Great Basin Naturalist Memoirs

Volume 7 *Biology of Desert Rodents* Article 6

8-1-1983

Behavior of desert heteromyids

O. J. Reichman
Division of Biology, Kansas State University, Manhattan, Kansas 66506

Recommended Citation

Reichman, O. J. (1983) "Behavior of desert heteromyids," *Great Basin Naturalist Memoirs*: Vol. 7 , Article 6.
Available at: https://scholarsarchive.byu.edu/gbnm/vol7/iss1/6

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.

---

[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] 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.

ACKNOWLEDGMENTS

My thanks are extended to Dr. Robert Kruh, dean of the Graduate School at Kansas State University, who provided support for this symposium. I also thank Jim Brown for his efforts on behalf of the symposium, and Mary Price, Jan Randall, and Cindy Rebar for their helpful comments. An anonymous reviewer also provided essential assistance.

LITERATURE CITED

ANDERSON, A. O., AND D. M. ALLRED. 1964. Kangaroo rat burrows at the Nevada Test Site. Great Basin Nat. 92:93–101.

BARTHOLOMEW, G. A., AND G. R. CARY. 1954. Locomotion in pocket mice. J. Mammal. 35:386–392.

BARTHOLOMEW, G. A., AND H. CASWELL. 1951. Locomotion in kangaroo rats and its adaptive significance. J. Mammal. 32:155–169.

BARTHOLOMEW, G. A., AND R. E. MACMILLEN. 1961. Oxygen consumption, estivation, and hibernation in the kangaroo mouse, *Microdipodops pallidus*. Physiol. Zool. 34:177–183.

BEHRENDS, P. 1981. Copulatory behavior of *Dipodomys microps* (Heteromyidae). Southwest. Nat. 25:562–563.

BENSON, S. B. 1933. Concealing coloration among some desert rodents of the southwestern United States. Univ. California Publ. Zool. 40:1–70.

BENSON, S. 1935. A protective habit of *Dipodomys deserti*. J. Mammal. 16:67–68.

BEST, T. 1972. Mound development by a pioneer population of bannertailed kangaroo rats, *Dipodomys spectabalis baileyi* Goldman in eastern New Mexico. Amer. Midl. Nat. 87:201–206.

BIEWENER, A., R. M. ALEXANDER, AND N. C. HEGLUND. 1981. Elastic energy storage in the hopping of kangaroo rats (*Dipodomys spectabalis*). J. Zool. 195:369–383.

BLAIR, W. F. 1937. Burrows and food of the prairie pocket mouse. J. Mammal. 18:188–191.

______. 1943. Populations of deer mice associated with small mammals in the mesquite areas of south New Mexico. Cont. Lab. Vert. Biol., Univ. Mich. 21:1–40.

BLAUSTEIN, A., AND A. RISSER. 1974. Dominance relationships of the dark kangaroo mouse (*Microdipodops megacephalus*) and the little pocket mouse (*Perognathus longimembris*) in captivity. Great Basin Nat. 34:312–316.

______. 1976. Interspecific interactions between three sympatric species of kangaroo rats (*Dipodomys*). Anim. Behav. 24:381–385.

BORCHETT, P., J. GRISWOLD, AND R. S. BRANCHEK. 1976. An analysis of sandbathing and grooming in the kangaroo rat (*Dipodomys merriami*). Anim. Behav. 24:347–353.

BOWERS, M. 1982. Foraging behavior in heteromyid rodents: field evidence of resource partitioning. J. Mammal. 63:361–367.

BOWERS, M., AND J. H. BROWN. 1982. Body size and coexistence in desert rodents: chance or community structure? Ecology 63:391–400.

BRADLEY, W. G., AND R. MAUER. 1971. Reproduction and food habits of Merriam's kangaroo rat, *Dipodomys merriami*. J. Mammal. 52:497–507.

BROWN, J. H. 1975. Geographical ecology of desert rodents. Pages 315–341 *in* M. L. Cody and J. Diamond, eds. Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts.

BROWN, J. H., AND G. A. BARTHOLOMEW. 1969. Periodicity and energetics of torpor in the kangaroo mouse, *Microdipodops pallidus*. Ecology 50:705–709.

