established. Competition is important as well, but predation and parasitism have received little consideration. *Distribution*: Patterns of distribution have been shown to correspond to temperature, moisture, substrate, or vegetative parameters. An important question that remains is to determine the relative importance of physiological specialization vs. interspecific interactions leading to habitat specialization. *Genetic Structure*: Despite a number of studies on desert rodent systematics, little is known of the genetic structure of desert rodent populations. Behavioral, demographic, indirect genetic, and direct genetic evidence can be used to detect deviations from panmixia.

Although desert rodents have been the subject of hundreds of studies on a number of levels (e.g., physiology, behavior, population ecology, community ecology, and systematics), it is not yet feasible to make general conclusions as to the relative importance of various factors in determining the abundance, distribution, and genetic structure of populations of desert rodents. This article is designed to help remedy this problem. We consider the possible importance of each of a number of factors, reviewing the relevant literature to determine what is known at present, then suggesting ways in which the gaps in our knowledge can be filled.

With few exceptions, we have limited our treatment to the nocturnal rodents that inhabit the deserts of North America. In addition, much of our treatment concerns rodents of the family Heteromyidae, a bias that results in large part from the greater amount of work done on that group relative to other groups.

Abundance and Dynamics

Discussion of factors affecting the abundance and dynamics of desert rodent populations has, in the past, centered on the importance of food, water, and vegetation. More recently studies have focused on interactions among rodent species. In addition to discussing these factors, we consider predation and parasitism and argue that both are worthy of study, although little evidence exists concerning their importance.

Food and Water

Perhaps the best-documented pattern of desert rodent abundance is increased population growth and reproduction following rainfall and the growth of plants, particularly annuals. This pattern has been shown to hold for many rodent species in many geographical areas (Reynolds 1958, Chew and Butterworth 1964, Beatley 1969, Bradley and Mauer 1971, Van de Graff and Balda 1973, Newsome and Corbett 1975, O'Farrell et al. 1975, Reichman and Van de Graff 1975, Whitford 1976, Dunigan et al. 1980, Petryszyn 1982). The exact timing of rainfall is at least as important as the total amount. Both Beatley (1974) and Petryszyn (1982), working in deserts with very different precipitation patterns, have shown that rainfall early in winter is important in germination and early growth, and rainfall in the spring is necessary for further growth and flowering.

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[2]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.

[3]Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907.

Several hypotheses have been proposed to account for this apparent dependence of rodent populations on plant growth; all are based primarily on reproductive responses to external factors, not on effects on survivorship. First, Chew and Butterworth (1964) suggested that rodents may consume hormonal substances within the plants that initiate reproduction. Such a triggering mechanism has been demonstrated for microtines (Berger et al. 1981 and refs. therein). Second, Chew and Butterworth (1964) and Van de Graaff and Balda (1973) found that rodents gained weight at times of plant growth or in areas where green vegetation was present and argued that ingesting green vegetation improves general body condition, enabling individuals to reproduce. Third, Beatley (1969), Bradley and Mauer (1971), and Reichman and Van de Graaff (1975) found an increased availability or consumption of green vegetation during or prior to reproduction and argued that water and vitamins in the plants are necessary to compensate for increased demands during gestation and lactation. Deficiencies in vitamins (such as A or E) can lead to sterility or fetal death (Wright 1953). Finally, based on the common trend that increased growth of annuals is a prelude to increased availability of seeds and insects, O'Farrell et al. (1975), Reichman and Van de Graaff (1975), Whitford (1976), and Dunigan et al. (1980) suggested that increased reproduction may depend on increased food availability.

The problem of distinguishing among these hypotheses can be made more tractable if we recast them to reflect requirements that are common to all animals: water, energy, and nonenergetic nutrition (simply termed *nutrition* below; includes essential fatty acids, amino acids, vitamins, and minerals). First, the "hormonal substances" hypothesis is probably based on a proximate mechanism. Rodents should not come to rely on an external cue, such as a hormonal substance, unless that cue is tied to some ultimate benefit such as water, energy, or nutrients. Second, increased "general body condition" is probably due to the increased availability of water, energy, and/or nutrients. Finally, "increased food availability" confounds the effects of energy and nutrition. The problem, then, is to distinguish among the relative importance of water, energy, and nutrients (all of which are more available following favorable weather conditions) in leading to population increases of desert rodents.

Several studies and observations, other than the above correlative studies that led to the formulation of these hypotheses, bear on this question. Breed (1975) showed that water deprivation resulted in reduced reproductive activity in female Australian hopping mice (*Notomys alexis*), as measured by ovarian and uterine weights and follicular development. In another laboratory experiment, Yahr and Kessler (1975) found that reproductive activity ceased in Mongolian gerbils (*Meriones unguiculatus*) that received lettuce only once a week but continued in control animals that received daily lettuce rations. In this study, the effect of water and nutrient availability are confounded because lettuce may contain required nutrients as well as water. Soholt (1977) found that free water intake in lactating *Dipodomys merriami* increased by more than 200 percent over that of nonreproductive females, though gestating females exhibited no increase. However, because carrots were used as the source of free water, it is not possible to distinguish between the importance of water and any nutrients that carrots may contain. Furthermore, these experiments do not demonstrate an absolute need for free water during lactation because females were not actually deprived of free water; they simply showed an increase in water use.

Two studies have shown a correlation between the density of *Neotoma* populations and the local abundance of *Opuntia* cactus (Brown et al. 1972, Cameron and Rainey 1972, Olsen 1976), although it is unknown whether the correlation is due to increased food and water availability or to increased protection against predators (woodrats often used cactus joints in constructing nests; Brown et al. 1972). In addition, Petryszyn (1982) found that *N. albigula* densities failed to respond to a single winter of higher than average rainfall, but did respond to two consecutive good years. This can be interpreted to indicate that the abundance of annual plants (which would respond to a single good winter) does not limit woodrat populations

but the growth of perennial plants (which perhaps only respond to consecutive good years) may limit woodrat populations (Petryszyn pers. comm.).

By providing a source of supplemental water, Christian (1979a) was able to cause an increase in reproductive activity in two species and increased density in one species in a community of three species of Namib Desert rodents. The species most ecologically similar to North American heteromyids because of its superior ability to conserve water (*Desmodillus auricularis*; Christian 1979b) was little affected; Christian (1979a) argued that factors other than the availability of water determine its population size. The two species more similar to North American desert cricetids or sciurids (they are poorer at water conservation than *D. auricularis*; Christian 1979b) did respond to supplemental water, indicating that the availability of water is important in determining the abundance of these species.

Two observations indicate that availability of green matter and the water or nutrients contained therein are not a requisite for reproduction. O'Farrell et al. (1975) found that female *Perognathus parvus* sometimes remained lactating for more than a month after vegetation had dried up; vegetation may have been required for initiation of reproduction, but not for lactation. Whitford (1976) observed a population increase during a year in which there was virtually no growth of green matter.

The importance of energy or nutrients is indicated by two studies in which seeds were added to experimental plots. Addition of seeds to plots in short grass prairie caused an invasion of seed-eating *Dipodomys ordii* (Abramsky 1978). Addition of seeds to plots in the western Chihuahuan desert caused a threefold increase in numbers of the largest species at the site (*D. spectabilis*) but a slight decrease in numbers of smaller species (Brown and Munger, in preparation).

The results of the studies discussed here indicate that it is unlikely that variation in a single factor, whether it be water, energy, or nutrients, will be able to account for all situations where desert rodent population increases are correlated with bouts of rainfall. There are several reasons for this. First, species of desert rodents may vary in their requirements. This is illustrated by Christian's (1979a) finding that three species of Namib Desert rodent responded in different ways to the addition of water. It is apparent that physiological differences among species must be considered when assessing the effects of various factors on abundance.

Second, geographical differences in the stressfulness of the environment may be important. For example, all studies that showed population responses not tied to increased water availability were carried out in relatively benign (with respect to water stress) environments: south central Washington (O'Farrell et al. 1975), Chihuahuan Desert above 1000 m elevation (Whitford 1976, Brown and Munger, in preparation), and short grass prairie (Abramsky 1978). The studies that showed an apparent reproduction dependence on free water were carried out in the more stressful lower Sonoran Desert, Mojave Desert, and Namib Desert. To resolve this problem, water and food addition experiments should be performed in the harsher lower deserts as well as in the relatively benign higher deserts.

Third, insects, whose populations often respond to increased plant growth, may provide a source of moisture for several months after annual plants have died.

Finally, although these hypotheses have been couched in terms of the effects of various factors on reproduction, these same factors are likely to affect survivorship as well. Probably because of the energetic and nutritive demands of reproduction, survivorship of breeding adults tends to be negatively associated with the degree of reproductive activity (French et al. 1974, Conley et al. 1977) and thereby negatively correlated with the amount of rain-induced plant growth (Christian 1980). Juvenile survivorship, on the other hand, should be increased by the increased availability of food and water. This pattern was found by Whitford (1976), who showed that the survivorship of young heteromyids was much lower in a year with a poor seed crop than in years with good crops. Increased juvenile survivorship may have contributed directly to increased densities shown by the studies cited above, or indirectly via

reproduction in adults: increased probability of survivorship of young during years of high plant growth and subsequent plant availability may be the ultimate factor that leads adults to reproduce in those years (Reichman and Van de Graaff 1975).

As noted above, desert rodent populations appear to be strongly influenced by the growth of plants following sufficient rainfall. One might ask then whether it is necessary to even consider factors other than food and water, since the availability of water, energy, and nutrients seems to explain a large part, if not all, of the variation in desert rodent abundance. We strongly feel that other factors should be considered, if only to rule them out. Below we describe a series of studies on desert annual plants that illustrates the need to consider other factors.

The abundance of desert annual plants is, as mentioned above, dependent on the pattern and amount of rainfall. Other factors have been shown to be important as well. First, intraspecific evidence appears to limit the number of seeds that germinate (Inouye 1980). Second, large-seeded species of annual plants appear to be able to outcompete small-seeded species, but seed predators (especially rodents) apparently prefer larger seeds. Rodents decrease the abundance of large-seeded species, thereby indirectly increasing the abundance of small-seeded species (Inouye et al. 1980). And third, if large-seeded species do attain high densities (as they do in rodent exclosures) they are subject to attack by a parasitic fungus that causes a large decrease in fecundity (Inouye 1981). With this example in mind, we proceed to consider the importance of interspecific interactions, predation, and parasitism in determining the abundance of desert rodents.

Interspecific Interactions

A population of a given species of desert rodent does not live in the absence of other organisms. In the following section, we address the possible importance of interspecific interaction in determining the abundance of desert rodents.

For competition among species to occur, some resource must be limiting. A substantial amount of evidence, much of it indirect, argues that food is limiting for many species of desert rodents, especially granivorous species. As discussed above, increases in population density follow periods of high precipitation and seed production (Reynolds 1958, Beatley 1969, 1976, French et al. 1974, O'Farrell et al. 1975, Whitford 1976, Dunigan et al. 1980, Petryzsyn 1982), and invasions or population increases of seed-eating rodents follow the addition of seeds (Abramsky 1978, Brown and Munger, in preparation). In addition, densities of seed-eating rodents increased in response to the removal of ants (Brown and Davidson 1979) and, along a geographic gradient of increasing precipitation and productivity, population density, biomass, and species diversity of seed-eating rodents tend to increase (Brown 1973, 1975). Furthermore, woodrat populations appear to be limited by the amount of green matter available to them (Brown et al. 1972, Cameron and Rainey 1972, Olsen 1976).

A number of studies indicate the probable importance of rodent-rodent interactions. Cameron (1971) concluded that, where the two species are sympatric, *Neotoma fuscipes* excludes *N. lepida* from their preferred food plant. Frye (in press) showed experimentally that *Dipodomys merriami* were excluded from seed resources near the mounds of the larger *D. spectabilis*. A number of authors have shown that desert rodents differentially utilize microhabitats (Brown and Lieberman 1973, Brown 1973, 1975, Lemen and Rosenzweig 1978, Price 1978a, Wondolleck 1978) or habitats (Rosenzweig 1973, Schroeder and Rosenzweig 1975, Hoover et al. 1977, Warren 1979). That this differential use is caused by interspecific interactions is indicated by studies that have shown a shift in microhabitat use as a result of experimental removal (Price 1978a, Wondolleck 1978) or a natural lack (Larsen 1978) of putative competitor species. In addition, although food may not be the basis of the response, the granivorous *D. ordii* expanded its microhabitat use in response to removal of the omnivore *Onychomys leucogaster* (Rebar and Conley, in preparation). Exclusion of one species by another from a preferred resource or microhabitat can potentially lead to a reduction in population size for the former species.

Removal experiments that measure numerical response are even stronger evidence of the importance of interspecific interaction. Unfortunately, few such studies have been done. Schroeder and Rosenzweig (1975) performed reciprocal removals of *D. ordii* and *D. merriami* but found that neither species responded to removal of the other. Munger and Brown (1981) found a 3.5-fold increase in the population density of small granivorous rodents following the absolute removal of three species of *Dipodomys*. In a third study, Eidemiller (1982) performed reciprocal removals of the herbivorous *Neotoma lepida* and the granivorous *Perognathus fallax*. Three species of omnivorous *Peromyscus* responded with a twofold increase to *N. lepida* removal but failed to respond to *P. fallax* removal. The response of *N. lepida* to the removal of *P. fallax* and the reciprocal response were minor.

To further assess the importance of interspecific interactions, more removal experiments must be performed. To be of value, these experiments must be properly replicated; a surprising number of studies appearing in the literature lack experimental replication (Hayne 1975).

A number of questions can be addressed with these studies. First, how general are the results of the experiments discussed here? Another, is the result affected by the identity of the species studied, by the habitat in which the study was conducted, by the presence of other competitor or predator species (which may be affected by historical factors such as colonization events or ecological bottlenecks), by the season in which the study was performed, or by the temporal pattern of resource availability? One tenuous pattern that emerges is that similar-sized species failed to respond to removals (Schroeder and Rosenzweig 1975), whereas dissimilar-sized species responded to removals (Munger and Brown 1981; although this was not true in all cases for Eidemiller 1982). Such a generalization contradicts other studies that suggest that the intensity of pair-wise interactions among granivorous rodents increases with body-size similarity (Brown 1973, 1975, Brown and Lieberman 1973, Mares and Williams 1975, Bowers and Brown 1982). As discussed by Schroder and Rosenzweig (1975), it may be that the interaction between similar-sized species has been sufficient, over evolutionary time, to discourage utilization of a common set of resources (see discussion under habitat selection).

Second, by examining the bases of these interactions in detail, a great deal can be learned about their impact on population dynamics. For what resource are these rodents competing? Does the interaction involve exploitation or interference competition?

Predation

The most direct way to assess the effect of predation on desert rodent populations is to remove predators then measure any response there may be in the abundance and distribution of the rodents. Much information about predator-prey interactions can also be gathered through detailed observations of population numbers, distribution, and behaviors of predators and prey as shown by what is undoubtedly the most complete study of the effects of predation on the population dynamics of a small mammal: the work of Errington (1943, 1946) on muskrats (*Ondatra zibethica*) and their primary predator, mink (*Mustela vison*). Unfortunately, no study approaching this quality has been performed on desert rodents and their predators (perhaps because much of their activity is nocturnal); therefore, we must rely primarily on indirect evidence in this section.

