FORAGING IN KANGAROO RATS AND ITS ADAPTIVE SIGNIFICANCE

By

Robert David Burns

AN ABSTRACT

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Robert D. Burns

THESIS ABSTRACT

The kangaroo rat (Dipodomys) is classified with the family Heteromyidae whose members are found in the arid and semi-arid regions of North America where the soil is pliable and sandy. Morphologically the family is characterized by well developed hindlimbs and smaller weaker forelimbs. This study was undertaken in an attempt to gain an increased understanding of foraging behavior, and its relationship to some of the morphological adaptations of kangaroo rats.

Observations were recorded of four species, Dipodomys, panamintinus, D. merriami, D. agilis, and D. deserti. Two controlled experiments, the sand-seed test and the bead-seed test, were carried out. D. merriami and D. deserti were used in the former and D. panamintinus, D. merriami, and D. agilis in the latter. Data was obtained by observations and by the use of high speed photography. The observations were recorded orally on a tape recorder while the experiments were in progress.

When finding food, the experimental animals primarily used the sense of smell but depended relatively more upon the tactile senses when searching for food with little or perhaps no odor. Kangaroo rats sifted and picked up objects from the soil with their manus. The claws on the manus made an effective rake.

When seeds were buried five to ten millimeters under fine, dry sand, individuals did not locate buried food by smell, but did locate piles of buried seeds if they chanced to touch or uncover them during random sifting and digging activities. Limited data suggests that the sense of smell was useful in locating buried seeds when the relative humidity was at least 50 percent.

More critical discrimination was accomplished by means of manipulation by the manus and nibbling with the incisors. When glass beads were mixed with food, kangaroo rats were not able to distinguish between beads and seeds until they had been sampled by use of the incisors and manus. The animals exhibited an ability to make a decision at some level. After sampling a limited number of objects the remainder of the material was either rejected or accepted without further sampling.

Kangaroo rats demonstrated that they were able to place objects inside their cheek pouches at amazing speeds. An individual can reach out under the tip of the nose, pick up a seed, and place it inside its cheek pouch at a modal rate of one seed in 0.2 second.

The members of this genus exhibit a marked ability to manipulate seeds by means of their claws. The claws were used separately and in combination with the palmar pad. During hulling operations the claws were used to pull away the loosened hull. Discarded material was thrown with the manus backwards between the hindlimbs or sometimes to the side. Seeds were sorted after collecting by emptying the pouches, and selecting certain types which were carried to a different area. Individuals covered the emptied contents of their cheek pouches with loose soil when the material was stored.

The possible evolutionary and distributional implications of the animals' foraging adaptations and related behavior are discussed.

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INTRODUCTION

The kangaroo rat (Dipodomys) is classified with the family Heteromyidae whose members are found in the arid and semi-arid areas of North America where the soil is pliable and sandy. Morphologically the family is characterized by well developed hind limbs, and smaller, weaker forelimbs. Specialized, englarged auditory bullae and fur-lined cheek pouches which open externally on either side of the mouth are present.

The genus Dipodomys resembles the other members of its family with regard to the above characteristics and, in addition, the tail is longer than the body. The genus lends itself to behavioral studies because of its docile habits. Although quick motions and loud noises sometimes attract their attention, individuals in captivity normally pay little attention to human observers.

Dipodomys is fossorial and spends much of its life underground making quick excursions outside the burrow when foraging for food. The four species, D. panamintinus, D. merriami, D. agilis and D. deserti, used in these observations all plug the entrances of their burrows with soil from the inside, and generally venture out of their dens only after dark. Food is gathered directly from the standing vegetation or sifted from loose soil on the surface of the ground. The material is carried in the external cheek pouches and buried near or inside the den.

This study is an outgrowth of an earlier work concerned with the adaptive significance of locomotion in heteromyid rodents (Bartholomew, et al., 1951, 1954) where it was suggested the the possible evolution of bipedalism in heteromyid rodents may have been primarily a by-product of specialized foraging habits and that strictly locomotor factors may have been of secondary significance. Since the details of foraging were unknown, this study was undertaken in an attempt to gain an increased understanding of such behavior. Because direct observations were almost impossible, high speed photography and slow-motion pictures were used in recording foraging and discriminatory behavior in the laboratory. Howell (1932:382) stated, "I have watched long and intently in an effort to learn the actions involved in the use of the external cheek pouches, but unsuccessfully."

MATERIALS AND METHODS

Capture and Housing of Animals

The experimental animals were captured in box-type live-traps baited with dry rolled oats, and were taken in the vicinities of the Lovejoy Buttes and Llano in the Mohave Desert, Los Angeles County, California. The traps were inspected about two hours after dark, and again at dawn. The animals captured were then transferred to metal cans containing sawdust and rolled oats and shipped within two days to East Lansing. The bead-seed and sand-seed tests, which will be described later, were completed within two weeks after capture. Observations which were made prior to the above tests were made on animals which had been in capivity for periods up to one year.

With the exception of 15 D. merriami used during the sand-seed tests, which were housed in metal cans 4-1/2" in diameter and 11-1/2" long, the experimental animals were housed in cages 8" X 10" X 8", and were supplied with sawdust and/or dry sand, grain, and water. The cans in which the former were housed were placed on their sides and fine sand and grain was given, but no water was provided. All of the individuals were housed separately. The temperature in the laboratory ranged from 72° to 80° F. The light was subdued.

Methods of Recording Data

Observations were recorded on tape while the experiments were in progress, and the tapes were later transcribed.

A Speed Graphic camera (3-1/4" X 4-1/4") equipped with a stroboscopic flash was used with a 152 mm Kodak Ektar lens to take still pictures. The duration of the flash was reputed by the manufacturer to be 1/1000 second. Motion pictures were taken at 64 frames per second with a 16mm Bell and Howell camera. A one-inch lens and a three-inch telephoto lens with a +3 close-up attachment were used with the motion picture camera.

Cages

Two cages were used for observation and photography. These consisted of an 8" X 14" X 12" cage constructed of plate glass which was used in conjunction with a mirror so adjusted that photographs could be taken from the side and underneath simultaneously (Figure 1), and a larger 22" X 48" X 14" tank which was filled with eight inches of damp sand in which individuals were able to burrow and forage for growing plants and seeds.

Experiments

After detailed observations were made of foraging behavior, there appeared to be two distinct actions involved: (1) Food finding--the activities involved in locating the place where food was present; (2) Food discrimination--the manipulating and nibbling behavior involved in separating the desired food from a heterogeneous mixture of soil and plant material.