BROWN, J. H., O. J. REICHMAN, AND D. W. DAVIDSON. 1979. Granivory in desert ecosystems. Ann. Rev. Ecol. Syst. 10:201–227.

BUTTERWORTH, B. B. 1961. The breeding of *Dipodomys deserti* in the laboratory. J. Mammal. 42:413–414.

______. 1964. Parental relations and the behavior of juvenile kangaroo rats (*Dipodomys*) in captivity. Southwest. Nat. 8:213–220.

CHAPMAN, B., AND R. L. PACKARD. 1974. An ecological study of Merriam's pocket mouse in southern Texas. Southwest. Nat. 19:281–291.

CHEW, R., AND B. B. BUTTERWORTH. 1964. Ecology of rodents in Indian Cove (Mojave Desert) Joshua Tree National Monument, California. J. Mammal. 45:203–225.

CLARK, W. H., AND P. COMANOR. 1973. The use of western harvester ant, *Pogonomyrmex occidentalis* (Cresson), seed stores by heteromyid rodents. Occas. Papers Biol. Soc. of Nevada 34:1–6.

COMPTON, L. V., AND R. F. HEDGE. 1943. Kangaroo rat burrows in earthen structures. J. Wildl. Mgt. 7:306–316.

CONGDON, J. 1974. Effect of habitat quality of diets of three sympatric species of desert rodents. J. Mammal. 55:659–662.

CSUTI, B. 1979. Patterns of adaptation and variation in the Great Basin kangaroo rat (*Dipodomys microps*). Univ. California Publ. Zool. 111:1–69.

CULBERTSON, A. E. 1946. Observations of the natural history of the Fresno kangaroo rat. J. Mammal. 27:189–203.

DALY, M., M. WILSON, AND P. BAHRENDS. 1980. Factors affecting rodents' responses to odors encountered in the field: experiments with odor-baited traps. Behav. Ecol. and Sociobiol. 6:323–329.

DAY, B., H. J. EGOSCUE, AND A. WOODBURY. 1956. Ord's kangaroo rat in captivity. Science 124:485–486.

DENYES, H. A. 1954. Habitat structure and the digging ability of certain pocket mice. J. Mammal. 35:453.

DEWSBURY, D. 1972. Patterns of copulatory behavior in male mammals. Quart. Rev. Biol. 47:1–33.

DIXON, K. L. 1959. Spatial organization in a population of Nelson's pocket mouse. Southwest. Nat. 3:107–113.

EISENBERG, J. 1963. The behavior of heteromyid rodents. Univ. California Publ. Zool. 69:1–100.

______. 1975. The behavior patterns of desert rodents. Pages 189–224 *in* I. Prakash and P. K. Ghosh, eds. Rodents in desert environments. W. Junk, The Hague, The Netherlands.

______. 1981. The mammalian radiations. Univ. of Chicago Press, Chicago. 610 pp.

Eisenberg, J., and D. E. Isaac. 1963. The reproduction of heteromyid rodents in captivity. J. Mammal. 44:61–67.

Engler, M., and R. C. Dowler. 1981. Field observations of mating behavior in *Dipodomys ordii*. J. Mammal. 62:384–386.

Fitch, H. S. 1948. Habits and economic relationships of the Tulare kangaroo rat. J. Mammal. 29:5–35.

Flake, L., and C. D. Jorgensen. 1969. Invasion of a "trapped out" southern Nevada habitat by *Perognathus longimembris*. Great Basin Nat. 29:143–149.

French, A. 1976. Selection of high temperatures for hibernation by the pocket mouse, *Perognathus longimembris*: ecological advantages and energetic consequences. Ecology 57:185–191.

French, N. 1975. Activity patterns of a desert rodent. Pages 225–239 *in* I. Prakash and P. Ghosh, eds. Rodents in desert environments. W. Junk, The Hague, The Netherlands.

Frye, R. J., and M. L. Rosenzweig. 1980. Clump size selection: a field test with two species of *Dipodomys*. Oecologia 47:323–327.