Errington's work illustrates a further point: the scale on which the results are viewed drastically affects the interpretation. Although large numbers of muskrats are killed by mink and other predators, Errington (1946, 1956) argued that predation is overrated as a factor controlling muskrat populations. Instead, he argued that population size is controlled by the availability of territories; predation primarily affects the surplus individuals (those without territories) of a population and is only one of a number of factors that affect surplus animals of the population. Although he may be correct that territory number limits population numbers and density within a marsh, it is predation that makes areas outside the marsh unsafe, ultimately limiting the number of territories that can be safely occupied. If it is the presence of

mink that prevents muskrats from successfully colonizing areas near the marsh (where food and water are accessible), then predation would have to be considered to be a factor important in limiting distribution and therefore total population size of muskrats. On a within-habitat scale, predation appears to be unimportant. On a between-habitat scale, it may contribute substantially to the limitation of the population.

Errington's studies illustrate both a direct effect (increased death rate: those individuals that do not possess safe territories are often killed) and an indirect effect (habitat selection: given a choice, muskrats will selectively live in habitats that are relatively safe) of predation on abundance and distribution. In desert rodent populations, direct effects of predation have yet to be demonstrated, though a number of studies have shown that desert rodents are, in fact, killed by a number of predators, e.g., owls, carnivores, and snakes (French et al. 1967, Egoscue 1962, Webster and Webster 1971, Lay 1974, Ryckman et al. 1981, Munger, pers. obs., Jones, pers. obs.).

French et al. (1967) tried to estimate the direct effect of kit fox (*Vulpes macrotis*) predation on the survivorship of desert rodents by comparing longevity (which included loss by emigration) in unfenced populations (subject to losses by emigration and predation by kit foxes and other predators such as snakes) with longevity in fenced populations (from which kit foxes were excluded and out of which emigration was not possible). The effect of emigration (measured in another study at 25 percent per year) was subtracted from the sum of all effects on longevity of the fenced population. They concluded that kit fox predation was unimportant in affecting longevity, though predation by other predators may have been important. Although this approach was novel, it suffers an important flaw: the calculations of French et al. (1967) are overly sensitive to the values entered into their equations. For example, a decrease in the emigration value used from 25 to 24 percent results in a sixfold increase in the apparent importance of kit fox predation. Since no confidence intervals are given for any of their values, the exact importance of this sensitivity is unknown.

The effect of other factors, such as productivity, competition, and parasitism, may be manifest primarily through predation. It is likely that a decrease in productivity, an increase in competition, and an increase in parasitic load will all require rodents to spend more time foraging to meet energetic requirements. This, in turn, will increase their exposure to predators, and potentially directly affect abundance.

It is somewhat easier to examine indirect effects of predation because these often involve morphologies and behaviors that may be more easily studied than density effects. Behaviors and morphologies that lead to a reduction in the probability of being killed should evolve in desert rodents. If these behaviors and/or morphologies are costly or reduce resources available to a population (for example by restricting foraging to certain microhabitats), then predation can potentially have an indirect effect of lowering population size.

Several studies indicate that one indirect effect involves microhabitat selection. Quadrupedal desert rodents forage substantially more under and around bushes than out in the open (Brown and Lieberman 1973, Rosenzweig 1973, Price 1978a, Wondolleck 1978, Thompson 1982a). Though this may be due in part to differences in resource availability (Reichman 1975, Brown et al. 1979a), a number of authors have argued that these rodents favor bush microhabitats to avoid attacks by visually oriented predators (Rosenzweig 1973, O'Dowd and Hay 1980, Thompson 1982a, Kotler, in press).

Four studies provide experimental evidence consistent with the notion that predation importantly affects microhabitat selection. Thompson (1982b) was able to increase the density of quadrupedal rodents in an area by constructing artificial shelters in the open spaces between bushes. By increasing the amount of cover available, the shelters may have allowed the rodents to utilize areas they previously avoided, resulting in an increased population size. Because measures of seed density failed to show any effect by the shelters on resource distribution, it is unlikely that the density increase was caused by changes in the resource base. Rosenzweig (1973) decreased the number of *Perognathus*

penicillatus captured by experimentally removing shrubby vegetation. The rapidity of the response indicates that it is unlikely that the rodents were responding to a change in resources. O'Dowd and Hay (1980) showed that the probability that desert rodents exploit artificial seed patches varies with the distance of those seeds to the nearest bush (presumably a measure of the danger of being preyed upon) but not with the quality of those patches.

The results of these three studies are open to an alternate explanation. The ultimate reason that quadrupedal rodents prefer bushy microhabitats may be that bushes have been associated (over evolutionary time) with particular resource distributions and are presently used by rodents as proximate cues to favorable resource patches. In the studies of Rosenzweig (1973) and Thompson (1982b), the rodents may have responded to changes in the proximate cue even though the ultimate factor remained unchanged. The opposite may have occurred in the study of O'Dowd and Hay (1980): the rodents may have failed to respond to changes in the ultimate factor (seeds) because there was no change in the proximate cue.

By manipulating a factor other than microhabitat, Kotler (in press) avoided this problem. He reasoned that, because many predators of nocturnal desert rodents rely on visual cues, the rodents should use the amount of illumination in the environment to assess their risk of being preyed upon. Using artificial light sources, Kotler experimentally increased the amount of illumination, causing four of the six species at his study site to reduce their use of open habitats, indicating that the utilization of microhabitats by these species is sensitive to the risk of being preyed upon. It is interesting to note that one species, *D. deserti*, responded to increased light only when resources in bushy microhabitats were augmented, indicating that resource availability and risk of predation may interact in affecting behavior. The two remaining species made little use of open microhabitats prior to experimental treatment; a decrease in the use of open areas by these species would therefore be difficult to cause or detect.

Several other studies indicate that predation may be an important selective force in desert rodents. First, timing of foraging activity is sensitive to moonlight; presumably increased light increases the probability of being preyed upon (Lockard and Owings 1974, Rosenzweig 1974, Kaufman and Kaufman 1982). Second, individuals of the island-dwelling *Neotoma lepida latirostra* spend more time away from the nest and travel in more open areas than their mainland counterparts, presumably due to a lack of predators on the island (Vaughan and Schwartz 1980). Third, desert rodents in several families possess auditory and locomotory specializations (Bartholomew and Caswell 1951, Webster 1962, Webster and Webster 1975, Lay 1972) that have shown to be important in aiding these rodents in avoiding attacks of predators (Webster and Webster 1971). These rodents also possess pelages which match the substrate on which they occur (Dice and Blossom 1973). It should be noted, however, that demonstrating the importance of predation on the evolution of behavioral and morphological traits does *not* demonstrate its importance in affecting abundance and distribution.

Obviously, much work needs to be done before the importance of predation can be assessed. Indirect studies need to be bolstered by determining whether the ultimate factor responsible for such behaviors as avoidance of open microhabitats is based on resource distribution or predator avoidance. This task will prove difficult if behaviors are inflexibly tied to proximate cues. Studies that measure the direct effect of predation on abundance and local distribution should be attempted as well, perhaps using island systems (cf. Vaughan and Schwartz 1980) or areas where predators have been subjected to control programs.

Parasitism

The role that parasitism may play in affecting the abundance and distribution of desert rodents has been given little consideration, even in comparison with the small amount of attention given predation. There are several reasons for this. First, antiparasite adaptations (such as immune response) are

not easily recognized and the effects of parasites are often indirect and subtle. Second, because it is difficult to manipulate parasite loads under field conditions, it is not easy to study the importance of parasites. Third and perhaps most important, biologists often believe that parasites have little ecological importance (but see Price 1980 and Anderson and May, 1982a). This is based on the notion that parasites should evolve to minimize their effect on their hosts: by damaging its host, a parasite would supposedly reduce its chances of reproducing.

In arguing that parasites are worthy of consideration in the population biology of desert rodents, we will consider two questions. First, how might parasites affect abundance and distribution and, second, what is the evidence that parasites can be important in affecting abundance and distribution? For this latter question, we consider a number of systems outside desert rodents as well as reviewing the meager evidence pertaining to desert rodents.

Parasites (which we consider here to include viruses through parasitic arthropods) can affect abundance both by lowering survivorship and by consuming energy that might otherwise go to host reproduction, thereby reducing fecundity. Anderson and May (1978, 1979, 1982b), Anderson (1978), and May and Anderson (1978, 1979) provide excellent discussions of the dynamics of parasite and host populations. They argue that the ability of a parasite to regulate a host population is enhanced by factors that promote the stability of the parasite-host dynamics, such as overdispersion of parasites, density-dependent restraints on the growth of parasites within hosts, and a nonlinear relationship between parasite burden and host death rate. They do not mention another very important stabilizing factor: the presence of a second host species that does not suffer pathological effects from infection—a reservoir for the parasite (Baltazard et al. 1952, cited in Nelson 1980). Reservoir hosts may be especially important in affecting distribution (see discussion below).

If parasites are to be important in regulating the abundance of the host, they must maintain enough virulence to reduce the survivorship or fecundity of the host (the following discussion is based on Anderson and May, 1982a).

The reproductive rate (and therefore fitness) of a parasite is governed by three factors. A higher reproductive rate will result from (all else being equal): higher probability of infection in an uninfected host when encountered by an infected host (higher transmission rate), lower rate at which a host recovers from a parasitic infection (lower recovery rate), and lower probability that a host dies as a result of an infection (lower virulence). If the reproductive rate of a parasite depended solely on its virulence, but if virulence was not tied to the transmission rate or recovery rate, it would be reasonable to expect the parasite to evolve to have a negligible effect on the host. However, these parameters are interrelated, at least in some systems. In the myxoma virus–rabbit system for instance, hosts infected with more virulent strains of virus had a slower recovery rate and a higher transmission rate than hosts infected with strains of low virulence (Anderson and May, 1982a). Given the character of these interrelationships, parasites should evolve to some intermediate rate of virulence, low enough to prevent a premature death of the host but high enough to retard recovery and facilitate transmission. This is what has happened in the myxoma–rabbit system (Fenner and Ratcliff 1965, Anderson and May, 1982a). The virus introduced was extremely virulent; nearly 100 percent of the infected rabbits died quickly. Eventually the system stabilized such that the most prevalent viral strains were of neither very high nor very low virulence, but somewhat intermediate in their effect.

Studies of the effect of parasites on small mammal hosts are relatively rare. In addition, a number of these studies have questionable worth in assessing the importance of parasites in natural situations. First, some studies use laboratory animals as hosts, a practice that ignores the importance of coevolution of parasites and their hosts. Second, many studies are correlative: a measure of host condition is tied to parasite load. Such correlative studies do not allow us to assign cause, since some other factor, such as poor nutrition, may have led to both poor condition and high parasite

load. Laboratory studies that utilize experimental variations in parasite load will allow us to assess the effect of parasites on survivorship and fecundity. Only by performing field studies in which parasite loads are manipulated on the scale of the population will we know if the effects of parasites on survivorship and fecundity translate into actual effects of population regulation. For illustrative purposes, we will list several examples of apparent importance of parasites on demographic parameters of mammals (other examples can be found in Davis and Anderson 1971, and Price 1980): Infections of *Peromyscus leucopus* by *Cuterebra fontinella* (bot fly) are correlated with reduced hematocrit (Childs and Cosgrove 1966); delayed female maturity, delayed litter production, and reduced male fertility (Cranford 1980); they may also cause reduced size of reproductive organs in subadult males, but have no discernible effect on the size of adult reproductive organs (Timm and Cook 1979). Epizootics occasionally decimate populations of *Ondatra zibethica* (Errington 1954). Infections by lungworms (*Protostrongylus* spp.) are thought to be very important in decreasing survivorship in bighorn sheep in North America (Forrester 1971).

What evidence exists that the abundance of desert rodents may be affected by parasitism? Numerous studies have shown that desert rodents are often infected by a number of parasites—plague virus, nematodes, cestodes, spirochaetes, mites, fleas, and ticks (Eads and Hightower 1952, Read and Milleman 1953, Grundman 1957, 1958, Reisen and Best 1973, Bienek and Klikoff 1974, King and Babero 1974, Whitaker and Wilson 1974, O'Farrell 1975, Egoscue 1976, Garner et al. 1976, Maser and Whitaker 1980, Ryckman et al. 1981). However, to our knowledge, very few studies have mentioned the effects of these parasites on their hosts. Garner et al. (1976) indicated that *Dipodomys ordii* individuals infected with cestodes had a reduced amount of axillary and groin fat. Several studies of gastric parasites have noted that the stomach of the host appears distended, irritated, or simply filled with parasites (Garner et al. 1976, Grundman 1958, King and Barbero 1974). No study has assessed the effect of parasitism on population size.

Two strategies of study can increase our knowledge of the importance of parasitism in desert rodent populations. First, laboratory studies utilizing wild rodents and their natural parasites can be used to make precise quantitative measures of the effect of parasite loads on parameters important to the demography of a population. Second, field studies should be attempted in which internal parasite loads are manipulated by administering the appropriate drug to a portion of a population and external parasites are manipulated, perhaps at burrow sites, using techniques used to control the ectoparasites of domestic animals (e.g., flea collars). Such studies should yield further information on the effects of parasitism demographic parameters and, perhaps, on the effect of parasitism on rodent abundance.

DISTRIBUTION

In this section, we address two basic questions. First, what factors are important in defining the geographic ranges of desert rodents? Second, within the range of a species, why doesn't that species occur ubiquitously over all habitats? That is, what factors lead to patterns of local distribution? As will be seen, many of the factors important in determining abundance should also affect patterns of local geographic distribution.

After a brief discussion of physical barriers, we will address the importance of three abiotic factors (temperature, moisture, and substrate) and four biotic factors (vegetation, competition, predation, and parasitism) to local and geographic distribution. It is common for two or more factors to interact in a synergistic manner. In the discussion below, the most common example of synergism is the interaction of temperature, moisture, and substrate to produce patterns in the distribution of vegetation, which in turn appears to affect the distribution of desert rodents.

Physical Barriers

Physical barriers (e.g., habitat discontinuities, mountain ranges, rivers) often persist over long periods of time, are readily discernible, and, for desert rodents, can be put on maps (e.g., Hall 1946, Durrant 1952,

Hall and Kelson 1959, Hall 1981). In general these barriers represent both the proximate and ultimate factors that circumscribe the geographic distributions of species.