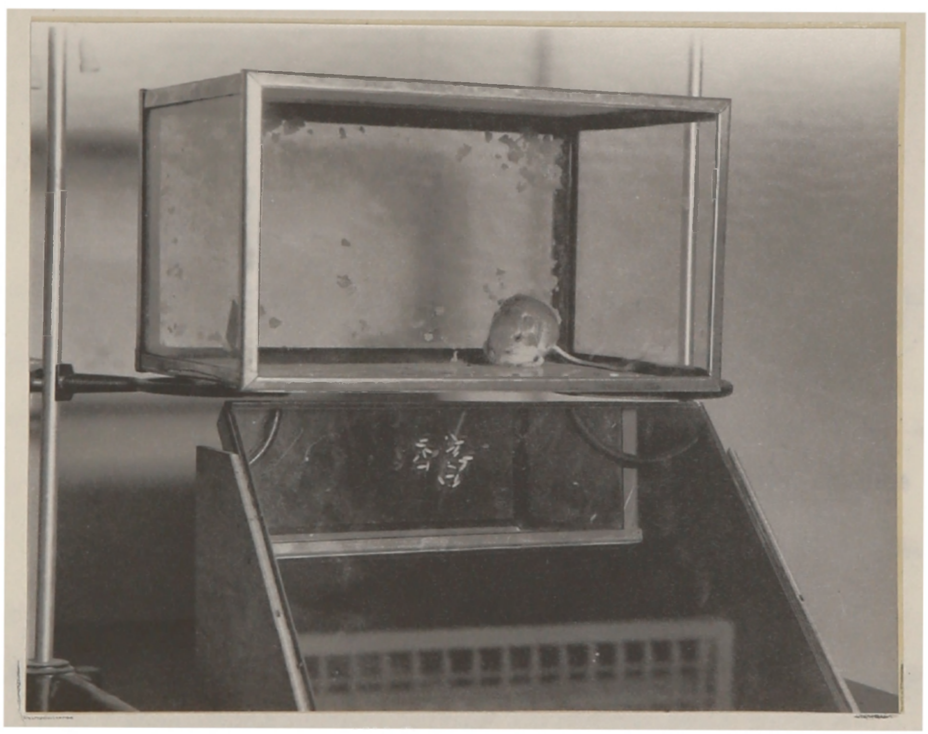


Figure 1. Observation cage with mirror in which food handling behavior was photographed.

The sand-seed test was devised to approximate arid conditions such as kangaroo rats would encounter in the wild. Since discriminatory behavior could not be observed by means of this test, another test was designed in which observations could be made from beneath the animals. Although the glass surface did not resemble the conditions of the desert floor, the activity after the objects were picked up from the glass should be the same as in nature. This second test was called the bead-seed test.

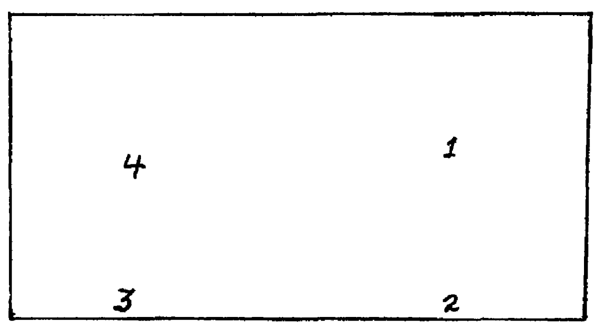


Figure 2. Diagram illustrating the positions of the piles of seeds used in the sand-seed tests.

For the sand-seed test a cage was constructed of plate glass 8" x 14" x 12" and fine sorted sand was added to a depth of about five centimeters. Seeds were placed in four areas which were numbered from one to four (Figure 2). The seeds in the right center of the cage were designated position number one, and the rest were numbered in a clockwise direction. The seeds in position number one were placed on the surface of the sand, while those at the other three loci were buried 5 to 10 millimeters deep. Positions two and three were next to the glass sides of the cage and were visible to the observer. Each pile contained three milliliters of mixed seed (sunflower, wheat, oats, and millets).

Four pieces of cardboard three millimeters square, one commercial rabbit-food pellet, and a small ball of cotton 10 mm in diameter were placed at random on the surface. These objects were used as a means of distinguishing between the use of touch and olfaction since two of the objects were not food, and the remaining one was an odoriferous food pellet. The amounts of sniffing and sampling were considered to indicate the relative importance of olfaction and touch.

Feeding was discontinued during the 24 hours prior to each experiment. As each test was begun, an individual was placed at the opposite end of the cage from position one. The activity of the animal determined the length of each test which was usually about five to seven minutes. The seeds on the surface in pile one served to determine if the subjects were hungry and interested in food. If an individual picked up the seeds in pile one and sifted over the surface of the sand, it was assumed that it would have also picked out the buried seeds if it were able to locate them.

The same plate glass cage was used for the bead-seed test as was described for the previous test. The bottom of the cage was cleaned to permit observations and photographs to be made from beneath. In each experiment four glass oat-pearls, four glass cylinders and eight glass spheres were mixed with the seed (Figure 3). The seed consisted of hulled wheat grains, unhulled oats, and various spherical millets. The beads had shapes and sizes similar to those of the seeds. In addition there were small pieces of crushed granite among the seeds.

The mixture of beads and seeds was placed in the center of the experimental cage and an individual which had not been fed for 24 hours was introduced. A test was completed when all of the food was placed inside the cheek pouches, or when an individual exhibited no more interest in the food. By counting the remaining number of beads in the cage, the number in the pouches was calculated.

As will be evident from information presented below, after food had been discovered, the relative importance of vision and olfaction decreased (vision completely) and that of the tactile sense, as evidenced by manipulation with the manus or nibbling, increased. Thus, food-finding and food-discrimination must be considered as two separate steps in the feeding behavior of these species. The bead-seed test is concerned with the latter.

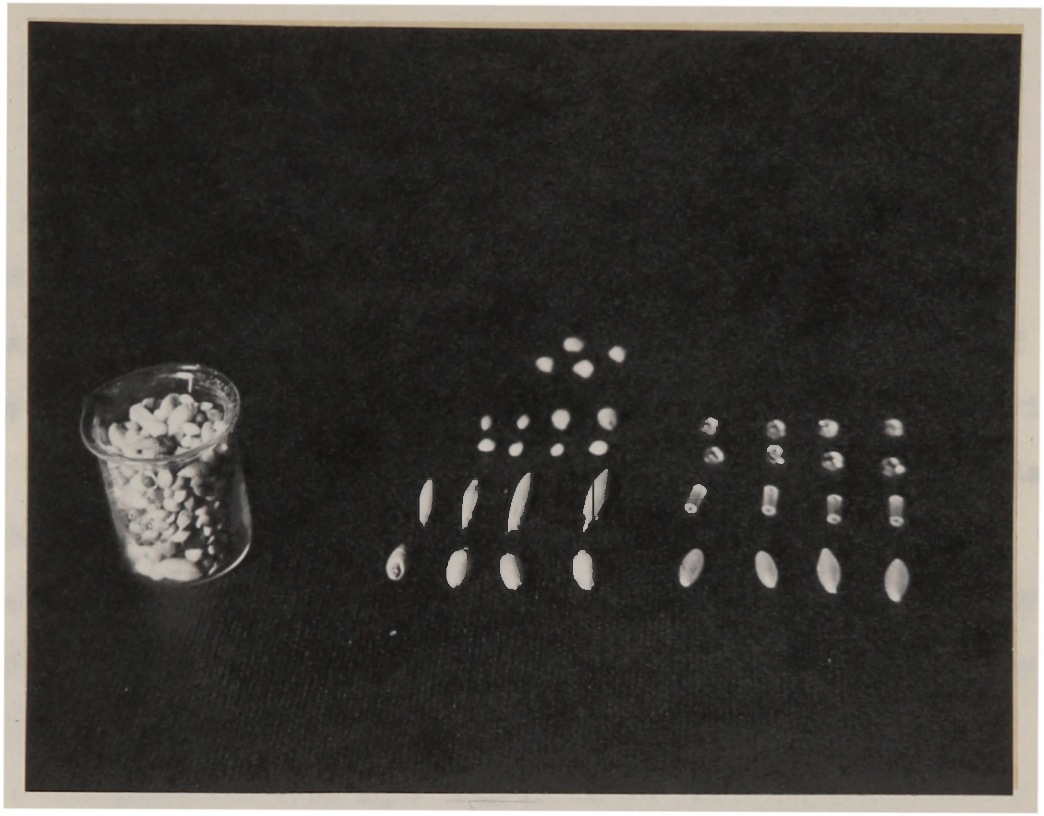


Figure 3. The material presented to the experimental animals during the bead-seed test. At the left is a 5 ml beaker filled with mixed bird seed. At the far right the beads are arranged in rows corresponding to the shape and sizes of the seeds (center group). The bottom row contains four hulled wheat grains and four oat-pearls. The next contains four oat grains with hulls and four glass cylinders. Row three contains eight millet seeds and eight spheres. The objects at the top are pieces of crushed granite which came mixed with the commercial bird seed.