Garner, H., L. W. Richardson, and L. Felts. 1976. Alimentary helminths of *Dipodomys ordii*: effects on the host population. Southwest. Nat. 21:327–334.

Griswold, J., G. Borchett, P. Branchek, and J. Bensko. 1977. Condition of the pelage regulates grooming behavior in the kangaroo rat (*Dipodomys merriami*). Anim. Behav. 25:602–608.

Hall, E. R. 1946. Mammals of Nevada. Univ. of California Press, Los Angeles. 710 pp.

Hall, E. R., and K. Kelson. 1959. Mammals of North America. Ronald Press, New York.

Hawbrecker, A. C. 1940. The burrowing and feeding habits of *Dipodomys venustus*. J. Mammal. 22:388–396.

Hay, M. E., and P. J. Fuller. 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. Ecology 62:1395–1399.

Hayden, P., J. J. Gambino, and R. G. Lindberg. 1966. Laboratory breeding of the little pocket mouse, *Perognathus longimembris*. J. Mammal. 47:412–423.

Heffner, H., and B. Masterson. 1981. Hearing in Glires, domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. J. Accoustical Soc. Amer. 68:1584–1599.

Holdenreid, R. 1957. Natural history of the bannertailed kangaroo rat in New Mexico. J. Mammal. 38:330–350.

Hoover, K., W. G. Whitford, and P. Flavill. 1977. Factors influencing the distribution of two species of *Perognathus*. Ecology 58:877–884.

Hutto, R. 1978. A mechanism for resource allocation among sympatric heteromyid rodent species. Oecologia 33:115–126.

Johnson, T., and C. Jorgensen. 1981. Ability of desert rodents to find buried seeds. J. Range Mgt. 34:312–314.

Kaufman, D., and G. Kaufman. 1982. Effects of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). J. Mammal. 63:309–312.

Kenagy, G. J. 1972. Saltbush leaves: excision of hypersaline tissue by a kangaroo rat. Science 178:1094–1096.

______. 1973a. Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. Ecology 54:1201–1219.

______. 1973b. Adaptations for leaf-eating in the Great Basin kangaroo rat, *Dipodomys microps*. Oecologia 12:383–412.

______. 1976a. The periodicity of daily activity and its seasonal changes in free-ranging and captive kangaroo rats. Oecologia 24:105–140.

______. 1976b. Field observations of male fighting, drumming, and copulation in the Great Basin kangaroo rat, *Dipodomys microps*. J. Mammal. 57:781–785.

Kenagy, G. J., and G. A. Bartholomew. 1981. Effects of day length, temperature, and green food on testicular development in a desert pocket mouse *Perognathus formosus*. Physiol. Zool. 54:62–73.

Kenagy, G. J., and J. T. Enright. 1980. Animal behavior as a predictor of earthquakes: an analysis of rodent activity rhythms. Zeit. Tierpsychol. 52:269–284.

Kenagy, G. J., and D. Hoyt. 1980. Reingestion of feces in rodents and its daily rhythmicity. Oecologia 44:403–409.

Laine, H., and J. G. Griswold. 1976. Sandbathing in kangaroo rats (*Dipodomys spectabalis*). J. Mammal. 57:408–410.

Lawhon, D., and M. Hafner. 1981. Tactile discriminatory ability and foraging strategies in kangaroo rats and pocket mice (Rodentia:Heteromyidae). Oecologia 50:303–309.

Lemon, C. 1978. Seed size selection in heteromyids: a second look. Oecologia 35:13–19.

Lemon, C., and M. L. Rosenzweig. 1978. Microhabitat selection in two species of heteromyid rodents. Oecologia 33:127–135.

LaVick, J. P. 1982. Maternal response to neonate vocalizations in Ord's kangaroo rat (*Dipodomys ordii*). Southwest. Nat. 27:122–123.

Lockard, R. B. 1978. Seasonal change in the activity pattern of *Dipodomys spectabalis*. J. Mammal. 59:563–568.

Lockard, R. B., and J. S. Lockard. 1971. Seed preference and buried seed retrieval of *Dipodomys deserti*. J. Mammal. 52:219–221.