Hall (1946), Durrant (1952) and, more recently, Brown (1973, 1975), and Brown and Lieberman (1973) noted striking differences in the composition of rodent communities in the eastern and western Great Basin desert. They suggested that eastern Great Basin desert communities are depauperate and that orographic barriers have limited certain species (e.g., *D. deserti*, *D. merriami*, *Microdipodops pallidus*) to western habitats. Physical barriers often can be invoked to account for the limits of spatial distribution on at least one range boundary of many desert heteromyid, cricetid, and sciurid species in North America (Hall and Kelson 1959, Hall 1981). Besides orographic barriers, rivers appear to play a significant role in limiting the distribution of populations of a species. Range boundaries of *Perognathus formosus*, *P. spinatus*, *P. penicillatus*, *P. intermedius*, *Ammospermophilus leucurus*, and *A. harrisii* are partially coincident with the Colorado River. The high frequency with which physical barriers limit species' distributions corroborate other empirical data that suggest that mammals are relatively poor dispersers across unsuitable habitats (Carlquist 1965; Brown 1971, 1975).

Abiotic Factors: Temperature, Moisture, Substrate

Abiotic factors that vary in a continuous or mosaic manner are also important in circumscribing geographic ranges and affecting local distribution, although their effects are usually more subtle than those of the highly visible physical barriers just discussed. In many situations, cause and effect relationships may be confounded by synergistic interactions among variables and by an inability to distinguish proximate from ultimate factors. In the next section, we first discuss how single abiotic factors can limit distributions, then deal with the problem of synergism.

Correlations between the distribution of desert rodent species and various measures of temperature have been reported in the literature for many years. Sixty years ago, Grinnell (1922) suggested that temperature was important in creating barriers to dispersal and, ultimately, could be used to account for the distribution of *Dipodomys* in California. The observations that *D. merriami* has relatively little ability to regulate body temperature (Dawson 1955) and that the northern extent of its distribution is coincident with the 30 F isotherm for average January temperatures (Reynolds 1958) suggests that low winter temperatures may limit the range of this species to warm desert habitats. Gaby (1972) found that *D. merriami* (an inhabitant of low, hot deserts) and *D. ordii* (which tends to inhabit higher, cooler deserts) have interspecific differences in temperature-dependent metabolic rates that correspond to the different requirements of their ranges. In these experiments *D. ordii* was less tolerant of high temperatures than *D. merriami*; *D. merriami* had a higher metabolic rate at low ambient temperatures. Unfortunately, it is unclear what role these intrinsic differences play in affecting geographic distributions. The question becomes one of cause and effect: are *D. merriami* populations limited to warm desert regions because they are unable to cope physiologically with colder temperatures, or are the metabolic differences between these kangaroo rats merely a result of local adaptation to contrasting environmental conditions?

Physiological research has long demonstrated, through the study of functional adaptations, the high premiums placed on water conservation for rodents in desert habitats (Howell and Gersh 1935, Schmidt-Nielsen et al. 1948, Schmidt-Nielsen and Schmidt-Nielsen 1951). More recently, negative effect of increased ambient temperature on water balance has been elucidated (MacMillen and Christopher 1975). Beatley (1969a, 1976) noted that a species must necessarily be limited to areas where positive water balance (a function of interaction of temperature, available moisture, and the physiology of the species in question) can be maintained.

Howell and Gersh (1935) first quantified the urine-concentrating capacities of *Dipodomys* and found substantial interspecific variation. That this capacity at least corresponds to distribution is indicated by studies comparing *D. merriami* and *Dipodomys* of less arid habitats: *D. merriami* has a higher

urine-concentrating ability (comparison with *D. agilis*; Carpenter 1966) and a lower rate of body water turnover (comparison with *D. microps*; Mullen 1971).

Substrate characteristics also appear to affect distributional patterns of desert rodents. Grinnell (1922) suggested that desert rodents are limited in geographic distribution via the matching of pelage coloration with color tone of the background, though this may be a matter of local adaptation. Other studies contend that both local and geographical distributions of desert rodents are limited to those areas with soil conditions that do not inhibit the burrowing habits of a given species. *Dipodomys deserti* appears to be restricted to deep sand areas, a substrate that is conducive to the construction of large, deep burrow systems (Grinnell 1914, Hall 1946, Reynolds 1958, Roth 1978). *Dipodomys merriami* is often excluded from areas that have a surface layer of rocks, heavy clay, sulphate crust, or hard-pan because of the difficulty in digging burrows in such soil types (Vorhies and Taylor 1922, Hardy 1945, Hall 1946, Huey 1951, Reynolds 1958). In fact, Huey (1951) suggested that this was the main factor controlling the geographic distribution of *D. merriami* below 4500 feet in western North America.

The complex nature of physiological interactions (primarily through the dissipation of heat and conservation of water) with burrow environments suggests that local distributions may be affected by soil type (Gaby 1972, Hoover 1973) as well as the potential for burrow ventilation via surface winds (Kay and Whitford 1978). Such speculation is supported by some novel work that employs physiological and behavioral data to account for the distribution of two species of *Perognathus* in New Mexico. This work (Hoover et al. 1977) suggests that *P. intermedius* can tolerate a wide range of burrow microclimates but is behaviorally excluded by *P. penicillatus* from substrates that have a high heat buffering capacity (the preferred burrow sites of *P. penicillatus*). If *P. penicillatus* can tolerate only a small range of burrow microclimates and is behaviorally dominant to *P. intermedius*, this is an example of an included niche (Colwell and Fuentes 1975). Unfortunately, definitive experiments in which *P. penicillatus* is experimentally removed to see if *P. intermedius* is, in fact, behaviorally relegated to less-preferred habitats by *P. penicillatus* were not performed. Nevertheless, the data strongly suggest that physiological differences between these species mediate the interspecific interactions that determine the local distributions of these species.

More recently, hypotheses that focus on interspecific interactions and differential foraging behaviors have been invoked to account for patterns of substrate philopatry in some rodent species. Reichman and Oberstein (1977) and Price (1978b) have suggested that divergent body sizes and morphologies of heteromyid species reflect adaptations for exploiting different seed dispersions. Seed density and dispersion appear to be affected by microtopography and soil structure (Reichman and Oberstein 1977, Bowers 1979, 1982). Areas with fine substrates permit the accumulation of dense seed aggregations by trapping windblown seeds in depressions, whereas on substrates consisting of larger soil particles, seeds are trapped individually. Because of their larger size and saltatorial locomotion, *Dipodomys* are thought to specialize on the exploitation of seed clumps that provide large energy returns per unit time. Therefore, the distribution of *Dipodomys* should be coincident with fine substrates. In contrast, the smaller, quadrupedal *Perognathus* are thought to forage for more dispersed (individual) seeds and, consequently, should prefer areas with larger soil particle sizes. Differential substrate utilization between these genera has been documented at the local habitat level (Wondolleck 1978, Bowers 1979); there is no *a priori* reason why the same mechanism might not be working to affect geographical distributional patterns as well.

Vegetation

Possibly the greatest effect of temperature, moisture, and substrate is a synergistic one, affecting the local patterns of vegetative structure and the distribution of certain plant species. Dice and Blossom (1937) suggested that the physiognomy of the vegetation was

an important factor in determining the distribution of desert rodent species. More recently, positive relationships between annual precipitation and perennial plant species diversity, density and size (Beatley 1969, Brown 1973, Hafner 1977), as well as perennial and annual seed standing crop (Lieberman 1974) have been established. That *D. merriami* is limited in geographic distribution to areas receiving less than 25 cm of annual precipitation (Reynolds 1958) and prefers habitats of little vegetative cover (Hall 1946, Lidicker 1960, Brown and Lieberman 1973, Rosenzweig 1973, Schroder and Rosenzweig 1975) suggest an indirect effect of moisture on limiting habitat characteristics for some species. By comparison, *D. ordii* is apparently limited in distribution to more grassy habitats that have an annual precipitation of more than 25 cm (Reynolds 1958, Schroder and Rosenzweig 1975). A similar relationship may occur on a geographic scale: *D. merriami* has expanded its geographic range to include overgrazed grassland (now desert scrub) habitats that once were more typical of *D. ordii* habitats (Reynolds 1958).

Precipitation, through its effect on the quantity of available food (seed) resources, may also affect the geographical distribution of some desert rodent species. Frye (pers. comm.) found that most species of large (> 100 g) *Dipodomys* species are restricted to those areas that predictably receive substantial annual precipitation. It is likely that the relatively large amount of food resources required by rodents of large body size coupled with the constraints of finite foraging areas limits large species to more productive areas. A potential exception to this pattern is *D. deserti,* which often occurs in areas of the Mojave and southwestern Great Basin deserts that receive little precipitation. Although the total amount of resources produced in these areas is probably comparatively small, *D. deserti* is restricted to sand-dune habitats, which should be richer than surrounding habitats. This is because food resources will be concentrated in dune areas on two different scales by the action of surface winds. First, the same wind patterns that transport sand from the surrounding valley and concentrate it into dunes will transport seeds to dune areas as well. Second, on the dunes themselves, seeds will tend to accumulate in depressions, thereby further concentrating the resource, making it more efficient for kangaroo rats to harvest.

The interaction of climatic and substrate variables affect the distribution of certain plant species or types (e.g., the associations of Shelford 1913) to which, in turn, are closely tied the distribution of some desert rodents. For example, it is well documented that the distribution of *D. microps* is coincident with the distribution of chenopods of the genus *Atriplex* (Grinnell 1933, Jorgensen 1963, Kenagy 1972a, b), upon which it is physiologically and morphologically adapted to feed (Kenagy 1972a, b; but see Csuti 1979). *Atriplex,* in turn, is usually limited to alkali flats surrounding dry basins of Pleistocene Lakes (Hall and Dale 1939, Munz and Keck 1959).

Field observations (Hall 1946, Cameron 1971, Brown et al. 1972, Cameron and Rainey 1972, Olsen 1975) have documented relationships between the presence of cricetid rodents and succulent desert vegetation. It is likely that this pattern results from the need of some species of *Peromyscus* and *Neotoma* to consume succulent vegetation to maintain positive water balance (Olsen 1975).

Interspecific Interactions

Comparative physiological data do not always account for differences in the local distribution of closely related species, and other causal and effect mechanisms must be invoked. Lee (1963), in an investigation of the physiological adaptations of *N. lepida* and *N. fuscipes* to arid and semiarid habitats, found no physiological bases for the observed differences in local distribution where the species ranges overlap. A study focusing on the competitive relationship of these species in the Mojave Desert of southeastern California found that these species are distinctly separated in most aspects of the habitat (Cameron 1971). Dietary studies, however, revealed that, when allopatric, both *N. fuscipes* and *N. lepida* prefer a common food plant (*Quercus turbinella*), whereas *N. lepida* switches to a less preferred species (*Juniperus californica*) when sympatric with *N. fuscipes.* An investigation of behavioral interactions

(Cameron 1971) suggested that *N. fuscipes* is dominant over *N. lepida*, relegating the latter to areas of low *Quercus* density, and controlling the preferred food resource via habitat selection and defense. Such data support the premise that interspecific competition for limited food resources affects patterns of local distribution.

The differential occurrence of *Dipodomys* and *Perognathus* in different, but contiguous, microhabitats has been documented by numerous studies focusing on the local distribution of these genera. This body of data represents the best-documented pattern of habitat use by desert rodents. *Perognathus* tend to inhabit areas of high vegetation cover (Arnold 1942, Hall 1946, Reynolds and Haskel 1949, Reynolds 1950, Rosenzweig and Winakur 1969, Feldhammer 1979, Brown and Lieberman 1973, Rosenzweig 1973, Price 1978a, Wondolleck 1978) and coarse substrate types (Hardy 1945, Hall 1946, Rosenzweig and Winakur 1969, Brown 1975, Hoover et al. 1977, Wondolleck 1978). In contrast, *Dipodomys*, on a local scale, tend to be found in more open microhabitats with finer substrate (Hall 1946, Lidicker 1960, Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Wondolleck 1978, Price 1978a; for a complete review, see Brown et al. 1979b; but see Thompson 1982a).

In the section on abundance, we briefly discussed two mechanisms, based on competition and predation, that have been hypothesized to account for differential utilization of microhabitats by *Dipodomys* and *Perognathus*. The predation hypothesis is based on the early observations that *Dipodomys* is better adapted to avoid predation, via locomotory (Bartholomew and Caswell 1951) and auditory (Webster 1962) specializations, when compared with the more quadrupedal *Perognathus* (although *Perognathus* was subsequently shown to share most of the auditory specializations found in *Dipodomys*; Webster and Webster 1975). Consequently, *Perognathus* are thought to occupy areas of high vegetative cover mainly as a result of predation pressure that covaries with local vegetative physiognomy (Rosenzweig 1973, Thompson 1982a). Even though recent work of Thompson (1982a) has demonstrated that *Dipodomys* also use areas of high vegetative cover, perhaps as a refuge from predation, it is thought that saltatorial kangaroo rats use open, poorly vegetated areas to a significant extent in the exploitation of food resources. The experimental work of Thompson (1982b), O'Dowd and Hay (1980), and Kotler (in press) provides evidence that predation is important in determining microhabitat use.

However, predation is not the sole factor influencing microhabitat use. If predation alone affects the differential use of microhabitats and habitats by *Perognathus* and *Dipodomys*, the experimental removals of *Dipodomys* by Wondolleck (1978) and Price (1978a) should not have caused shift in microhabitat use by *Perognathus*. In all probability, properties of the resource base that vary according to habitat microtopography interact with locomotory differences in foraging of *Dipodomys* and *Perognathus* to help produce the observed differences in habitats utilized. The competition hypothesis couches patterns of habitat use in terms of the ability of a species to exploit a resource base that varies on a spatial scale. But there are several variations on this general theme, and even the mode of competition (e.g., exploitation vs. interference) has been a subject of much discussion.

Much evidence suggests that desert granivorous rodents subdivide seed resources by exploiting different seed dispersions. As discussed above, seed density and dispersion appear to be influenced by microtopography and vegetative structure (Reichman and Oberstein 1977). Consequently, it is hypothesized that the microhabitat affinities shown by desert rodents may exist because microhabitats differ in the degree to which they contain clumped seeds. Large saltatorial *Dipodomys* forage mainly in open, vegetation-free habitats where windblown seeds accumulate in depressions or adjacent to objects acting as windbreaks (Reichman and Oberstein 1977, Bowers 1982). Thus, bipedal kangaroo rats are thought to forage from seed clump to seed clump, spending little time in the interspersed seed-poor areas (but see Frye and Rosenzweig 1980). By contrast, *Perognathus* and other quadrupeds forage under bushes (Brown and Lieberman 1973, Rosenzweig et al. 1975, Price 1978a), where seeds are more uniformly distributed.

Although such a scheme is supported by both theoretical (Reichman 1980) and empirical (see Brown et al. 1979b for a review) data, the actual mechanisms resulting in spatial segregation of *Dipodomys* and *Perognathus* on a local level are unclear. In particular, do *Dipodomys* use aggression to competitively exclude *Perognathus* from the seed-rich, open areas as suggested by Hutto (1978) and Trombulak and Kenagy (1980), or are the patterns of microhabitat use merely the result of more proficient exploitation of seed clumps by *Dipodomys* relative to *Perognathus* (Reichman and Oberstein 1977, Wondolleck 1978, Price 1978b)?