RESULTS

Food Finding

Smelling. The sense of smell was used to locate groups of seeds which were on or just beneath the surface of the soil. Individuals found buried seeds more rapidly in loose damp soil than in powdery dry soil. Under the conditions of the sand-seed test *D. merriami* failed to locate by smelling piles of seeds buried 15 to 20 millimeters beneath the surface. However, when the relative humidity in the laboratory was 50 to 85 percent, all four species detected some of the piles of buried seeds. Since individuals went directly to the places where seeds were buried, it was inferred that they must have smelled them.

When food was found on the surface or exposed by digging, the external nares were located directly over the seeds which were picked up. In the laboratory the sense of smell was used to locate a spot where food was present, while the manus and incisors were used for more precise discrimination. For instance, individuals recently captured were never observed to rely only on smell when placing seeds in their cheek pouches, and this sense was always used in conjunction with touch before objects were accepted.

Sifting. Both manus were used to sift. They were simultaneously extended to the tip of the nose and drawn back under the mouth. Only the claws extended into the sand. Small grooves made by them were visible for an instant as the spread digits were drawn through the powder-dry sand. Solid objects were raked from the sand and sampled. When the manus was in a pronated position, the claws were pointed down and they made an effective rake. The digits were flexed when an object was touched. As the object was lifted from the sand, the grains of sand fell out from between the claws.

The expeditiousness with which individuals sifted varied among the four species observed. The sifting strokes of D. merriami were very dainty, and only the surface of the sand was lightly raked. The estimated depth to which the claws went into the sand was between two to five millimeters. D. deserti, which in nature is restricted to sandy regions, differed chiefly by the use of more powerful digging strokes interspersed during sifting. The latter sifted deeper and more vigorously than the merriami. Further, the larger manus and longer reach of D. deserti allowed for more rapid coverage of the test cage area. This species sometimes sifted all the sand in the test cage (224 cubic inches) within a five minute period while the more methodical merriami, at best, sifted only the entire surface (112 square inches) and rarely deeper than one inch in one or two places. D. agilis and D. panamintinus were much alike with regard to their sifting behavior, which was intermediate between that of deserti and merriami.

The digging strokes which occurred during sifting were made with both manus simultaneously, and usually never more than three or four strokes occurring in sequence. Digging while sifting was distinguished from sifting alone since sand was excavated during digging while the manus merely raked through the sand during sifting.

Digging. In this study digging is distinguished both from sifting and the digging strokes made during sifting activities. The method of digging was similar to that of most other rodents in that alternate strokes were taken very rapidly. The soil was loosened with the forepaws and kicked away by simultaneous backward strokes of the pes. This behavior was used for excavating buried roots, constructing burrows and making depressions for food caches.

When digging, kangaroo rats frequently packed down the loose excavated soil with the manus. The soil pushed over food caches was packed down in a similar fashion, namely, by patting it down with the palm.

Sand-seed Test. The sand-seed test was devised to help establish the relative importance of olfaction and touch during food finding. In each test one group of seeds was placed on the surface of the sand while the others were buried. Olfaction was measured by observing the length of time it took for the surface and buried seeds to be located. If olfaction was always used to locate buried seeds, an individual would be expected to locate both groups of seeds, and dig them out of the sand. If the tactile senses were sometimes depended upon, then they would be expected to miss buried seeds unless these were touched with the manus while sifting or digging, and thus brought closer to the surface where they could be smelled. The latter behavior occurred under dry conditions when the relative humidity was about 35 percent, and in individuals which were recently captured from the wild.

The following account of D. merriami is considered typical for that species during the sand-seed test. Individuals first walked around the cage sniffing and sifting at random until the scent of the surface seeds was detected. The surface seeds were detected almost at once, and gleaned from the surface. As can be seen in Table I, the surface seeds in pile one were always picked up. The buried seeds were never picked up first.

The manus was used to pick up food from the sand. Kangaroo rats were never observed to pick up small objects from the ground with their incisors. Both forepaws were extended anteriorly to the end of the nose, and were drawn back through the sand. During this operation, the claws alone penetrated the sand and only to a depth of three to six millimeters. The claws were used exclusively while sifting. Individuals usually backed up and reworked the material which accumulated between the hind legs during digging and sifting.

In a homogeneous mixture of sorted sand every foreign particle was picked up and sampled, including lumps of sand. The pieces of cardboard were usually discarded after being manipulated although three individuals actually placed them in their cheek pouches. In subsequent tests most of the animals observed discarded the cardboard with little or no sampling, but nevertheless picked them up in the manus before rejecting them. The commercial rabbit food pellet was picked up and sampled by almost every individual, but was never placed inside the pouches. The ball of cotton was also picked up and manipulated before it was discarded. There were two pieces of charcoal in the sand. These were picked up and sampled until they were completely ground to dust as a result of nibbling.

Individuals passed over the buried seeds several times without giving any indication that they were aware of the presence of food only five millimeters beneath them. An occasional seed located near the surface was found during random sifting. Generally this was sampled and placed inside one of the cheek pouches. The discovery of such a seed induced continued digging in the same area. However, under laboratory conditions seeds were sometimes buried deeper as a result of the digging activities of the animal itself, and large piles of seeds close to the digging site went undetected.

Digging in dry sand exposed seeds to the sides and in front of an individual. As the sand caved into the excavation, seeds rolled free and were sifted out like those in the surface piles. Seeds were discovered in 11 out of a possible 139 of the buried piles (see Table I). The buried seeds were located in two ways. Either an individual sifted and dug at random about the cage and located seeds when they were struck by the manus or the seeds were detected by smelling and a hole was dug until they were exposed.

Sometimes sifting and digging took place directly over a spot where seeds were buried, and the individual moved to another area before these foraging activities exposed them. When seeds were found by sifting, individuals tended to remain in the same spot, although sometimes the seeds were not completely uncovered when the direction of activity was to the side of the main pile. After several strokes were taken and no seeds were found, an individual would explore other areas in the test cage, but usually would return to the place where seeds had first been located. Sometimes subsequent digging and sifting would uncover the remaining seeds while at other times they would be missed.

There was evidence in two of the 11 cases in which buried seeds were located that the sense of smell was used. At the beginning of the sand-seed tests the sand over pile four contained some lumps of damp sand. Both individuals M-24 and M-25 dug directly over the seeds and uncovered the seeds in pile four (Table I). Since, in subsequent tests, all four species found buried seeds when the relative humidity was over 50 percent, it would seem that olfaction could be useful under moist conditions.