Lockard, R. B., and D. Owing. 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. J. Mammal. 55:189–193.

Mares, M., and D. F. Williams. 1977. Experimental support for food particle size resource allocation in heteromyid rodents. Ecology 58:1186–1190.

Martin, R. E. 1977. Species preference of allopatric and sympatric populations of silky pocket mice, Genus *Perognathus* (Rodentia:Heteromyidae). Amer. Midl. Nat. 198:124–136.

Maza, B., N. R. French, and A. P. Aschwanden. 1973. Home range dynamics in a population of heteromyid rodents. J. Mammal. 54:405–425.

McCue, P., and J. Caufield. 1979. Photographic documentation of predation on *Dipodomys ordii* by *Onychomys leucogaster*. Abstracts of the 59th meeting of the American Society of Mammalogists.

M'Closkey, R. 1980. Spatial patterns in types of seeds collected by four species of heteromyid rodents. Ecology 61:486–489.

———. 1981. Microhabitat use in coexisting desert rodents: the role of population density. Oecologia 50:310–315.

Monson, G. 1943. Food habits of bannertail kangaroo rats in Arizona. J. Wildl. Mgt. 7:98–102.

Monson, G., and W. Kessler. 1940. Life history notes on the bannertail kangaroo rat, Merriam's kangaroo rat, and the white-throated woodrat in southern Arizona and New Mexico. J. Wildl. Mgt. 4:37–43.

Morton, S., R. Hinds, and R. E. MacMillen. 1980. Cheek pouch capacity in heteromyid rodents. Oecologia 46:143–146.

O'Dowd, D. J., and M. Hay. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology 61:531–540.

O'Farrell, M. 1974. Seasonal activity patterns of rodents in a sagebrush community. J. Mammal. 55:809–823.

———. 1980. Spatial relationships of rodents in a sagebrush community. J. Mammal. 61:589–605.

Price, M. V. 1978. Seed dispersal preferences in coexisting desert rodents. J. Mammal. 59:624–626.

Quay, W. B. 1953. Seasonal and sexual differences in the dorsal skin gland of kangaroo rats (*Dipodomys*). J. Mammal. 34:1–14.

———. 1965. Variation and taxonomic significance in sebaceous caudal glands of pocket mice (Rodentia:Heteromyidae). Southwest. Nat. 10:282–287.

Randall, J. 1981a. Comparisons of sandbathing and grooming in two species of kangaroo rat. Anim. Behav. 29:1213–1219.

———. 1981b. Olfactory communication at sandbathing loci by sympatric species of kangaroo rats. J. Mammal. 62:12–19.

Reichman, O. J. 1975. Relationships of desert rodent diets to available resources. J. Mammal. 56:731–751.

———. 1977. Optimization of diets through food preferences by heteromyid rodents. Ecology 58:454–457.

———. 1978. Ecological aspects of the diets of Sonoran Desert rodents. Mus. North. Arizona Res. Rep. 15 96 pp.

———. 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology 60:1085–1092.

———. 1981. Factors influencing foraging in desert rodents. Pages 195–213 *in* A. C. Kamil and T. D. Sargent, eds. Foraging behavior: ecological, ethological, and psychological approaches. Garland-STMP Press, New York.

Reichman, O. J. In press. Spatial and temporal variation in seed distribution in Sonoran Desert soils. Jour. of Biogeography.

Reichman, O. J., and J. H. Brown. 1979. The use of torpor by *Perognathus amplus* in relation to resource distribution. J. Mammal. 60:550–555.

Reichman, O. J., and D. Oberstein. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. Ecology 58:636–643.

Reichman, O. J., and K. Van De Graaff. 1973. Seasonal reproductive and activity patterns of five species of Sonoran Desert rodents. Amer. Midl. Nat. 90:118–126.

———. 1975. Influence of green vegetation on desert rodent reproduction. J. Mammal. 53:503–506.

Reynolds, H. G. 1958. Ecology of Merriam's kangaroo rat on the grazing lands of southern Arizona. Ecology 31:456–463.

Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid species. Ecology 54:111–117.