Congdon (1974) reported an instance where interspecific aggression of *D. deserti* toward *D. merriami* appeared to be dependent on the amount of available resources. In periods of low resource availability, *D. merriami* and *D. deserti* cooccurred in habitats with sand substrates, but when the resource base was augmented, indirectly, by an intense summer storm, *D. merriami* moved into nonsandy habitats, presumably to avoid the aggressively dominant *D. deserti* (Congdon 1974). This pattern may result from several factors. First, resources may have become dense enough following the storm to become economically defensible (Brown 1964) by *D. deserti*. Second, increased resource availability may have allowed *D. deserti* to spend less time foraging and more time engaged in aggressive interactions (see Caraco 1979).

Although instances of aggression in desert rodents have been reported many times (Hall 1946, Eisenberg 1963, Christopher 1973, Kenagy 1976, Blaustein and Risser 1976, Hutto 1978, Trombulak and Kenagy 1980), its role in determining local distributions is unclear. In most cases, the appropriate experiments have not been done (but see Frye, in press). In fact, some authors (Brown and Lieberman 1973, Brown et al. 1979, Bowers and Brown 1982) contend that for granivorous desert rodents it is very rare that the distribution of resources is sufficiently dense for interspecific aggression to be an economically feasible strategy.

Interspecific interactions that affect patterns of habitat use, on a local scale (Rosenzweig et al. 1975, Price 1978a, Brown et al. 1979b), might also play a role in limiting the geographic distributions of certain rodent species. Bowers and Brown (1982) found that those rodent species that *a priori* were most likely to compete (e.g., similar-sized species of the granivore guild) overlapped less in their geographic ranges and cooccur less often in local communities than a null model predicted. In contrast, overlaps between and cooccurrences of pairs with different trophic affinities (e.g., interguild comparisons) did not differ from the random model.

Body Size

Body-size, *per se*, may also play a role in determining the distribution of desert rodent species by affecting the way rodents use certain resources. Grinnell (1914) and Hall (1946) noted that an intermediate-sized heteromyid, *D. merriami*, was found in nearly every desert habitat, whereas the larger *D. deserti* was more restricted in habitat. From this pattern Grinnell (1914) concluded that larger species usually have more restricted habitat utilization patterns and more circumscribed geographic ranges than their smaller relatives. More recently, Mares and Williams (1977) reported the result that intermediate-sized species of *Perognathus* and *Dipodomys* occupy the northern and eastern range limits of the family, whereas, in the center of heteromyid diversity, an array of smaller and larger species are syntopic with intermediate-sized species. Bowers (in preparation) investigated the relationship between geographic range and body size for 46 heteromyid species and suggested that body size is an important factor in affecting the extent of a species distribution. Intermediate and very small species are characterized by having large distributions, but small and large heteromyids have relatively small ranges. As many economic, physiologic, and behavioral characteristics covary with body size (Eisenberg 1963, Rosenzweig and Sterner 1970, French 1976, Reichman and Brown 1979), it is difficult to attach cause and effect relationships between certain biological properties and geographic range. However, patterns of resource use and the propensity of a species to enter food-induced torpor, both of which change with body size (Rosenzweig and Sterner 1970, Brown and Lieberman 1973, Mares

and Williams 1977, Reichman and Brown 1979), appear to be of particular importance in the determination of geographic distribution.

Hypotheses regarding geographic distribution are almost impossible to test via manipulation. However, it seems plausible that many of the ecological factors important in affecting local distribution should also affect the extent of the geographical distribution of a species and, therefore, that geographic distribution can be studied, via inference, through studies at the local level. At best, the projection of locally studied factors to explain large scale patterns is myopic. However, such an approach has been employed in other systems with apparent success (see Glazier 1980, Reaka 1980, Brown 1981).

Habitat Selection

Throughout our discussion of distribution, we have given many examples of habitat or microhabitat affinity. An important problem that remains is to determine whether these affinities are completely due to physiological or physical limitation (which has often been implicit in our discussion, especially of abiotic factors), or whether these affinities result at least in part from habitat selection originating from competitive interactions. Rosenzweig (1979, 1981) has developed models of competition-based habitat selection that can be illustrated as follows. Imagine a species, *A*, that prefers habitat type *a* over a different type, *b*, perhaps because it is more efficient at harvesting resources in *a*. At low densities, all *A* will be found in habitat *a*. As the density of *A* increases, however, the fitness of individual *A* in habitat *a* will gradually decrease (because of resource degradation); eventually, habitat *a* will be degraded to a point where *a* and *b* are equal in quality. At this point, *A* should inhabit *b* as well as *a*; an observer would detect no habitat affinity (though a difference in density could exist). Now introduce species *B*, which prefers habitat *b* because it is more efficient at harvesting resources there. Because they prefer *b* over *a*, B will tend to degrade habitat *b*, reducing the fitness of *A* on *b*, leading *A* to inhabit only habitat *a*.

Such competition-based habitat selection neither requires nor precludes interspecific aggression. Furthermore, habitat selection may be dependent on contemporary interactions or, if interactions occur over a very long time, species may evolve inflexible behavioral, morphological, or physiological adaptations that can enforce habitat selection even in the temporary absence of the competitor species. The evolution of inflexible habitat selection was invoked by Shroeder and Rosenzweig (1975) to explain the result that reciprocal removals of *D. merriami* and *D. ordii* failed to result in either a wider range of habitats used or density change in the target species when the congener was absent.

How can it be determined if a specific case of affinity for a certain type of substrate or vegetation results from competition-based habitat selection? If habitat selection is based on contemporary interactions, removal experiments (as we called for in the *Perognathus intermedius–P. penicillatus* system) should suffice. If, on the other hand, habitat selection has evolved to inflexibility, then simple removal experiments will not distinguish between competition-based habitat selection and a complete lack of competition: no response would be expected in either case. Study of "natural experiments" is then called for. If a species expands its use of habitats in geographic areas where the putative competitor is absent, then the contention that competition is important in causing habitat selection is supported.

Predation and Parasitism

Distribution may also be affected by predation and parasitism. The probability of being preyed upon may be so high in certain habitats that some species are either exterminated in those areas or individuals are unwilling to enter them. Although there are no documented cases of habitat or range restriction that are directly attributable to predation, it has been speculated (Brown, pers. comm.) that the range of the kangaroo mouse, *Microdipodops pallidus*, may be restricted by the presence of the sidewinder rattlesnake (*Crotalus cerastes*); these two dune specialists do not appear to cooccur on

dune systems even though their ranges abut. This pattern may occur because the kangaroo mice appear to be particularly vulnerable to attacks by sidewinders (which are pit vipers); instead of hopping away when attacked by a predator (as kangaroo rats do; Webster and Webster 1971), they simply remain motionless (Brown, pers. comm.).

Parasites may be important in determining distribution as well. Barbehenn (1969) developed a hypothesis in which competitive exclusion of one species by another species is resisted by "germ warfare" on the part of the competitively inferior species. In the simplest scenario discussed by Barbehenn, if the inferior species harbors a parasite to which it has evolved resistance and if the parasite is restricted to certain habitats by requirements of the intermediate host or vectors, then those habitats will provide refuges for the inferior species; individuals of the competitively superior species that invade this habitat will be killed by parasites. Cornell (1974) extended this hypothesis in an attempt to explain distributional gaps between congeners. In this case, each host species carries a strain or species of parasite (to which it is resistant) but is killed when infected by the parasite carried by the other host species. Where the ranges of these host species abut, individuals of both species would be killed by parasites carried by the other species. In both these models, the interactions between the parasite and the resistant host are relatively stable; therefore it is unlikely that reduced virulence need evolve.

One example of the effect of parasites on distributions is the contraction of the range of the moose (*Alces alces*) in the face of the expansion of the whitetail deer (*Odocoileus virginianus*) range, which is thought to be caused by meningeal worms harbored by the whitetail deer that are fatal to the moose (Price 1980). Another possible example involves *Peromyscus maniculatus* and *Neotoma cinerea* inhabiting lava caves in northeastern California. *Peromyscus maniculatus* harbors bubonic plague; populations of *N. cinerea* in these caves are occasionally exterminated by outbreaks of disease (Nelson and Smith 1976).

Absolutely nothing is known of the impact of parasites on the distribution of desert rodents. To gain this knowledge will require extensive study of host-parasite dynamics within each system considered.

POPULATION STRUCTURE

In this section we will discuss two aspects of population structure: breeding structure (who mates with whom) and certain aspects of spatial structure, primarily home range use and dispersal. We are mainly interested in the effects of these on population genetic structure, which we define here as the way in which a population deviates from panmixia. Deviation from panmixia can have several important effects on the evolutionary dynamics of populations.

1. Fixation of alleles by random drift is more likely to occur with small, effective population size and discrete subpopulations, than in large panmictic populations. Drift is important in one model of evolution, embodied in the shifting balance theory of Wright (1977), but is unnecessary or even a hindrance for evolution in models that assume panmixia (Haldane 1924, Fisher 1930).

2. Localized extinctions, which are important in most scenarios of group selection (e.g., Wilson 1977, Gilpin 1975) and island biogeography (MacArthur and Wilson 1967, Brown 1971), are more likely to occur in subpopulations that are small and discrete.

3. Demic structure and resistance to immigration may reduce the impact that gene flow has in maintaining species integrity and thereby make interpopulation divergence more likely (Anderson 1970; but see Baker 1981).

4. The evolution of some social and altruistic behaviors is thought to partially depend on subpopulation groupings that are based on kin ties (e.g., Hamilton 1972, Sherman 1977, Michod 1979, 1980) or possession of traits common to members of a group (Wilson 1977).

5. High variance in reproductive success can result from competition for mating opportunities (typically among males), active choice of mates by members of one sex, or differential survival of young. Differential reproductive success among members of one or both sexes will not only lead to reduced effective population size (Wright 1940, Patton and Feder 1981), but it will also lead to more

rapid evolution within populations since selective pressures due to variance in reproductive success are more pronounced than when mating is random within populations (Wilson et al. 1975).

At least four types of evidence can be used to study population structure: behavioral, demographic, indirect genetic, and direct genetic. We will treat each in turn and describe what is known for desert rodents, covering primarily heteromyids.

Behavioral Evidence

Behavioral evidence can be used to infer the importance and probable effect of various mechanisms in structuring populations. In some desert rodents, male dominance may play an important role in breeding structure. There is evidence suggesting that, among some kangaroo rats, certain males may defend the burrows of females against other males. Kenagy (1976) observed two male *D. microps* fighting at the mound of a female, and saw the winner copulate with the female. Similarly, Randall (pers. comm.) observed one *D. spectabilis* defend the mound of a female against several other males. In the thorn-forest-inhabiting heteromyid *Liomys salvini*, Fleming (1974) found that size was a good predictor of dominance and that larger males were surrounded by more potential mates than were smaller males.

In the northern grasshopper mouse, *Onychomys leucogaster*, there is some evidence that males and females form at least temporary pair bonds, a behavior that would tend to reduce variance in male reproductive success. First, Ruffer (1965) observed male parental care in the laboratory. Second, Egoscue (1960) found that, even at low densities, members of a male-female pair of *O. leucogaster* were often caught in adjacent traps, indicating that they lived or traveled together. A similar pattern occurs in *Peromyscus eremicus* (Munger, unpubl. data).

Patterns of home range overlap can also be used to infer breeding structure. For instance, if males defend the burrows of females, as has been observed for *D. spectabilis* and *D. microps*, there might be little home range overlap between males, and the home ranges of certain males might include the mounds of some females exclusive of other males. On the other hand, if males do not defend the areas of females, one expects to find extensive overlap between males; exclusive access to females by certain males should be rare. This latter pattern of home range overlap characterizes *D. merriami*; male-male overlap of home ranges is extensive and the home range of each female is overlapped by the home ranges of several males (O'Farrell 1980; Jones, 1982).

Data on dispersal behavior are also useful in understanding population structure. Dispersal data are lacking for most desert rodents, but in those species that have been studied there appears to be a low degree of individual vagility. Jones (1982) measured distances moved by juvenile *D. spectabilis* and *D. merriami*. He was able to detect successful dispersal moves of up to 0.9 km (15 to 20 home range diameters), yet he found that among those juveniles surviving to reproductive maturity, less than 25 percent of *D. spectabilis* and only 11 percent of *D. merriami* dispersed to areas not adjacent to their natal sites. Most of these cases of dispersal involved movements of less than three home range diameters. The possibility of long distance dispersal (>0.9 km) cannot be ruled out, though. French et al. (1974) measured dispersal up to 0.9 km in *Perognathus formosus* (whose home range diameter is less than half that of *D. merriami*; Maza et al. 1973) and determined that more individuals dispersed short distances and more dispersed long distances than would be expected if individuals simply moved to the nearest vacancy. In other words, although most individuals made only very short dispersal moves (as was shown for *D. merriami* and *D. spectabilis*), there were a few *P. formosus* individuals that moved a great distance. The possibility that *D. merriami* and *D. spectabilis* make similar long distance moves needs to be checked by studying dispersal in these species over at least 40 home range diameters (2 km).

Information on the extent of dispersal in other desert rodents is sketchy. Allred and Beck (1963) found that the average distances between most widely separated capture locations for each individual were greatest for *Onychomys torridus* males and *Peromyscus*

maniculatus males, somewhat less for *O. torridus* females, *P. maniculatus* females, and *D. merriami,* and still less for *D. microps* and *Perognathus longimembris.* Among *D. microps,* for which the average distance between capture locations was about 76 m, 79 percent of males (n = 183) and 87 percent of females (n = 126) ranged less than 122 m. Among *P. longimembris* most animals of both sexes ranged less than 30 m (n = 102). Such data suggest that *D. microps* and *P. longimembris* are quite sedentary. Roberts and Packard (1973) reported that the average home range size in the Texas kangaroo rat *D. elator* was .08 ha, and that the maximum distance moved between traps was 87 m for males and 109 m for females. It is not clear what portion of the movements in either study represent daily movements about the home range as opposed to dispersal or shifts in home range boundaries. To understand the effects of these movements on population genetic structure, we need to know the distribution of movements in terms of home range to determine what fraction of an animal's movements bring it into contact with individuals they do not normally encounter within their own home ranges. It is also unclear from these data which movements represent permanent shifts in home ranges vs. temporary excursions out of the usual home range.

We emphasize that these sorts of behavioral data are, by themselves, insufficient to determine how populations are structured. There are several reasons for this. First, though some dominant males may defend females, subordinate males may steal copulations and thus dilute the effects of territorial defense. Second, the timing of mating may be crucial. An observer might see several males copulating with a female, but it may be that only the male that mates with her at peak receptivity during estrus will successfully fertilize her. Third, among heteromyids, individuals occasionally make long forays (3 to 4 home range diameters) away from their usual home ranges. Maza et al. (1973) reported that these long distance excursions are correlated with reproductive activity in *P. formosus.* Long-distance forays also occur in *D. merriami* and *D. microps* (Allred and Beck 1963) and in *D. spectabilis* (Jones, 1982). The actual influence of these excursions on the breeding structure of a population is unknown, but it seems that they would increase the number of female home ranges to which a given male has access. And fourth, dispersers will have no effect on population structure unless they breed or otherwise disrupt the breeding structure of the residents. Liebold and Munger (in preparation) have shown that dispersing female *D. merriami* tend to be less successful at breeding than their nondispersing counterparts, indicating that their effect on population genetic structure might be less than would be expected from examining dispersal behavior alone.