TABLE I

Sand-seed Test

Individual	Trial 1				Trial 2				Trial 3			
	Pile Number				Pile Number				Pile Number			
	1	2	3	4	1	2	3	4	1	2	3	4
M-10	+	0	0	0								
M-11	+	0	0	0								
M-12	+	0	+	0	+	0	0	0	+	0	0	0
M-13	+	+	0	0	+	+	0	0	+	+	0	0
M-14					+	0	0	0	+	+	0	0
M-15					+	+	0	0	+	0	0	0
M-16	+	0	0	0	+	0	0	0	+	0	0	0
M-18	+	0	0	0	+	+	0	0	+	0	0	0
M-19	+	0	0	0	+	0	0	0	+	0	0	0
M-21	+	0	0	0	+	0	+	0	+	0	0	0
M-22	+	0	+	0	+	+	0	0	+	0	+	0
M-23 ♂	+	0	0	0	+	0	0	0	+	0	0	0
M-24	+	0	0	+					+	0	0	0
M-25 ♀	+	0	0	+					+	0	0	0
M-26	+	0	0	0	+	0	0	0	+	0	0	0
M-28	+	0	0	0								
M-29	+	0	0	0								
M-31	+	0	0	+					+	0	0	0
M-32	+	+	0	0								
M-33	+	0	0	0	+	0	0	0				
M-34	+	0	0	0								

A plus sign (+) indicates that the individual located the pile of seeds and placed them inside its cheek pouches. Zero (0) indicates the pile of seeds was not found. When the experimental subjects exhibited no interest in the food, the space is left blank.

Food Discrimination

Sampling. Sampling is defined here as nibbling with the incisors, and possible use of the tongue for testing. The precise role of the sense of taste during sampling was not determined. Large stones in the cage exhibited a damp spot after an individual had sampled them, indicating that some objects were licked. It was thought that although taste was used sometimes, it was not very useful when sampling tastless objects, e.g., the beads in the bead-seed test.

Some of the musculature around the mouth (buccinatorius) is highly specialized (Howell, 1932:420), and the part of the mouth posterior to the incisors can be tightly closed. This was probably the condition during sampling. It was observed, however, that a small opening could be formed in the center of the closed lips. The tongue was extended through this opening when individuals licked the glass on the sides of their cages. Thus it would be possible for kangaroo rats to taste what they were sampling without opening the mouth.

Seeds which had been sampled had portions which had been bitten away (Figure 4). Sometimes fragments of a hulled seed were seen to drop to the ground during sampling activity. When no particles were observed it was assumed that any loosened

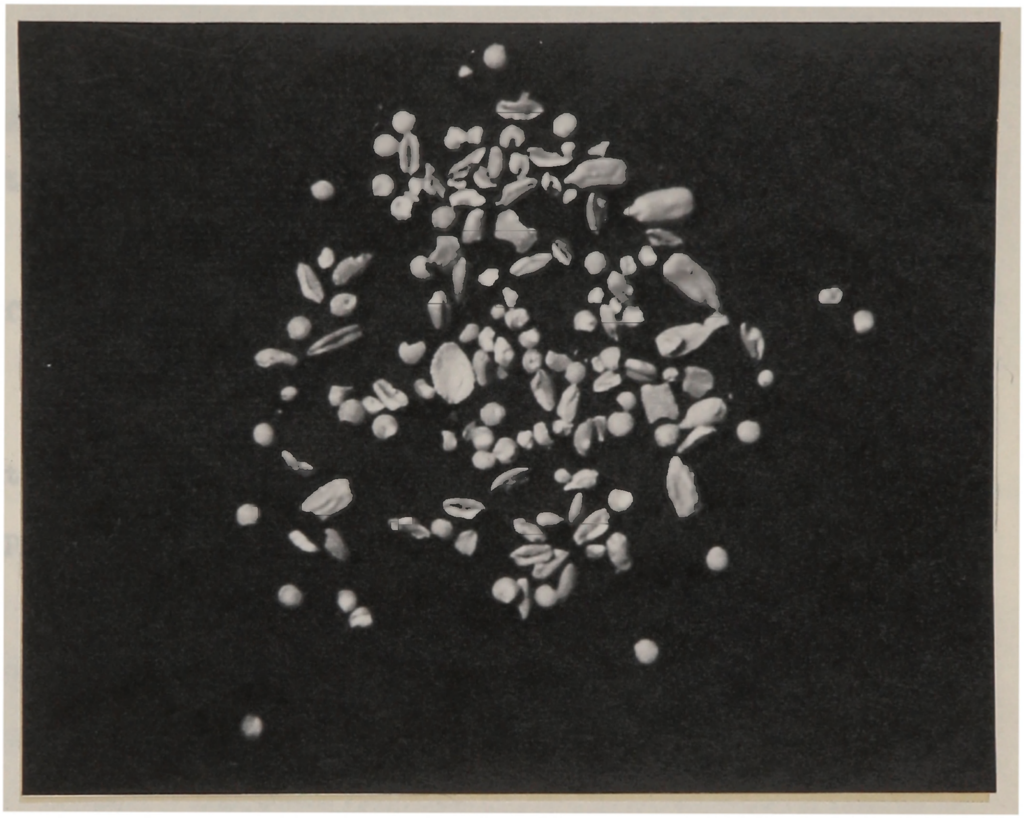


Figure 4. The contents which were removed from the pouches of a D. panamintinus. Note that most of the seeds have portions which have been eaten away.

parts of the seed were eaten. Slow motion pictures showed that the two lower incisors were spread apart slightly when the jaw was lowered while the upper incisors appeared fixed in position. When the observer's finger was offered for sampling, it was grasped with the manus and lightly pinched with the incisors at first. As nibbling continued, it became more intense. At no time could the investigator detect any use of the tongue when his finger was sampled.

Bead-seed Test. This test was devised to establish the relative importance of the size and shape of the food particles, as opposed to their odor, in food discrimination, and to determine the relative values of the tactile and olfactory senses. If the latter were of primary importance, an individual would be expected to distinguish between seeds and glass beads. If the tactile senses were paramount, the animals should pick up beads with sizes and shapes similar to those of the seeds actually used in the tests. The latter occurred.

When first subjected to this test kangaroo rats of the species observed (*D. merriami*, *D. panamintinus*, *D. agilis*) first tilted their heads slightly upwards and sniffed the air. Then they went directly to the mixture of seeds and beads placed in the center of the glass cage. Immediately after discovering the pile the animals began to pick items from it with their forepaws; the items first picked up were then nibbled, or further manipulated with the forepaws, or both. Both seeds and beads were taken, and certain of these, which were removed manually from the cheek-pouches by the observer, are shown in Figure 5. Note that the marks of nibbling are plainly visible. The numbers of beads placed in the pouches are recorded in Table 2.

In general, _D. panamintinus_ picked up more beads than did the smaller species, _D. merriami_ (Table 2). The _panamintinus_ were less discriminating, picked up objects more quickly, and did less sampling. Upon locating beads and seeds, the first objects picked up were sampled. Sampling behavior consisted of manipulating the objects with the manus and/or nibbling them with the incisors. If the first few (approximately 1 to 4) objects were ALL seeds, the remaining objects were placed in the pouches without much sampling. Those individuals which sampled more frequently, placed fewer beads in their pouches. When animals were starved for 24 hours, they sampled less, and placed in their pouches all the objects presented to them including bits of crushed granite which came with the mixed commercial bird-seed. On the other hand, if the first objects picked up were beads, they were sampled, and after the first test beads were usually discarded. Sampling continued

TABLE 2

The Numbers of Beads Placed Inside the

Pouches During the Bead-seed Test

Individual		Test														
		1st			2nd			3rd			4th			5th		
D. panamintinus																
P-01	♂	+	+	+	2	1	5	3	2	4	0	0	3			
P-02	♀	4	4	8	0	0	0	0	0	2	1	0	1			
P-03	♂	4	3	6	4	2	3	4	0	2						
P-04	♀	-	-	-	0	0	1									
P-05	♂	4	4	6	4	4	8	4	4	8	4	4	7	3	0	7
P-06	♂	4	4	8	4	3	8	0	0	1	0	0	0	0	0	0
P-07	♀	4	0		3	0	5	1	0	3	0	0	0			
P-08	♂	3	1	1	4	0	2	4	0	1	0	0	0			
P-09	♀	4	4	7												
P-10	♀	4	4	7												
P-11	♂	0	0	2	4	4	6	0	0	1						
P-13	♀	0	0	3	2	1	3	0	0	0	0	0	3			
D. merriami																
M-01	♂	4	1	4	1	0	2	0	0	0						
M-02	♂	-	-	-	-	-	-	1	1	8						
M-03	♂	0	0	6	1	0	2	-	-	-	0	0	2			
M-04	♀	2	0	7	-	-	-	0	0	3						
M-05	♀	+	+	+	0	0	8	-	-	-						
M-06	♀	2	5	5	2	0	5	-	-	-						

The first column in each test indicates the number of oat-pearls, the second indicates the number of cylinders, and the third the number of spheres. A plus sign (+) indicates that beads were placed in the pouches but not counted. A dash (-) indicates that the test was given but the animal did not pick up either seeds or beads.