———. 1974. On the optimal above ground activity of bannertail kangaroo rats. J. Mammal. 55:193–199.

Rosenzweig, M. L., and P. Sterner. 1970. Population ecology of desert rodent communities: body size and seed husking as a basis for heteromyid coexistence. Ecology 51:217–224.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of rodent communities: habitats and environmental complexity. Ecology 50:558–572.

Scheffer, T. H. 1938. The pocket mice of Washington and Oregon in relation to agriculture. USDA Tech. Bull. 608. 15pp.

Schmidley, D. J., and R. L. Packard. 1967. Swimming ability in pocket mice. Southwest. Nat. 12:480–482.

Schmidt-Nielsen, K., B. Schmidt-Nielsen, and A. Brokaw. 1948. Urea excretion in desert rodents exposed to high protein diets. J. Cell. Physiol. 32:361–380.

Schreiber, K. 1973. Bioenergetics of rodents in the northern Great Basin desert. Unpublished dissertation. Univ. of Idaho, Moscow.

Schroder, G. D. 1979. Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabalis*). Ecology 60:657–665.

Schroder, G. D., and K. N. Geluso. 1975. Spatial distribution of *Dipodomys spectabalis* mounds. J. Mammal. 56:363–368.

Shaw, W. T. 1934. The ability of the giant kangaroo rat as a harvester and storer of seeds. J. Mammal. 15:275–286.

Smigel, B., and M. L. Rosenzweig. 1974. Seed selection in *Dipodomys merriami* and *Perognathus penicillatus*. Ecology 55:329–339.

Stamp, N., and R. Ohmart. 1978. Resource utilization by desert rodents in the Lower Sonoran Desert. Ecology 59:700–707.

Stock, D. 1972. Swimming ability in kangaroo rats. Southwest. Nat. 17:98–99.

Tappe, D. T. 1941. Natural history of the Tulare kangaroo rat. J. Mammal. 22:117–148.

Thompson, S. D. 1982a. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology 63:1303–1312.

———. 1982b. Structure and species composition of desert heteromyid species assemblages: effects of a simple habitat manipulation. Ecology 63:1313–1321.

———. In press. Bipedal hopping and seed dispersion selection by heteromyid rodents: the role of locomotion energetics. Ecology 65.

THOMPSON, S. D., R. E. MACMILLEN, E. M. BURKE, AND C. R. TAYLOR. 1980. The energetic costs of bipedal hopping in small mammals. Nature 287:223–224.

TROMBULAK, S. C., AND G. J. KENAGY. 1980. Effects of seed distribution and competitors on seed harvesting efficiency in heteromyid rodents. Oecologia 44:342–346.

VAN DE GRAAFF, K. 1973. Comparative developmental osteology in three species of desert rodents, *Peromyscus eremicus*, *Perognathus intermedius*, and *Dipodomys merriami*. J. Mammal. 54:729–41.

VAN DE GRAAFF, K., AND R. P. BALDA. 1973. Importance of green vegetation for reproduction in the kangaroo rat, *Dipodomys merriami merriami*. J. Mammal. 54:509–512.

VORHIES, C. T., AND W. P. TAYLOR. 1922. Life history of the kangaroo rat *Dipodomys spectabalis spectabalis* Merriam. Bull. U.S.D.A. 1091-1-40.

VOORHIES, M. R. 1974. Fossil pocket mouse burrows in Nebraska. Amer. Midl. Nat. 91:492–498.

WEBSTER, D. 1962. A function of the enlarged middle ear cavities of the kangaroo rat, *Dipodomys*. Physiol. Zool. 35:248–255.

WEBSTER, D., AND M. WEBSTER. 1971. Adaptive values of hearing and vision in kangaroo rat predator avoidance. Brain Behav. Res. 4:310–322.

———. 1972. Kangaroo rat auditory threshold before and after middle ear reduction. Brain Behav. Res. 5:41–53.

———. 1980. Morphological adaptations of the ears in the rodent family Heteromyidae. Amer. Zool. 20:247–254.

WONDOLLECK, J. T. 1978. Foraging-area separation and overlap in heteromyid rodents. J. Mammal. 59:510–518.