Demographic Evidence

Breeding structure is also partially dependent on demography. The number of breeding individuals and the variance in their lifetime reproductive success may be influenced by survivorship and longevity. For example, a few individuals may survive to adulthood and live through several breeding seasons, but most individuals either do not survive to reproductive maturity or reproduce only once. In this situation, the reproductive output of a population is concentrated in a small number of long-lived adults. The contrasting situation is one in which longevity is nearly equal for all adults so that those individuals reaching reproductive maturity all reproduce once or twice and then die. In this case the lifetime reproductive contributions of all adults might be more nearly equal than in the former situation. Both of these age structures are found in heteromyids. The latter characterizes *L. salvini.* Annual turnover is nearly complete; young are born in the spring and by the next breeding season yearlings make up nearly 100 percent of the population (Fleming 1974). *Dipodomys spectabilis* appears to be an example of the other situation. Holdenreid (1957) studied a population near Santa Fe for 27 months, and stated that "the population was composed of a few well-established individuals remaining continually on the area and a much larger number of animals that remained for only a few days or months" (p. 338). In general, desert rodents tend to be long lived relative to nondesert rodents (Smith and Jorgensen 1975, Conley et al. 1976; members of some

Perognathus species may live up to five years, French et al. 1967). In most cases, however, it is unknown whether there is a high variance in survivorship that might lead to a large differential in reproductive success.

Indirect Genetic Evidence

Indirect genetic evidence concerning population structure can be gathered by determining if genotypic frequencies deviate from an expectation based on random mating. Rasmussen (1964) found a deficiency of heterozygotes of blood group loci in *Peromyscus maniculatus*, implied that inbreeding was the cause, and calculated a relatively small genetic neighborhood size of 10–75 individuals. Selander (1970) found a deficiency of heterozygotes in a population of house mice and from this inferred that the population was structured into small demes (but see Baker 1981). He strengthened his assertion by citing behavioral studies that showed an organization into families or tribes. Patton and Feder (1981) calculated F statistics (Wright 1965, Nei 1975) for populations of *Thomomys bottae*. The measure of random mating within a population (F_{IT}) can be decomposed into two parts, deviation from random mating among subpopulations (F_{ST}) and nonrandom mating within a subpopulation (F_{IS}). Patton and Feder showed a significant amount of divergence among subpopulations, but results were equivocal for within-subpopulation matings. Schwartz and Armitage (1980) similarly calculated F statistics from electrophoretic data on yellow-bellied marmots *Marmota flaviventris*. They found evidence for considerable gene flow between colonies and no evidence for inbreeding, and thus concluded that it is unlikely that evolution in these marmots is accelerated by fixation of alleles via inbreeding within colonies.

Relatively little indirect genetic evidence exists concerning the breeding structure of desert rodent populations. Studies that measure allelic diversity are typically concerned with systematics at the subspecies level or above, or with describing the amount of variation that exists in populations. The published data are usually genic, not genotypic, frequencies and values of overall heterozygosity and polymorphism; genotypic frequencies are required to detect deviations from random mating. Furthermore, sample sizes from any one population are often too small to allow statistical tests. Finally, it is not possible to determine if the samples from any one study site are from one or several subpopulations; population structure will affect the interpretation (Patton and Feder 1981).

Two studies do provide some indirect genetic evidence concerning structure in desert rodent populations. Using a pelage character, Blair (1947) showed no deviation from random expectation within subpopulations of *Peromyscus maniculatus blandus*. In addition, there was little divergence of subpopulations from nearby (less than 5 km) subpopulations, indicating that dispersal between subpopulations does occur. More distantly separated subpopulations did diverge, however. Johnson and Selander (1970) gave diagrams showing the spatial associations of genotypes at four loci in *D. merriami*, and described two of the loci as having clumped distributions of alleles. They suggested that this pattern might indicate a low level of dispersal and some inbreeding, though no statistical test of the pattern was presented. Their findings are at least consistent with the findings of Jones (1982) for dispersal distances of *D. merriami*.

Direct Genetic Evidence

Indirect evidence yields only the knowledge that some deviation from panmixia has occurred, but does not determine which mechanism causes the deviation. This is illustrated by the findings of Patton and Feder (1981): the deviations from random mating they observed within subpopulations of gophers may not have been due to inbreeding but instead to demic structure within the subpopulation.

Direct genetic evidence, on the other hand, ties a genetic effect to the mechanism causing it. For instance, by identifying genotypes at a number of polymorphic loci for all individuals within a population, it is often possible to determine precisely what successful matings have occurred in the population. Patton and Feder (1981) used this technique to show that relatively few males of the pocket gopher *Thomomys bottae* fathered most of the young in their study area.

Hanken and Sherman (1981) used it to demonstrate multiple paternity in Belding's ground squirrel (*Spermophilus beldingi* litters. Foltz and Hoogland (1981) determined that most litters of the black-tailed prairie dog *Cynomys ludovicianus* were sired by resident males within the home coterie, indicating that coteries were the units of reproduction within the population as well as the units of social structure. Foltz (1981) also used genetic evidence to determine that female oldfield mice *Peromyscus polionotus* usually mate with the same male for consecutive litters, thus demonstrating long-term monogamy in this species. As yet, there are no published studies showing direct genetic evidence of structure in desert rodent populations, but work is under way for two species, *D. spectabilis* and *D. merriami.*

Clearly, there are opportunities for more research on the structure of desert rodent populations, and what we now know suggests some interesting possibilities. One of these concerns deme size and the extent of substructuring of populations. Two lines of evidence, the description by Johnson and Selander (1970) of clumped distributions of alleles and observations by Jones (1982) of short dispersal distances, suggest a substantial demic structure in *D. merriami* populations. The extent of gene flow within populations is uncertain, though. Turnover rates are quite high in *D. merriami* (80–90 percent annually; Jones, 1982), which would tend to increase gene flow. Furthermore, we do not know the extent of long-distance dispersal (greater than 20 home range diameters), nor do we understand what role, if any, is played by excursions to areas outside the usual home range. Do individuals making these excursions find mates in areas several home range diameters from their own home range, or are they more successful at finding mates among their immediate neighbors, with whom they are possibly more familiar? Genetic studies in which marker alleles are introduced in natural populations (cf. Anderson et al. 1964, Baker 1981) would help answer these questions and would aid in determining the rate of gene flow within and among subpopulations.

Other questions concern the effects of age and breeding structure on population genetic structure. We suggested above how differences in age structure, longevity, and survivorship schedules might lead to more or less variance in lifetime reproductive success of adults. In species like *D. spectabilis,* where a few individuals live through several breeding seasons but most individuals have much shorter lifespans, a core of long-lived individuals may make a disproportionately large contribution to later generations. It would be useful to know what proportion of the breeding adults in later generations are actually descendants of these long-lived individuals. And how does reproductive success vary with age? Are older males more successful at competing for mates? This would further increase variance in male reproductive success in situations where only a small proportion of males live into their second or third breeding season. These questions are probably best pursued in long-term mark-recapture studies of natural populations combined with direct genetic determination of maternity and paternity.

Population structure in desert rodents may also be related to fluctuations in density; such periodic decreases in population size are known to occur (Beatley 1969, French et al. 1974, Whitford 1976, Petryszyn 1982). These decreases may cause genetic bottlenecks, reducing the amount of genetic diversity within subpopulations. To what extent do these decreases in density affect effective population size? Furthermore, the rate of dispersal between subpopulations may vary with density. Higher interdemic dispersal rates at peak densities might partially or completely offset the reductions in variability that possibly result from population crashes. Determining the importance of density fluctuations and interdemic dispersal for population genetic structure would require monitoring genetic makeup over large areas and over a time long enough to cover at least one, and preferably more, cycle(s) of population decline and increase.

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PATTERNS OF MORPHOLOGY AND RESOURCE USE IN NORTH AMERICAN DESERT RODENT COMMUNITIES[1]

M. V. Price[2] and J. H. Brown[3]

ABSTRACT.— As is true of many assemblages of ecologically similar organisms, coexisting heteromyid rodent species differ conspicuously in morphology and in microhabitat affinity. These patterns are so common that their explanation represents a central problem of community ecology. In the case of desert rodents, two very different factors, predation and competition, have been advanced as the ultimate cause of the patterns. We outline the way in which each of these factors could produce observed community-level patterns and review the evidence for the action of each factor. We conclude that the "competition" hypothesis has more support at the moment, but that this is partly a result of the general lack of good experimental studies of predation in terrestrial vertebrate systems. We outline a general protocol for distinguishing the effects of predation and competition through careful examination of relationships between morphology, foraging and predator-avoidance abilities, and behavior. We think such "microecological" analysis of the consequences of morphology holds much promise for improving our understanding of community-level patterns of morphology and resource use.

Among the basic concerns of community ecology is identification of factors that determine the number, relative abundances, and phenotypic attributes of coexisting species. Rodents of North American deserts were important in the development of this major subdiscipline of ecology, mostly through the work of several influential naturalists—among them Joseph Grinnell and C. Hart Merriam—who developed their ideas about limits to animal distributions in large part from observing small mammals in the western United States. Their ideas have subsequently been incorporated into a sophisticated body of mathematical theory, the recent development of which was stimulated primarily by G. Evelyn Hutchinson and Robert H. MacArthur (see MacArthur 1972, Hutchinson 1978). Desert rodents in general still figure heavily in community ecology, being widely used for testing general theories of community organization under field conditions. They are especially suitable for such studies because they are small, abundant, diverse, and easily captured in the field and observed in the laboratory, and because unrelated groups have independently colonized geographically isolated arid regions.

Our aim here is not to review exhaustively what is known about desert rodent communities, since several other authors have made recent contributions of this sort (Brown 1975, Rosenzweig et al. 1975, Brown et al. 1979). Instead, we will provide an updated overview of the general characteristics of these communities, discuss the alternative hypotheses that have been advanced to explain those characteristics, and outline the evidence that bears on the alternatives. Finally, we will suggest directions for further research. We will focus on the specialized seed-eaters of North American deserts because much less is known about other desert rodents, but we will attempt to indicate when observations from other dietary guilds or geographic regions fit the patterns we describe.

GENERAL PATTERNS

Natural History

The rodent fauna of North American deserts is dominated by members of the Heteromyidae, a New World family whose remarkable similarity to unrelated Old World and Australian desert forms is a textbook example of convergent evolution. Like jerboas,

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[2]Department of Biology, University of California, Riverside, California 92521.

[3]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721.

gerbils, and hopping mice, most heteromyids are primarily granivorous and can subsist without a source of free water. They are also nocturnal, live in burrows, and include both bipedal hopping (*Dipodomys*, *Microdipodops*) and quadrupedal bounding forms (*Perognathus*). A more complete analysis of morphological, behavioral, and ecological similarities among unrelated desert rodents can be found in Eisenberg (1975), Brown et al. (1979), and Mares (this volume).

Some of the convergent features of these groups, such as xerophytic physiology and burrowing habit, are clearly responses to the extreme temperatures and low rainfall that characterize deserts. Others, such as granivory, are probably indirect consequences of plant responses to frequent and unpredictable droughts. Many desert plants have adopted an "ephemeral" life history, in which they survive unfavorable periods as seeds or (less often) as underground storage organs (Noy-Meir 1973, Solbrig and Orians 1977); and the resulting pool of dormant seeds in the soil provides a relatively abundant and persistent food source for a variety of birds, rodents, and ants (Noy-Meir 1974, Brown et al. 1979). The significance of still other features of desert rodents, such as prevalence of bipedal locomotion, remains a matter of debate, but these features probably reflect constraints on predator avoidance or foraging strategies imposed by the physical structure of desert vegetation and soils (see Bartholomew and Caswell 1951, Brown et al. 1979, Thompson et al. 1980, Reichman 1981, Thompson 1982a,b).

Proximate Factors Affecting Abundance and Diversity

There is considerable evidence that individual reproductive success and population densities of rodents in North American deserts are limited by seed production of ephemeral plants, whose germination and growth is directly tied to the amount of precipitation falling during certain seasons (Noy-Meir 1973). Reproductive rates of individual rodents, as well as population densities, show extensive temporal and geographical fluctuations that are closely correlated with variation in precipitation (Brown 1973, 1975, French et al. 1974, Brown et al. 1979, M'Closkey 1980, Petryszyn 1982, Munger et al., this volume). Casual observation of climatic correlates of rodent "plagues" in other regions suggests that this is probably true in all deserts (see references in Prakash and Ghosh 1975).

Species diversity seems to be influenced by several factors, the most obvious of which is habitat complexity (Rosenzweig and Winakur 1969, M'Closkey 1978). Positive correlations between diversity and habitat complexity are common in animal communities (MacArthur 1972, Schoener 1974, Hutchinson 1978), and occur because coexisting species usually differ in affinities for areas of particular topographic or vegetation structure. If it is sufficiently productive, an area that is structurally complex can be inhabited by several species, each of which specializes on a different microhabitat. Interspecific differences in microhabitat affinity appear to be characteristic of all desert rodent communities that have been examined (cf. references in Prakash and Ghosh 1975). Among heteromyids, the bipedal kangaroo rats and kangaroo mice are associated with sparse perennial vegetation and tend to forage in open microhabitats, whereas the quadrupedal pocket mice are associated with dense perennial vegetation or rocky areas and prefer microhabitats under tree or shrub canopies (Rosenzweig and Winakur 1969, Rosenzweig 1973, Brown and Lieberman 1973, Brown 1975, Price 1978b, Harris unpublished, Price and Waser 1983). This pattern also appears to occur in African deserts where bipedal jerboas are associated with open areas more than are quadrupedal gerbils (e.g., Happold 1975).

Several experimental studies indicate that vegetation structure influences not just the number of species in North American communities, but also the identities and relative abundances of those species. Rosenzweig (1973) altered a number of small plots by clearing shrubs from some and augmenting brush on others. These manipulations resulted in significant local shifts in species composition: *Perognathus penicillatus* increased in density on augmented plots and decreased on cleared plots, but *Dipodomys merriami* responded in the opposite way. Similarly, Price

(1978b) removed half of the small shrubs from 25 sites within a 3.2 ha area and found predictable increases in the density of *D. merriami*, the species that showed the most pronounced preference for foraging in open spaces. Furthermore, the magnitude of local changes in density of this species was correlated with the amount of shrub cover removed. After adding cardboard "shelters" between shrubs to experimental plots, Thompson (1982b) observed increased abundance of species normally associated with shrubs and decreased abundance of kangaroo rats. "Natural" temporal or spatial changes in vegetation appear to result in similar shifts in rodent species composition that can be predicted from knowledge of microhabitat preferences (Rosenzweig and Winakur 1969, Beatley 1976, Hafner 1977, Price 1978b, Price and Waser 1983).