Figure 5. The material removed from the pouches of individual P-05 (D. panamintinus) immediately after the bead-seed test. Note the oat-pearls and glass spheres. There are no cylinders or unhulled seeds. Many of the seeds show where nibbling with the incisors took place. At the lower right is a round stone which was carried in its pouch before the test was given.

Figure 6. The coverings of the three oat-pearls in the upper row have been removed. At the extreme right is a covering. The bottom row contains oat-pearls in the original condition.

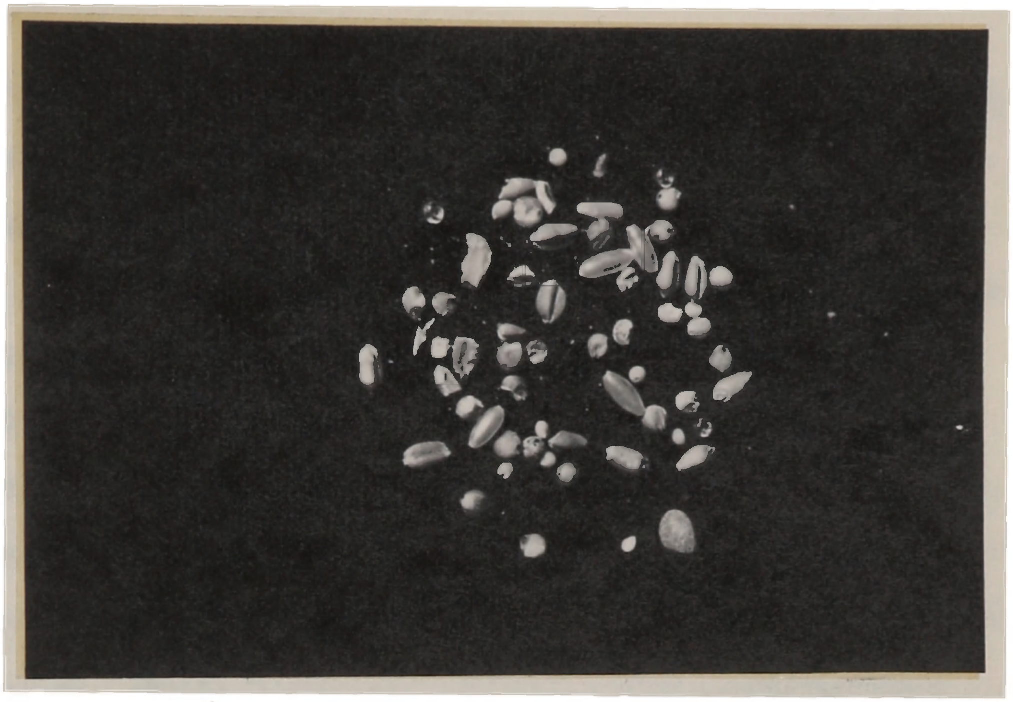


Figure 5.

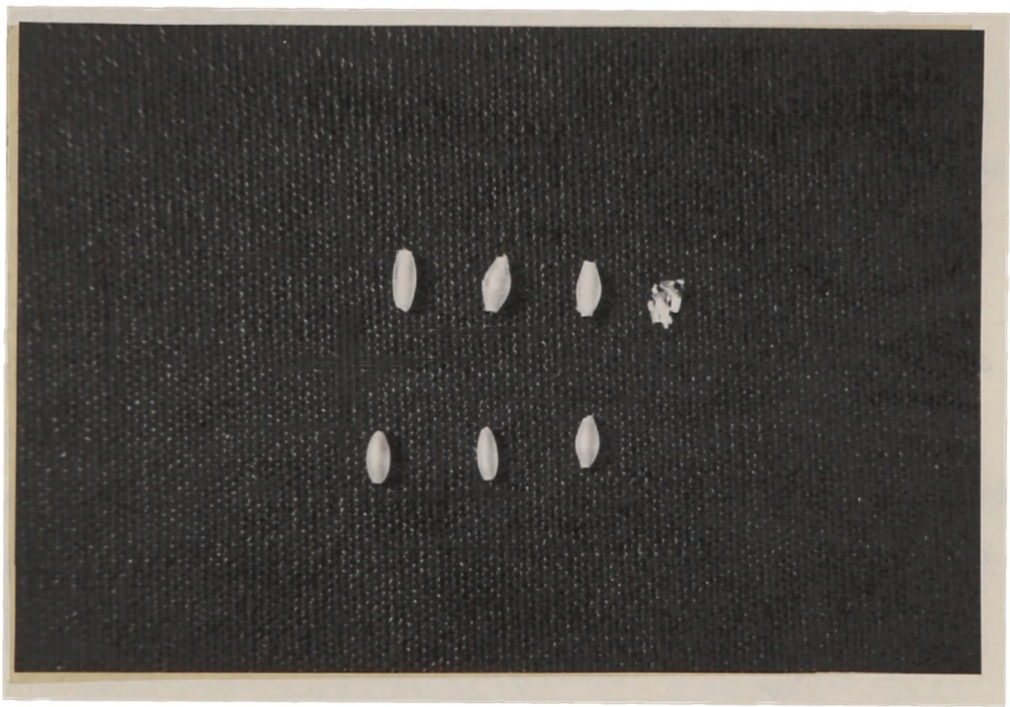


Figure 6.

until approximately two to five seeds were sampled in sequence, and subsequently, objects, including beads, were then placed directly into the cheek-pouches without sampling.

When certain individuals were confronted with this test for the first time, they actually attempted to hull the glass oat-pearls. In Figure 6 there are samples of oat-pearls with the pearl covering partially removed. The beads with no covering were also bitten, but no visible marks were observed. After sampling, the beads were either placed inside the pouches or discarded. In subsequent tests they were usually discarded after sampling as can be noted by the smaller numbers placed in the pouches (Table 2).

Individuals which sampled intermittently during the test placed fewer beads inside their pouches (Table 2 Individual P-07). Hungry individuals picked up objects more rapidly, did less sampling, and more beads were placed inside their pouches. Individual P-13 (Table 2) sampled frequently during the first test and placed only three glass beads in her pouches, but in the second, where she had been without food or water for 24 hours, there was an increase in the number of beads which were placed in the pouches.

Those individuals which showed a preference for a certain type of seed, showed a corresponding tendency to pick up beads of similar shape and size. For example, individual P-03 (Table 2) always picked up oat-pearls, but rejected some cylinders. He showed a corresponding preference for hulled wheat grains, and either removed the hulls from the oats or discarded such seeds. P-07 was an even more striking example. During the first test, all of the unhulled oats were rejected and no cylinders were placed in the pouches. On the second test some of the unhulled oats were hulled and placed in the pouches, but no cylinders were so treated. This animal was never observed to place an unhulled seed of any type inside its pouches. Here the tendency to sample and hull the seeds was correlated with a marked ability to distinguish beads from seeds. During the last test no beads were placed inside the pouches; however, the subject did not appear hungry, and sampled only some of the material.

D. merriami was generally more deliberate than *D. panamintinus*. Although certain individuals performed during the test, many instances were recorded where they did not pick up any of the material and place it inside the pouches. Some individuals appeared to sample almost every object, and, as a result, the beads were separated from the seeds. Even when starved for about 24 hours, less than 25 percent of the D. merriami observed (including those in the general observations) exhibited behavior similar to that of the D. panamintinus where the first few objects were sampled, and the remaining ones were rapidly placed inside of the pouches.

D. merriami exhibited a definite preference for the smaller seeds. Sunflower seeds were actually rejected by animals recently removed from the desert. W ithin two or three days, however, they were accepted. During the bead-seed tests, the small millet seeds were usually picked up first, and the larger seeds either remained on the ground or were picked up and placed in the pouches last. There was a corresponding tendency for the small glass spheres rather than the larger beads to be placed inside the pouches (Table 2). The small millet seeds possessed a thin hull which was removed easily by D. merriami. The seeds were manipulated so rapidly that even the slow-motion movies failed to reveal how the hulling was accomplished.

As its scientific name implies, D. agilis was by far the most dexterous and nimble of the Dipodomys observed during the study. These excitable creatures did a minimum of sampling, and indiscriminately and expeditiously placed all the objects inside their pouches. The members of this species which were tested

Figure 7. The contents which were removed from the pouches of *D. agilis*. Note that the oats were not hulled, and that there are several of the glass cylinders present. This individual did little sampling, and placed beads and seeds in its pouches in about the same proportions as were presented.

had been in captivity for three years when the bead-seed test was administered. The bead-seed test was then modified in such a manner that the greater portion of the material presented consisted of beads. This apparently had no effect upon discrimination. When the contents were removed from the etherized subject's pouches, more beads were present than seeds. (Figure 7). The consistency observed before can be seen in the photograph, namely, the beads and seeds, which were placed in the pouches, have similar shapes and sizes.

Food Handling

Posture. Figure 8 illustrates the posture of a Merriam kangaroo rat when picking up objects from a glass surface. The weight of the body is distributed such that the center of gravity is over the hind feet. No difference was observed when individuals foraged in soil. This posture allowed the animals to walk or hop bipedally while feeding. When individuals moved while foraging, they stood on their toes (digitigrade). A plantigrade position was assumed when a rat remained in one location during sifting and hulling activities. The posture permitted a considerable amount of agility and adaptability. The various positions taken are well illustrated by Bartholomew and Caswell (1951), and will not be repeated here.

Figure 8. The posture of D. merriami during feeding activities. Note position of the body in relation to the hind feet. The vibrissae are in contact with the glass floor of the cage.

Use of Cheek Pouches. The manus was used to place objects inside the cheek pouches. Seeds the size of wheat grains and smaller were placed in the pouches "one-handed." The right manus was always used to place objects in the right cheek pouch; the left manus was used with the other pouch. When small seeds were placed in the cheek pouches, the manus was cupped and supinated as the seed was placed at the orifice of the pouch (Figure 9).

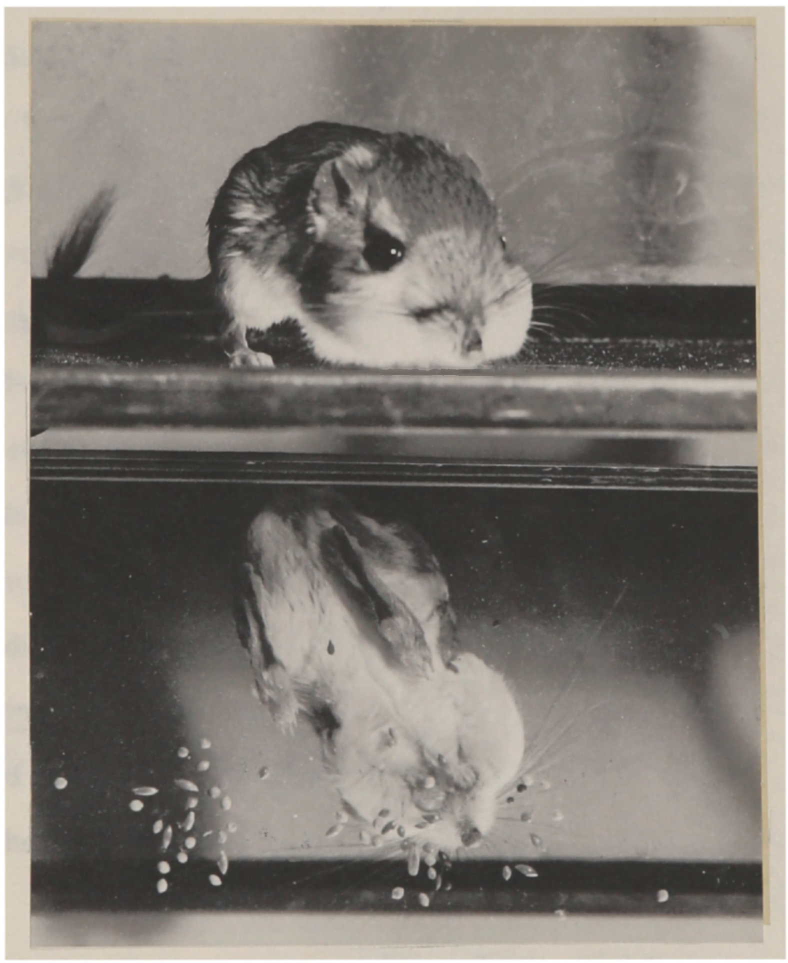


Figure 9. The individual's manus is cupped and in a supinated position when placing a seed inside the cheek pouches.

If an object was not placed far enough inside the pouch it was forced farther with the clenched manus. Slow-motion moving pictures revealed that this was a "two-operation" move. After the manus left the pouch it was returned a second time to force a seed inside which did not go completely in the first time.

Objects the size of sunflower seeds were oriented by means of the manus of the corresponding side so that the pointed end was directed toward the opening of the cheek pouch. In some instances the manus of the opposite side was used to push the guided object into the cheek pouch (Figure 10). The pouch musculature was relaxed in some cases when objects were brought to the opening. This was evidenced in the slow-motion moving pictures. The full pouches caused the opening to enlarge just before the seed was placed inside, but it closed afterwards.

When individuals appeared exceptionally hungry , they were so intent upon filling their cheek pouches that two or three other seeds dropped out while one seed was being placed inside. One D. merriami picked up millet seeds three or four times before it managed to get all of them inside.