Among habitats that are similar in structure, the number of rodent species increases with the amount and predictability of annual precipitation, which determines seed production as well as shrub density (Brown 1973, 1975, Hafner 1977, Brown et al. 1979). The most arid parts of the Colorado and Mojave deserts typically have only one or two species of heteromyids, whereas structurally similar but more productive areas in the Sonoran, Chihuahuan, and Great Basin deserts sometimes support as many as four or five species. As might be expected, average population densities and total rodent biomass also tend to be positively correlated with increased seed abundance, but it is less clear why species diversity should exhibit such a pattern. MacArthur (1969, 1972) showed that this correlation is expected of communities composed of species limited by a single resource. In such resource-limited systems, species that specialize on a subset of available resources can persist only when overall production is high enough to supply some minimal amount of the preferred subset during poor years. In unproductive regions, abundance of the appropriate resources may often fall below the threshold level, causing the consumer populations that depend on them to go extinct locally. Brown (1973) has proposed this explanation for geographic diversity–productivity correlations in heteromyid communities. A similar explanation would also account for seasonal variations in species occupying given habitats (cf. Congdon 1974, Meserve 1974) and for species turnover between local habitats that differ in structure. There is not as yet sufficient evidence to evaluate rigorously these productivity-based explanations of species diversity, although they are consistent with results of one experimental study: artificial augmentation of seeds in a short-grass prairie enhanced local species diversity by inducing invasion of a specialized granivore, *Dipodomys ordii* (Abramsky 1978).

Brown (1973, 1975) has pointed out that historical factors, in addition to productivity and habitat structure, can influence the number of species in heteromyid communities. He found that geographically isolated sand dunes were inhabited by fewer species than would be expected on the basis of their productivity, and attributed this to decreased colonization rates of isolated "islands" of suitable habitat. Historical constraints have also been invoked to account for the low diversity of rodents in South American and Australian deserts (Brown et al. 1979).

Morphological Configuration of Rodent Communities

In addition to pronounced divergence in microhabitat affinities, a salient feature of heteromyid communities is that coexisting species differ in body size more than would be expected if communities were random assemblages of species (Fig. 1; Brown 1973, 1975, Brown et al. 1979, Bowers and Brown 1982). Such body size divergence is by no means unique to desert rodent communities; in fact, it is so ubiquitous that nearly constant size ratios among coexisting species have been given the name "Hutchinson's ratios," after the ecologist who drew attention to them (Hutchinson 1959, Horn and May 1977, Lack 1971, MacArthur 1972). Heteromyid communities are, however, one of the few cases for which observed size spacing has been shown to be statistically different from random null models (cf. Strong et al. 1979, Bowers and Brown 1982, Petersen 1982, Simberloff and Boecklen 1981). It is interesting to note that desert cricetids do not show size patterns typical of heteromyids, and that including the omnivorous and carnivorous

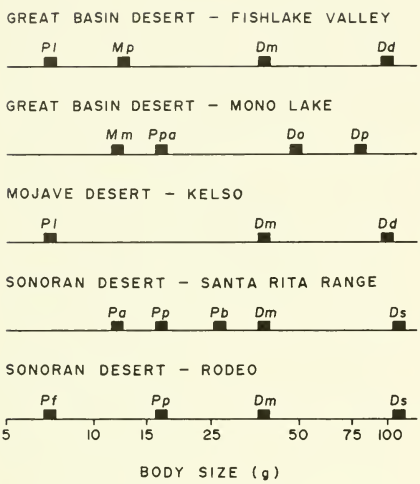

Fig. 1. Typical heteromyid rodent assemblages from three major North American deserts. The average body sizes of common species found at five sites are indicated by their position on the horizontal axis. Pl = *Perognathus longimembris*; Pf = *P. flavus*; Pa = *P. amplus*; Pp = *P. penicillatus*; Ppa = *P. parvus*; Pb = *P. baileyi*; Mm = *Microdipodops megacephalus*; Mp = *M. pallidus*; Dm = *Dipodomys merriami*; Do = *D. ordii*; Dp = *D. panamintinus*; Dd = *D. deserti*; Ds = *D. spectabilis*. Note that congeners of similar body size are not common at the same site. Data taken from Brown (1973) and Price (unpublished).

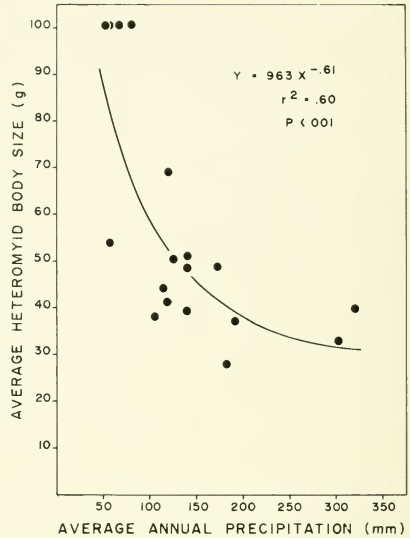

Fig. 2. Average body size of heteromyids resident on sand dunes that differ in annual precipitation, unweighted by relative species abundances. As species number decreases with decreasing precipitation, the smaller species drop out first. This causes a significant increase in average body size as productivity declines, until only the largest kangaroo rats remain on the most arid dunes. Data are from Brown (1973); the power fit shown on the figure is significant ($F_{1,16} = 24.43$; $P < .001$).

cricetids along with the heteromyids in a morphological analysis obscured patterns present within the granivore guild (Bowers and Brown 1982, Petersen 1982). There have been no studies of morphological structure similar to these for desert rodent systems in continents other than North America. This is unfortunate, because there are intriguing suggestions of size differences among coexisting gerbils in North Africa (Happold 1975:36) and among dipodids in the USSR (Naumov and Lobachev 1975:491).

Coexisting heteromyids differ in parameters of body shape related to locomotory gait as well as in size. Relative to quadrupedal forms, bipeds have elongated hind feet and tails, shortened vertebral columns, and reduced fore feet (Hatt 1932, Howell 1932). There is some association between shape and size; in general, bipedal forms are larger (12–150 g) than quadrupedal forms (7–40 g).

In addition to these within-community morphological patterns, there are striking geographical trends in body size for sand dune habitats. Figure 2 indicates that as species diversity declines along a gradient of decreasing precipitation, average size of heteromyids inhabiting sand dunes increases. This is not due to geographic variation in size within individual species, although such variation has been reported (Kennedy and Schnell 1978). Instead smaller species drop out first along the gradient, until only the largest species remain in the least productive regions. It remains to be seen whether similar patterns exist for other habitats.

Proposed Explanations for the Patterns

The Hypotheses

Two hypotheses have been advanced to account for the conspicuous interspecific diver-

gence in body size, shape, and microhabitat affinity that characterizes heteromyid rodent communities. The first proposes that these features reflect divergent predator avoidance strategies that have evolved because there can be no single "best" escape strategy in heterogeneous environments (cf. Rosenzweig 1973, Thompson 1982a,b, Webster and Webster 1980). An escape behavior that works well away from cover, for example, may be ineffective in dense brush either because shrubs impose physical constraints on movement or contain different types of predators. It is not difficult to imagine that morphology determines how easily an animal can be detected and which escape strategies it can use effectively. If each microhabitat requires a different escape strategy, then a particular morphology defines the relative risk associated with foraging in different microhabitats. The predation hypothesis can account for associations between heteromyid form and microhabitat if animals rank microhabitats on the basis of risk, and forage selectively in the safest areas. This would cause species differing in morphology to differ in their ranking and use of microhabitats. Predation could also interact with food availability to account for diversification of form within communities, if predation pressure restricts the microhabitats in which each species can forage efficiently, so that some microhabitats are initially utilized less intensively than others. In this case seeds would tend to accumulate in those microhabitats that are risky for resident species, and such microhabitats would eventually be colonized by species whose morphology and escape behavior allow their safe use.

The second hypothesis (cf. Brown 1975, Price 1978b, M'Closkey 1978) proposes that divergence in morphology and microhabitat affinity is the outcome of competition for seed resources. A predicted outcome of competition is divergence among competitors in use of limited resources, and in morphological and behavioral traits that influence the efficiency with which particular types of resources can be utilized (MacArthur 1972, Lawlor and Maynard Smith 1976). This hypothesis can account for observed microhabitat affinities if microhabitats differ in the types of seeds they contain or in the methods required to harvest seeds, and if body size and shape influence the efficiency of harvest in a particular microhabitat. Under these conditions, animals can be expected to rank and utilize microhabitats on the basis of harvest rates.

Little progress has been made in determining the relative importance of predation and harvest efficiency in shaping characteristics of heteromyid communities, although authors often invoke one or the other factor exclusively to explain microhabitat preferences or morphological attributes (cf. Eisenberg 1963, Rosenzweig 1973, Brown 1973, Price 1978b, Thompson et al. 1980, Webster and Webster 1980, Reichman 1981, Thompson 1982a, b). The problem with treating these as alternative hypotheses is that both factors may influence foraging behavior. According to optimal behavior models (cf. MacArthur and Pianka 1966, Pyke et al. 1977, Werner and Mittelbach 1981), animals should rank microhabitats according to the fitness gain realized while using them. Because fitness gain is a complex function of resource harvest rates discounted by expected costs or risks, interspecific differences in microhabitat choice could come about if species differ in their abilities to harvest resources and/or to avoid physiological stress or predation in particular microhabitats. It is difficult to devise an experimental protocol that would directly distinguish the relative importance of harvesting efficiency and predator avoidance in determining microhabitat choice, since this requires that each factor be varied separately—and predation risk is not especially susceptible to effective manipulation.

Until direct experimental tests of the "predation" and "harvest efficiency" hypotheses can be devised, we feel the best way to begin evaluating their importance is to examine in detail the plausibility of the assumptions about morphology and behavior upon which they are based, and to scrutinize community-wide patterns for any that might be inconsistent with one or the other hypothesis. We will concentrate on such an analysis in the rest of this section.

Evidence for the Role of Predation

There can be no doubt desert rodents represent a major food source for a variety of

predators. In North America, hawks, owls, snakes, and carnivorous mammals have been reported to take rodents, and populations of all these predators are dense enough to represent a significant source of mortality (cf. Pearson 1966). The importance of predation as a selective agent is further suggested by widespread correspondence between pelage and substrate colors in desert rodents (Benson 1933, Dice and Blossom 1937). This substrate matching has evolved because visually hunting predators selectively attack individuals that contrast with their background (Dice 1945, 1947, Smith et al. 1969, Bishop 1972, Kaufman 1974).

Estimates of potential predation rates for kangaroo rats have come from experiments comparing disappearance rates of marked individuals whose hearing had or had not been impaired experimentally (Webster and Webster 1971). Thirty-three percent of normal and sham-operated animals disappeared within a month of being released, along with 78 percent of the deafened animals. Most of the latter disappeared during the dark phase of the moon. Although it is impossible to tell what part of the 33 percent loss of normal animals was caused by predation rather than dispersal, the 45 percent increment in loss of deafened animals suggests that predators may be a potentially important source of mortality, at least for unwary or weakened animals.

There is some evidence that rodents respond behaviorally to risk of predation, but it is mostly inferred indirectly from evidence relating light intensity to rodent activity, or to predator success. Dice (1945) observed that owls have difficulty detecting immobile prey at light intensities lower than about 7.3×10^{-7} foot-candles (values equivalent to that under dense foliage on a cloudy night). Although owls can also use hearing to locate active prey, it is reasonable to expect hunting success to be higher on moonlit nights, unless prey experience a correspondingly greater ability at high light levels to detect and escape from approaching predators. Webster and Webster's (1971) observation that deafened kangaroo rats disappeared primarily in the dark phase of the moon would suggest that light can help prey as well as predator. In any event, Blair (1943) noted that deer mice exhibited reduced activity in the laboratory when light intensities exceeded levels typical of clear moonless nights. Similarly, Lockard and Owings (1974, but see Schroder 1979) reported reductions in visitation to feeding stations by free-ranging Banner-tailed Kangaroo Rats during periods of moonlight. Kaufman and Kaufman (1982) observed fewer kangaroo rats on standard nightly road censuses and observed more animals on shaded than unshaded sides of the road when the moon was up. Burt Kotler (pers. comm.) experimentally manipulated light levels in the field with lanterns and observed decreased foraging by desert rodents at seed trays when light levels approached those of bright moonlight. Although these authors concluded that overall kangaroo rat and deer-mouse activity is sensitive to risk of predation, there is no direct evidence that the effect of moonlight on activity has to do with predation risk. It is conceivable, for example, that animals avoid bright light simply because it is uncomfortable for dark-adapted eyes.

There is also little evidence that microhabitat use is influenced by predation risk. Dice (1947) found that artificial bushes reduced the number of deer mice taken by owls in experimental rooms, and Lay (1974) remarked that owls were less successful in attacking mice near an obstruction such as a wall; this leads one to expect that mice are safer in structurally complex areas. Blair (1943) did not note, however, that deer mice restricted their activity in the center of the room relative to low-risk areas near walls or the nest box when light intensities were high. Burt Kotler (pers. comm.) found that kangaroo rats spent a greater proportion of their time under shrubs when he had increased light levels experimentally with lanterns. Taken altogether, these studies suggest that light influences overall activity and microhabitat use, but the inference that these behavioral changes are responses to enhanced predation risk remains tenuous. Clearly, more experimental work needs to be done. It is especially important to determine the relationship between light intensity, microhabitat, and predation risk for different kinds of desert rodent.

Although there are interspecific differences in the ease with which rodents can escape detection or attack by particular predators, it is not known how these behaviors are related to differences in body size or shape. From the experiments of Dice (1947), Lay (1974), Kaufman (1974) and Webster (1962, Webster and Webster 1971), it appears that deer mice (*Peromyscus*) are much more vulnerable to owls than are kangaroo rats (*Dipodomys*) or gerbils (*Meriones*); the latter two groups often remained unscathed after a night's confinement in a bare room with a hungry owl. Several features of kangaroo rats have been related to their remarkable ability to avoid predators (Bartholomew and Caswell 1951, Webster 1962, Webster and Webster 1971, 1980). Their inflated middle ear cavities enhance sensitivity to the low-frequency sounds made by striking snakes and owls, and enlarged, dorsally placed eyes are sensitive to sudden movements in dim light. Kangaroo rats with either or both sensory modes intact readily avoid attack by leaping suddenly upward or backward out of reach of the predator. Elongated hind feet and tails appear to facilitate these maneuvers, which are effective for predators like owls and snakes that cannot easily change trajectory during an attack. Because deer mice lack ears specialized for detecting low-frequency sound as well as specialized anatomy to facilitate leaping, it is not clear whether they do not avoid owls effectively because they cannot detect them in time, or because they cannot use erratic leaping as an escape response. The former explanation seems more likely. Lay (1974) noted that *Peromyscus* made no attempt to escape owl attack until after they were captured, as though they were unaware of the predator's approach. He also noted that *Meriones*, which have enlarged auditory bullae like kangaroo rats but lack their extreme bipedal adaptations, could effectively jump or run out of the owl's way. Thus it appears that detection of predators is more critical for survival than leaping ability.