The cheek pouches were emptied by relaxing the pouch musculature. The forepaws were brought to bear on the posterior-ventral region of the pouch and by pushing up and forward the

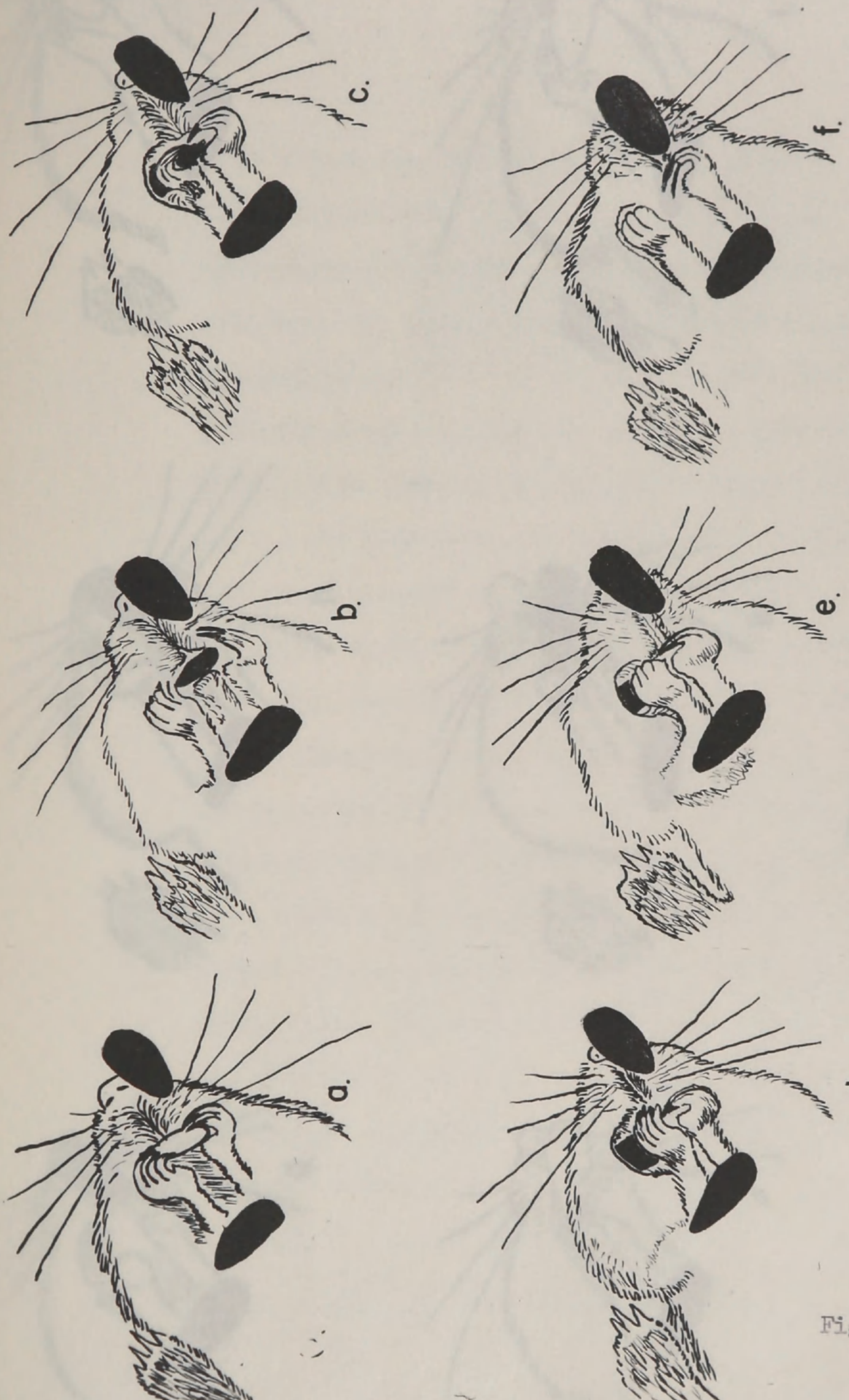
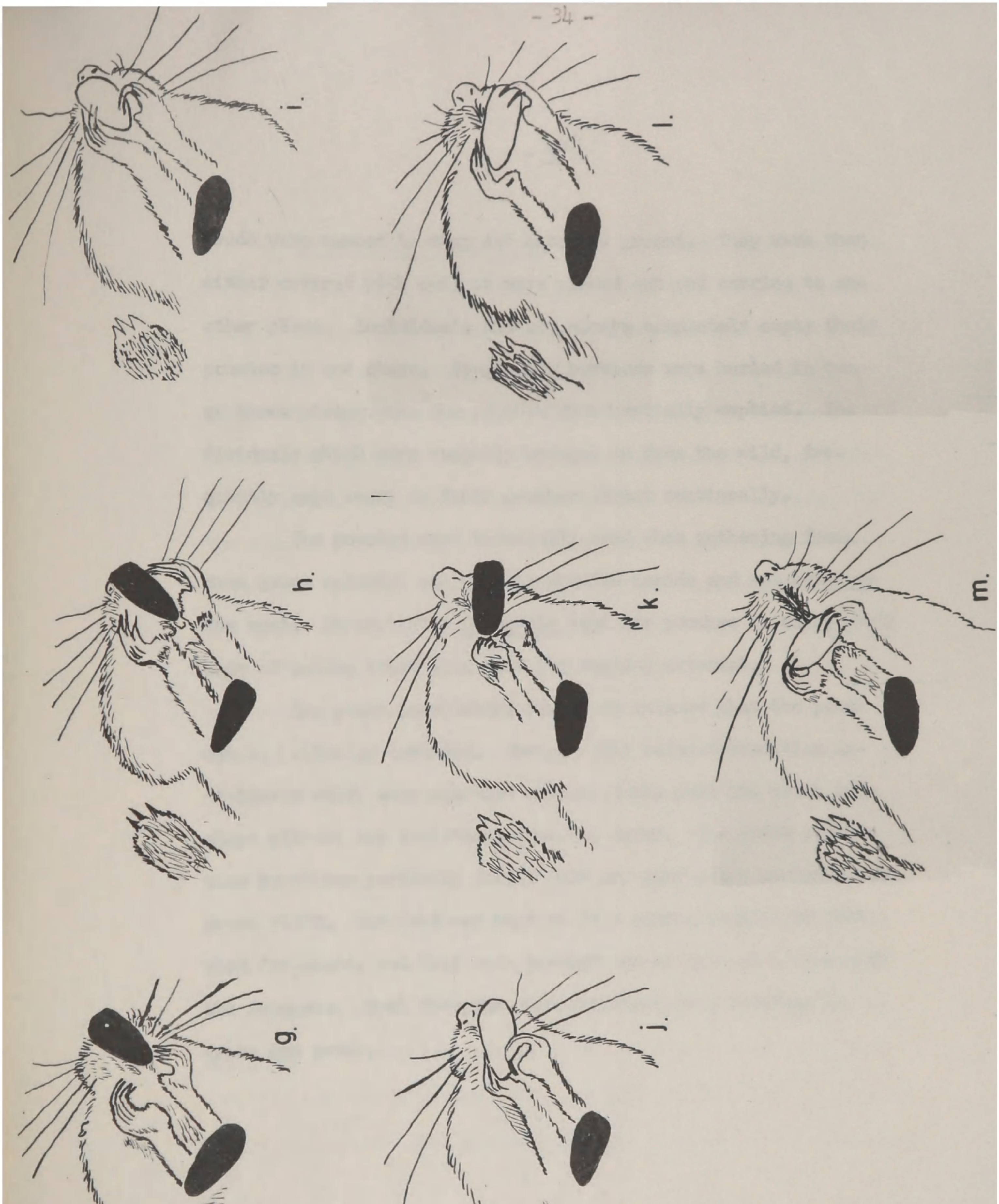


Figure 10.


i.
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seeds were caused to drop out onto the ground. They were then either covered with soil or were picked out and carried to another place. Individuals did not always completely empty their pouches in one place. Frequently portions were buried in two or three places when the pouches were partially emptied. Individuals which were recently brought in from the wild, frequently kept seeds in their pouches almost continually.