Although size apparently is important in determining prey choice by certain predators (cf. references in Hespenheide 1975, Wilson 1975), it is not obvious how size influences net predation risk among desert rodents. In general, small predators are less efficient at subduing large prey and therefore consume smaller prey on average than do large predators. In some animals, such as barnacles (cf. Connell 1975), an individual becomes immune to predation once it has grown to some threshold size. Large size in heteromyids may, therefore, confer some immunity from small predators on the one hand, but on the other could make them more conspicuous and desirable for larger predators, which would then concentrate their efforts on these preferred large prey.

It is unfortunate that nobody has compared predator escape abilities of pocket mice and kangaroo rats directly, because the former are often assumed to lack the kangaroo rat's facility in escaping predators. This assumption is based on differences in morphology between heteromyid genera that are qualitatively similar to differences between heteromyid and cricetid rodents as a whole. It may well be unwarranted. Webster and Webster (1975, 1980) have examined the morphology and sensory physiology of heteromyid ears. They calculate that ears of all three of the desert genera (*Dipodomys*, *Microdipodops*, *Perognathus*) have a theoretical best transmission of 94–100 percent of the incident acoustical energy reaching the outer ear. This theoretical efficiency is achieved by enlargement of the tympanic membrane in *Dipodomys* and *Microdipodops*, the two forms with inflated auditory bullae, whereas it is achieved by reduction of the stapes footplate in *Perognathus*. Actual sensitivity of *Dipodomys* and *Microdipodops* ears to low frequency sounds (less than about 3 k Hz) appears greater than that of *Perognathus*, judging from the sound intensity required to produce a 1 μV cochlear microphonic (Webster and Webster 1980). This is to be expected from the relatively greater reduction in stiffness relative to mass of the middle ear apparatus that is achieved by using enlarged tympanic membrane rather than reduced ossicle mass to achieve overall auditory sensitivity. Although suggestive, these results are not conclusive because cochlear microphonics do not show actual auditory thresholds; behavioral studies will be necessary to determine to what extent the lower sensitivity of *Perognathus* ears actually impairs their ability to detect predators in nature

(Webster and Webster 1971). If there is a difference between pocket mice and kangaroo rats in susceptibility to predation it is more likely a function of sensory than locomotory capabilities. There is no evidence that pocket mice are substantially less able than bipedal forms to use erratic leaping to avoid predators, even though they use quadrupedal bounding for straightaway running at high speeds. Bartholomew and Cary (1954) observed that pocket mice are adept at erratic leaping, an observation anyone who has tried to catch an escaped pocket mouse can confirm. Whether this ability to escape human pursuers implies equal facility with natural predators is, of course, not known.

We conclude from this survey that predation has undoubtedly been of general importance in the evolution of some aspects of desert rodent behavior and morphology, but its role in promoting divergence among coexisting heteromyids in morphology and microhabitat use has yet to be elucidated.

Evidence for the Role of Competition

The case for an important role of competition is stronger, but is by no means complete. Munger and Brown (1981) recently have provided experimental evidence that heteromyids compete: removal of kangaroo rats results in increased densities of smaller granivorous, but not omnivorous, rodents in experimental exclosures. This is the most robust sort of evidence for the existence of resource-based interspecific competition (cf. Connell 1975). Although such experiments document the existence of competition, they can tell us little about the evolutionary consequences of this interaction for community-level patterns of morphology and microhabitat affinity.

The fact that seed availability limits reproductive success of individuals indicates that, like predation, competition must have represented a strong agent of natural selection, in this case for efficient seed harvest. Anecdotal evidence suggests that heteromyids are indeed efficient "seed-vacuuming machines." Lockard and Lockard (1971) found that *Dipodomys deserti* could accurately pinpoint the location of a one-gram packet of millet seed buried 20 cm in the soil. We have observed desert rodents routinely collecting 90–100 percent of millet seeds widely dispersed on the soil surface in a night's time (Brown, unpublished); and oats sprinkled near traps during a recent field trip to Kelso Dunes, California, were harvested from 120 of 150 traps by *Dipodomys deserti* (Price, pers. obs.). In the laboratory, we have clocked pouching rates of 16 millet seeds per second in *D. deserti* (Price, unpublished). Finally, Monson (1943) found that *D. spectabilis* harvested and stored an average of about 20 qts of seed per month during fall seed production. The question remains, however, whether interspecific differences in morphology imply differences in the kinds of seed resources that can be harvested most efficiently.

Because differences in body size are so pronounced among coexisting heteromyids, the search for correlations between size and foraging behavior has been intense. Brown and Lieberman (1973; see also Brown 1975, Brown et al. 1979, Bowers and Brown 1982) initially proposed that heteromyids of different size partition resources in part by eating seeds of different size. They sieved seeds taken from cheek pouches and found a positive correlation between body weight and average seed size as measured by the size of sieves in which seeds settled. (This is a measure of seed linear dimensions.) Lemen (1978) subsequently reanalyzed their samples using weight of hulled seeds as the measure of seed size (rather than weight of the seed, hulled or unhulled, as it was found in the pouch) and found no correlation between rodent weight and average weight of seeds taken. Laboratory feeding trials generally support Lemen's (1978) conclusion that body size differences do not reflect differences in seed size selection (Rosenzweig and Sterner 1970, Hutto 1978; but see Mares and Williams 1977).

We have recently improved on these studies by offering caged heteromyids wheat ground to different sizes, rather than an array of seed species that differ in size. This controls for confounding effects of taste preferences. We find no indication that large heteromyids prefer large seeds; if anything, *D. deserti* harvests more small particles than do smaller species (Fig. 3a, b; Price unpublished). Results of these laboratory experiments are substantiated by field studies of

heteromyid food habitats, which indicate that sympatric rodents eat largely the same seed species (Smigel and Rosenzweig 1974, Reichman 1975, O'Connell 1979, Stamp and Ohmart 1978). Differences in diet may reflect spatial differences in what seeds are available where the animals forage rather than intrinsic differences in what seeds are selected once they have been encountered (Reichman 1975, O'Connell 1979, M'Closkey 1980). This lack of apparent differences in seed preference is supported by results of a preliminary laboratory study (Figure 3c; Price unpublished), in which no pronounced interspecific differences in consumption of eight seed species were observed.

The discrepancy between results Brown and Lieberman (1973) obtained by sieving cheek pouch contents and those Lemen (1978) obtained by weighing is intriguing. We believe it is real, and that it may be the result of a body-size-dependent difference in heteromyid foraging behavior. Such a discrepancy could come about if larger heteromyids more commonly take seed heads from plants directly rather than gleaning dispersed seeds from the soil (the seed head would have a larger linear dimension than a single detached seed), or if the small cheek pouch volume relative to metabolic demands of smaller heteromyids (Morton et al. 1980) requires them to remove bulky husks from seeds before pouching them (a husked seed has a smaller linear dimension than an unhusked one). The former possibility could result in partitioning of seed resources, but the latter would not. In both cases, sieving would show a positive relationship between rodent and seed size, but weighing hulled seeds would not.

There are other respects in which body size could influence foraging choices made by heteromyids. Price (1981, 1982a) has developed a simple model of a heteromyid foraging on a patchy seed resource. The model predicts that because harvest rates, travel speeds, and metabolic costs are allometric functions of body size, the degree to which an animal will specialize on the most profitable patches should depend on its size. Until we obtain accurate estimates of model parameters for the heteromyid system, however, we will not be able to determine

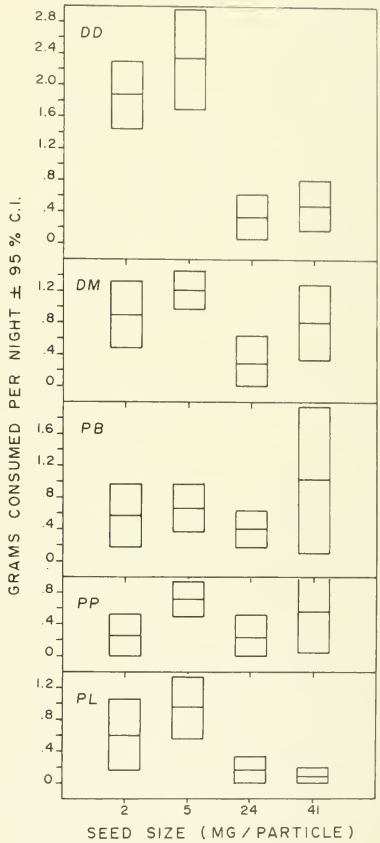

Fig. 3. Consumption of different sizes or species of seed by caged heteromyids having prior experience with the experimental food.

A. Animals were presented with equal weights of four size classes of ground wheat particles and left undisturbed to feed for a night. In the morning, remaining seeds were recovered by sieving and amounts of each size consumed determined by subtraction. Sample sizes were six runs for each rodent species. Abbreviations of specific names are as in Figure 1. MANOVA indicates a significant effect of species on consumption (Wilks' $L = .018$; $F_{16,37} = 7.65$; $P < .0001$), but discriminant analysis indicates the major interspecific difference is a simple effect of body size on consumption of all seed sizes ($\lambda = 22$), with a much less pronounced variation among species in the degree to which very large seeds are avoided ($\lambda = 2.4$). Notice that there is no correlation between body size and seed size selection.

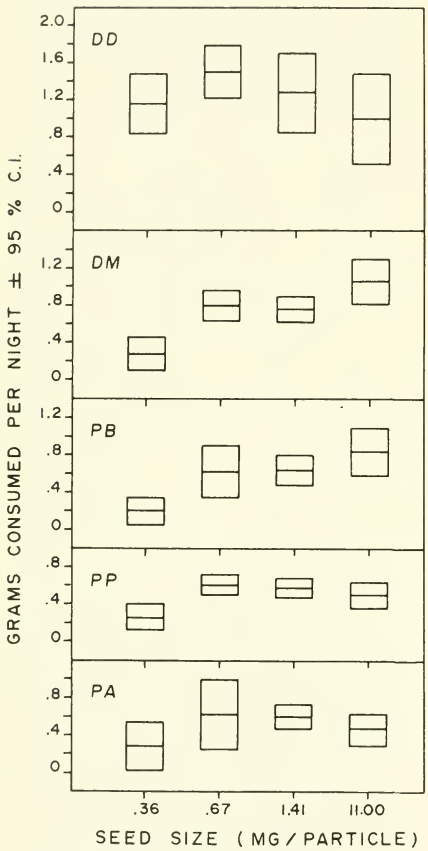

Fig. 3 continued.

B. Results of an experiment identical to that described above, but with smaller seed size classes and samples of ten runs per species. Again, the significant interspecific differences in consumption (Wilks' L = .040; $F_{16,55} = 6.50$, $P < .0001$) are largely due to the fact that large animals ate more of all sizes ($\lambda = 8.0$), with a minor difference ($\lambda = 1.8$) due to variation in the extent to which the smallest seeds are avoided. Note again that there is no tendency for larger species to prefer large seeds.

whether we should expect larger or smaller animals to specialize to the greater extent on profitable patches. Nevertheless, it appears from the model that body size may influence aspects of foraging behavior far more subtle than seed size choice alone. Some laboratory studies offer tentative support for this idea. Several authors (Reichman and Oberstein 1977, Price 1978a, Hutto 1978; but see Trombulak and Kenagy 1980) have observed differences between large and small heteromyids in use of seeds that occur in different local densities; the larger species specialize to a greater extent on dense seed aggregations. In contrast, the few studies of seed patch selection in the field provide no evidence that large species specialize on clumped seeds (Frye and Rosenzweig 1980, Price unpublished). This latter result may be an artifact of using millet sprinkled on the soil surface as bait. A single millet seed is five times larger than most naturally occurring seeds (cf. Reichman 1976) and may be perceived by all heteromyids as a "profitable patch." Indeed, movement patterns of heteromyids exploiting natural seed resources are consistent with the hypothesis that larger species use more widely spaced, rich patches (Bowers 1982). This discrepancy between conclusions drawn from baiting experiments and those based on observation of natural movement patterns underscores the great need for field experiments that mimic more accurately what heteromyids are encountering in nature.

Coexisting heteromyids differ not just in size, but also in morphological traits that are linked to the gait used in rapid locomotion. Reichman (1981) developed a graphical model that considers whether gait should influence seed patch choice. The model assumed that bipedal animals have lower energy expenditure at high speed than quadrupedal animals of similar size. This assumption leads to the expectation that bipedal forms should specialize to a greater extent than quadrupedal forms on clumped, widely spaced seed resources. Because bipedal heteromyid species are larger on average than quadrupedal species, Reichman's conclusions supplement those of Price (1981, 1982a). Recently, however, Thompson (1982c) and Thompson et al. (1980) have called into question the assumption that bipedal locomotion is more efficient than quadrupedal locomotion at high speeds. Their results suggest that the leveling-off of metabolic expenditure at high velocity reported by Dawson and Taylor (1973) and Dawson (1976) for bipedal animals may be a methodological artifact, and

that there are no obvious differences in metabolic rate between quadrupeds and bipeds traveling at the same speed. This finding does not, however, preclude the possibility that something more subtle is going on. Hoyt and Taylor (1981) were able to show that the relationship between metabolic rate and travel velocity is not linear within a gait, and that animals choose to travel at certain speeds because of this nonlinearity. If quadrupedal and bipedal animals have different preferred speeds, then there could be a real difference in their efficiency of travel that would be difficult to detect by measuring oxygen consumption of animals on a treadmill.

We conclude from these preliminary observations that morphological differences among coexisting heteromyids are likely to be associated with differences in the efficiency with which various seed resources can be harvested, and consequently with differences in resource use in nature. Exactly what form resource partitioning takes, though, is still in question. The diet data reviewed earlier suggest that direct partitioning of seeds on the basis of some intrinsic property such as size, nutritional quality, or husking difficulty is not sufficient to account for observed patterns of coexistence.

The conspicuous differences in microhabitat affinity among coexisting species could represent an indirect partitioning of seeds by differential patch choice if microhabitats differ in the seeds they contain or in the methods that must be used to harvest them. Detailed comparison of the seed reserves in different microhabitats has just begun, but preliminary results suggest substantial variation. Several workers have noted that average seed density in standard surface soil samples is higher under the canopy of shrubs than in open spaces between shrubs (cf. Goodall and Morgan 1974, Nelson and Chew 1977, Thompson 1982b). Furthermore, Reichman and Oberstein (1977) and Reichman (1981), working in the Sonoran Desert, found that the coefficient of variation in seed density is much higher for samples taken in open spaces than for those taken under shrubs. This suggests that seeds are more clumped in open spaces. Preliminary data from another Sonoran Desert site (Price and Reichman, unpublished) extend these findings

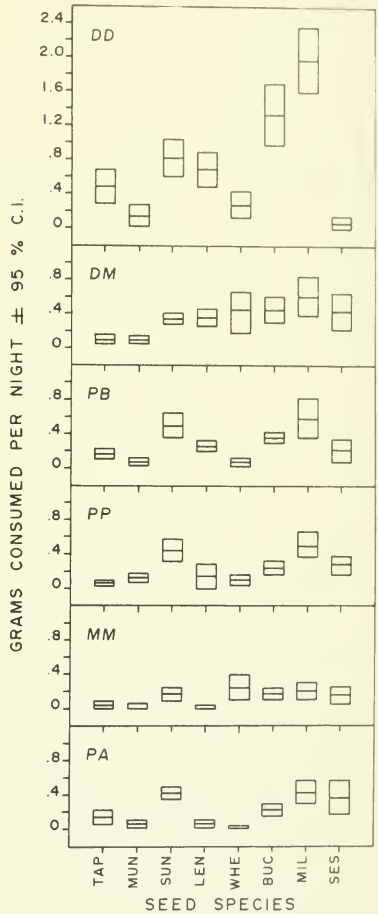

Fig. 3 continued.

C. Results of an experiment similar to those described above, except that animals were presented with equal weights of eight commercially available seed species that differ substantially in nutritional value. (TAP = tapioca; MUN = mung; SUN = sunflower; LEN = lentil; WHE = wheat; BUC = buckwheat; MIL = millet; SES = sesame). There were 14 runs per species. As before, significant differences between species in consumption (Wilks' L = .010; $F_{40,181} = 8.67$; $P < .0001$) are primarily those related to the effect of body size on consumption of preferred seeds ($\lambda = 25.5$). In general, preferences were similar across species, with sunflower, millet, and buckwheat taken most often. There was some variation in ranking of wheat and sesame ($\lambda = .86$), but this seems unrelated to body size or taxonomic similarity.

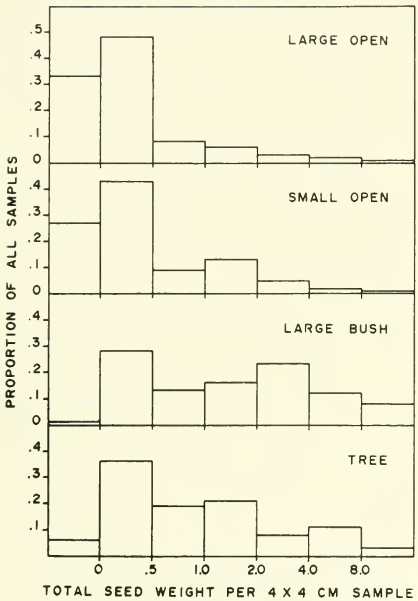

Fig. 4. Characteristics of seeds extracted from 160 4×4 cm soil samples taken in August 1980 from each of four microhabitats at the Santa Rita Experimental Range near Tucson, Arizona. Refer to Price (1978b) for a description of the study site and microhabitats, and to Reichman and Oberstein (1977) for a description of seed extraction techniques.

A. Distribution of total weights of seed (in mg) extracted per sample from Large Open, Small Open, Large Bush, and Tree microhabitats. There is significant heterogeneity among microhabitats in seed abundance ($G = 191$, d.f. $= 18$, $P < .005$), which is primarily due to differences between open and vegetated microhabitats (Large and Small Open form a homogeneous subset, as do Large Bush and Tree).

(Fig. 4) by indicating that microhabitats differ not only in seed abundance but also in the species of seed they contain and in the density and particle size of the soil matrix from which the seeds must be extracted. Soil under shrubs and trees contains much organic debris of about the same density and particle size as seeds. This could easily influence the method that must be used to separate seeds from the soil matrix. (It certainly influences the efficiency with which humans can extract seeds from soil samples!) Although it is intriguing that *D. merriami* prefers clumped seeds in the laboratory and also forages in open spaces, which appear to contain the most clumped seeds, we cannot yet be certain that any of these differences between microhabitats influence heteromyid harvest efficiencies or foraging choices; Price and her collaborators are currently studying foraging behavior in the laboratory and field to see whether this is the case.

Despite the fact that we are not certain that adaptations for efficient seed harvest are ultimately responsible for microhabitat affinities, there is good experimental evidence that interspecific differences in microhabitat use are sensitive to the presence of coexisting heteromyid species. Price (1978b) and Wondolleck (1978) observed expansion and contraction in the array of microhabitats used by heteromyids when potential competitor species were experimentally removed or added, respectively. These results suggest that microhabitat specialization would diminish substantially under pressure of intraspecific competition if interspecific competitors were removed permanently from an area (cf. Colwell and Fuentes 1975), and they further implicate competitive interactions as a major cause for microhabitat preferences. The possibility remains, however, that experimental changes in rodent densities in some way induced changes in predator density or behavior, and that the indirect effects of the experiments on predators were responsible for microhabitat shifts. We think this is unlikely, especially since the smallest pocket mouse species with the most generalized morphology was the one that most heavily used open spaces (presumably the "riskiest" microhabitat) following removal of *Dipodomys merriami* in both sets of experiments. Nevertheless, we hope experiments like those of Price and Wondolleck will be repeated with appropriate controls for effects of predation.

In summary, we have reviewed evidence that coexisting heteromyid rodents compete for limited seed resources; that differences in body size and shape appear to be associated with some differences in foraging behavior and abilities; that microhabitat use is sensitive to the presence of competitor species; that microhabitats appear to contain different seed resources; and that heteromyids may prefer the types of seeds that are contained

in the microhabitats they use in nature. All of these observations are consistent with the hypothesis that competition has played a major role in the evolution of two salient features of heteromyid communities: divergence between coexisting species in microhabitat affinities and in body size and shape.

SYNTHESIS AND PROSPECTUS

Communities of seed-eating desert rodents in North America have received such intensive study, especially in the last decade or so, that they are understood better than most other terrestrial vertebrate systems. As a consequence, current views of how communities in general are organized are influenced strongly by the perspectives taken by ecologists who work on desert rodents. This makes it imperative that we evaluate critically what is and is not known about this model system. In the remainder of this paper we outline a way of viewing communities that integrates the divergent perspectives that have been taken by desert rodent ecologists and suggests a general direction for further research.

As we have indicated in this review, a salient characteristic of heteromyid communities is that coexisting species differ in morphology and in microhabitat affinity. Few mammalogists would argue with this statement; indeed, it appears applicable to vertebrate communities in general. Most debate has focused not on the existence of these patterns, but instead on the nature of the causal mechanisms and the way that those determine the number and kinds of species that coexist in habitats of varying structure and productivity. There has been a tendency to treat different explanations as alternative, mutually exclusive hypotheses, with the implication that accepting one means rejecting the others. Traditionally, there have been two basic points of view. One emphasizes the importance of predation as a selective agent that has molded the evolution of heteromyid morphology, behavior, and community structure. The other emphasizes the importance of food scarcity caused by an unpredictable environment and the foraging activities of competitors.

These traditional "one-factor" perspectives naively assume that characteristics of animals

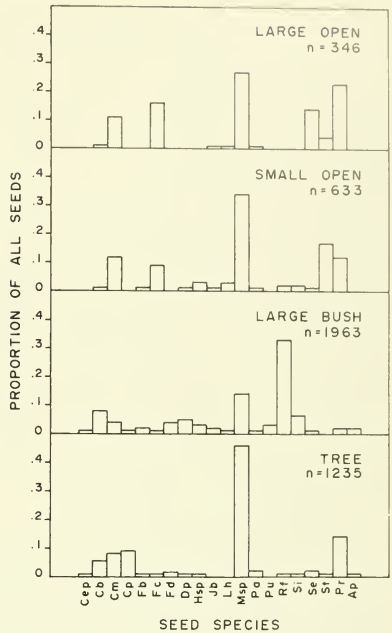

Fig. 4 continued.

B. Species composition of seeds extracted from different microhabitats. The proportional abundances of the 20 most common seed species are indicated, along with total numbers of seeds extracted (n). Again, there is significant overall heterogeneity among microhabitats in seed species composition ($G = 6023$, d.f. = 75, $P < .005$). Large Open and Small Open form a homogeneous subset that is different from Large Bush or Tree, each of which is different from all others. These data indicate that microhabitats differ not only in amounts, but also in species, of seed they contain. Cep = *Celtis pallida*; Cb = *Cryptantha barbigera*; Cm = *C. micrantha*; Cp = *C. pterocarpa*; Fb = "faceted ball"; Fc = *Filago california*; Fd = "flat disk"; Dp = *Daucus pusillus*; Hsp = *Haplopappus* sp.; Jb = "jelly banana"; Lh = *Lotus humistratus*; Msp = *Mollugo* sp.; Pa = "Panicum"; Pu = "pumpkin"; Rf = "reticulate football"; Si = "Sisymbrium"; Se = *Spermolepis echinata*; St = "strawberry"; Pr = *Pectocarya recurvata*; Ap = "Apium".

evolve in response to one overwhelmingly important selective force, and that, once an important force has been identified, the system has been understood. It must instead be the case that the behavior and morphology of an animal represent an integrated response to the diverse array of environmental factors that determine fitness. Therefore we feel that

the relevant question to address is not Which factor has been the most important? but instead What has been the role of each factor in producing the patterns we see? By adopting the broader perspective implicit in the second question, we reduce the risk of interpreting rodent communities simplistically in terms only of the factors we can study conveniently. To date, for example, there is little evidence that predation has had a significant effect on heteromyid community structure. We would be wrong, however, to conclude from this that competition is the only factor we need consider to account fully for characteristics of these communities. The apparently overwhelming importance of competition is probably more a function of the ease with which one can manipulate food, habitat structure, and competitor density, and the difficulty of manipulating predation risk, than a reflection of the true importance of competition relative to predation.

A number of approaches can be used to investigate the basis for particular community-level patterns. One that has been used extensively is analysis of the patterns themselves. In this approach the expected consequences of various factors for patterns of morphology or resource use are developed and compared with those exhibited by real communities. If two factors yield different expected patterns, then in principle one can be rejected (for example, see Price 1982b, Strong et al. 1979). Major problems with pattern analysis are that unambiguous expectations are often difficult to derive, and that very different factors often yield similar expectations.

Direct experimental manipulation is an alternative approach that has obvious virtues, but several disadvantages as well. First, it is often difficult to set up an appropriate and effective manipulation. For example, to determine the relative importance of predation directly, one must be able to manipulate it; and this is notoriously difficult to do in some terrestrial systems. Second, if there is no response to a manipulation, one often doesn't know why. The factor could indeed be important, but it is also possible that the manipulation was too small in scope to elicit a measurable response, or that for one reason or another the system simply lacks the capacity to respond.

A third approach is to use detailed analysis of the behavior of individuals as a vehicle for developing testable predictions about the properties of populations and communities (Pulliam 1976, Werner and Mittelbach 1981). Because this "microecological" approach has not yet been applied to heteromyid rodent communities, we will elaborate here on the method.

Consider the individual heteromyid rodent. To achieve genetic representation in future generations, it must be able to find sufficient energy and materials to grow, maintain itself, and reproduce in an environment characterized by low water availability and high diurnal and seasonal temperature fluctuations—and to avoid being eaten while acquiring energy and mates. The question of the relative importance of different factors for salient features of heteromyid community organization resolves itself into two questions at the individual level: (1) How is microhabitat choice influenced by relative harvest profitability, physiological cost, and predation risk? (2) How does the morphology of an individual influence its ability to harvest seeds and avoid predators in particular microhabitats?

The simplest way to attack these "microecological" questions is to use optimal foraging theory as a tool to derive predictions about how the microhabitat choice of morphologically distinct species ought to vary if individuals forage so as to maximize net rate of energy intake. By comparing observed with expected behaviors, one can ascertain whether constraints other than those of harvest efficiency (such as predator avoidance) must be incorporated into foraging models to explain the observed microhabitat choices of different rodent species. Of course, this approach is useful in distinguishing the relative importance of different constraints only if they yield different predicted optimal behaviors. If an animal behaving so as to minimize predation risk is predicted to behave in the same manner as one maximizing seed harvest rates, then this approach has no power in discriminating between two very different models of behavior. In general, however, we expect this will not be a problem, because it seems unlikely that the most profitable patches from a harvest efficiency point of

view will consistently be the least risky as well.

Developing predictions about optimal microhabitat selection is tedious, but straightforward because the theory is well developed (cf. Pyke et al. 1977, Werner and Mittelbach 1981). To apply it one needs to estimate known model parameters, such as how the seed resources contained in one microhabitat differ from those contained in another, how the expected net rate of energy harvest by an individual varies between microhabitats, and how morphology influences these foraging parameters. Armed with this knowledge, one can predict microhabitat preferences under natural or experimentally manipulated conditions, and test the predictions. If patterns of microhabitat use conform to those predicted, then it is in principle possible to develop testable models of niche relationships and competitive interactions between species based on the assumption that interactions are solely exploitative in nature (cf. MacArthur 1972, Pulliam 1976). The power of this approach lies in its ability to generate simple testable models of community structure whose assumptions and predictions are explicitly stated. If the model does not yield accurate predictions, then the assumptions about what constraints influence behavior or population dynamics must be wrong. Even if the model is wrong, progress in understanding nature has been made, for one knows that the next step is to modify the model so as to incorporate different assumptions, and test the new predictions. For examples and further discussion of these points, see Mittelbach (1981), Werner and Mittelbach (1981), and Sih (1980, 1982).

A major advantage of the microecological approach is that one can use it to detect the effects of factors like predation without having to manipulate predator populations directly in the field. A major disadvantage is that, although it is possible in principle to build models of communities from knowledge of individual behavior, in practice the number of variables one would have to incorporate into realistic behavioral models becomes so large that the approach may turn out to be unwieldy. Consider foraging behavior, for example. Microecological analyses may eventually enable us to understand and thus to predict how individual rodents respond to specified conditions, such as habitats with certain physical structure, patterns of food availability, and different kinds of predators. Unfortunately, however, these conditions themselves probably are not constants in nature, but instead are variables that are influenced by a wide variety of factors. The short- and long-term availability of food should depend in part on the foraging activities of intraspecific and interspecific competitors and the way these affect spatial distributions and recruitment in food plant populations. Similarly, the kinds of predators present will be affected by the other conspecific and heterospecific prey present in an area, and the predators in turn may influence the abundance and distribution of prey populations, thus affecting their interactions. If these sorts of complex feedbacks are important in the organization of desert rodent communities—and we suspect that they are—then they may be more easily detected and understood by macroecological experimental manipulations than microecological ones. For example, a recent experiment in which we added modest qualities of millet seeds to large areas of Chihuahuan desert habitat (Brown and Munger, in preparation) gave the interesting result that *Dipodomys spectabilis* increased in density and *D. merriami* and *D. ordii* decreased. Apparently the decline of the two smaller kangaroo rat species was a consequence of interference or exploitative competition from the larger *D. spectabilis*. This response would have been difficult to anticipate from microecological approaches, because all three *Dipodomys* species should have experienced increased foraging success after the manipulation.

All of this points out the limitations of our present knowledge and the need for additional research of many kinds. As much as we have learned about desert rodent communities in the last decade or two, we have only scratched the surface. Perhaps we have reached the stage where sufficient background work has been done to describe many of the important patterns of community organization and to suggest mechanistic hypotheses to account for these patterns. Clearly much imaginative work and many different approaches can contribute to testing these hypotheses.

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