The pouches were invariably used when gathering food. Even green material was usually stuffed inside and not eaten on the spot. In captivity D. agilis used its pouches to carry small wads of cotton which were used for nesting material.

The pouch musculature can be so relaxed that the pouch can be partially inverted. When in this relaxed condition individuals which were startled would quickly pull the pouch into shape without any assistance from the manus. The cheek pouches were sometimes partially filled with dry sand after carrying wet green stuff. The sand was emptied in a manner similar to that used for seeds, and they were groomed one or both at a time with the forepaws. Both forepaws were sometimes used together to groom one pouch.

Speed of Food Gathering. The speed with which kangaroo rats are able to pick up objects and place them in their cheek pouches is one of their more striking patterns of behavior. A great deal of variability was exhibited by each individual, apparently dependent upon the individual's state of hunger at the time of testing. For example, an animal which was extremely hungry picked up objects more rapidly than when it was not. If the animals were sleepy, the rate was very slow. Table 3 contains some examples of speeds computed from slow-motion moving pictures. Rates of speed of the four species were remarkably alike when they were starved for 24 hours prior to photographing. One-fifth second was the modal rate for hungry animals to pick up a seed, place it inside the pouch, and pick up the next seed. It should be mentioned that although the amount of time involved was approximately the same for the four species, the size of the seeds handled varied. For instance, merriami was not able to place sunflower seeds inside its pouches at the above stated rate, but it could handle the millet seeds at that rate. Because the millet seeds were completely hidden in the manus the rates computed for merriami were computed indirectly by placing 20 millet seeds in the cage, and using a stop watch to check the time it took to pick up all the seeds. This method was valid only when individuals did

TABLE 3

Speed of Placing Seeds Inside Cheek Pouches

Species	Number of Frames	Time in Seconds
D. agilis	21	0.31
	14	0.21
	8	0.12
	13	0.19
	16	0.24
	16	0.24
	19	0.28
D. agilis	30	0.42
	30	0.42
	33	0.49
	Hulling	
D. agilis	85	1.25
	190	2.79

The rates given refer to three series photographed at different times. Speeds were computed only from a series which clearly showed the seed throughout the operation. Sunflower seeds were used in all the above. The last column gives the time it took individuals to pick up a seed, hull it and place it inside the cheek pouch.

not sample. Since the rate (20 seeds in 4 seconds) approximated that computed for agilis from the films (1 seed in 0.2 second), the same method was used.

The computed food gathering rates for D. agilis do not include instances where seeds were fumbled. In such cases (Figure 10) the same seed was picked up more than once or in other cases it was knocked out of reach and another was picked up in its place. An individual was never observed to retrieve a fumbled seed if it was out of reach.

Manipulation The manus of the kangaroo rat is similar to that of fossorial Geomyidae (pocket gophers). Although the forelimbs of the heteromyids are not powerful, they do possess long pointed claws which are also characteristic of the geomyids. As will be seen from the results below, the claws played a major role in manipulation as well as during sifting. In Figure 10 are shown the common methods of holding seeds the size of sunflower seeds.

While manipulating seeds the phalanges were flexed and extended frequently. The slow-motion pictures revealed that this behavior took place many times when the manus were empty, and most frequently when reaching for seeds. It is worthy of note that Straus (1936) was able to reproduce this behavior by electrical stimulation of the higher brain centers (cerebral cortex) of *Dipodomys*.

Direct observations and photographs indicated that usually the forelimbs were extended simultaneously to the tip of the nose from under which seeds were picked up. Even if the seeds were closer to the mouth, only those directly under the nose and upper lip were picked up. Although the details of this behavior were not apparent from direct observation, the slow-motion pictures showed that there was a great deal of adaptation to meet the various situations with which individuals were confronted during manipulation. For example, when *agilis* was presented with a mixture of beads and seeds, it was noted that beads were picked up which were in contact with the vibrissae between the external nares and the mouth.

In Figure 10 a series of diagrams traced from the motion picture films illustrates the action involved in picking up two sunflower seeds. In Figure 10-a the seed has already been picked up and is held in both manus, and at each end. The seed is supported between the claws and the pad of the palm when brought to the mouth. Next it is apparently held between the incisors since both manus are free (Figure 10-b). The right manus has been brought closer to the center of the seed in part "c". It has been apparently pushed toward the right cheek pouch by the left manus while guided by the right. However, the right manus was used to shove the tip of the seed into the right cheek pouch (Figure 10-d). As the seed was forced into the pouch, a corresponding expansion of the outside of the pouch can be seen in Figure 10-e and 10-f. The external nares are directly over the next seed which will be picked up. The former seed was forced all the way into the cheek pouch with the right manus while the left was inactive (Figure 10-f). After the right manus had completed its task, both forelimbs were extended together to pick up the next seed (Figure 10-g). The position of the animal remained the same while only the forearms were extended. The following drawings (Figure 10-h, i, j and k), show a fumble. Apparently the seed was knocked out of the right manus by the left. The forelimbs were retracted empty, and the phalanges were flexed. The seed which is out of its original position was retrieved in the same manner as it was during the first try. The total time, including the fumble, was only 0.3 second. (Figure 10-a to k).

Small spherical seeds were held in the palm or against the pad by the claws. These small seeds were completely hidden from view when the manus was supinated (Figure 11). Photographs

Figure 11. Small seeds one to four millimeters in diameter were held in the manus. The manus was in a supinated position when seeds were being sampled.

showed that at least some were held between the pad and the claws when seeds were sampled, but more frequently the smallest seeds were held cupped in the supinated manus (Figure 11).

The manus can be seen at the orifice of the pouch as a small millet seed was placed inside (Figure 9). The pouch exhibits a distended position suggesting that the manus must be forced partly inside when placing small seeds there. The millets were handled with one manus, but during hulling activities the opposite manus was used to remove the hull fragments. The hull was removed with the claws and sometimes was grasped lightly with one manus between the claws and the pad while held securely with the other. Larger fragments were thrown backwards between the hind legs. Smaller fragments were also thrown but frequently dropped to the ground before they could be catapulted by the manus. Many rejected objects were thrown backwards between the hind feet, sometimes with such force that the object would ricochet off the sides of the experimental cage.

Hulling seeds. Seeds were hulled either before they were placed in the cheek pouches or later at the time when these were emptied. Usually the first seeds were sampled and hulled. Seeds the size of sunflower seeds were held by the ends with both manus, and crushed with the incisors. A claw was inserted where the hull was cracked and the hull was removed by pulling it away with one manus while it was held by the other. Since seeds about two millimeters in diameter were cupped in the palm, it was not possible to see the manner in which the hulls were loosened with the incisors. Intermediate sized seeds were hulled by using combinations of the above methods. The tendency to use both manus was greater with the larger seeds and vice versa.

Sorting. The pouches were used to help sort material in the following manner. In the laboratory a hungry individual picked up almost all of the various types of food which were placed before it. The material was carried in the cheek pouches to a corner of the cage where the latter were emptied. At this time a great deal of sampling and hulling activity took place. Certain seeds were picked up, placed in the cheek pouches once more, and carried to another location. This process was repeated and thus similar seeds were sorted out into separate piles. In captivity a great deal of what appeared to be needless sorting took place. There was a definite tendency to nibble a little from every available seed and eat only a part of it rather than to eat them one at a time. Rarely were seeds which had not been partially eaten found in an individual's cage.

Drinking. Individuals readily drank water in captivity. They exhibited difficulty at first when drinking from a dish. The external nares went beneath the surface when they attempted to drink directly with the mouth. Usually they dipped the manus into the water and licked off the drops. The relative position of the mouth and external nares made it almost impossible for kangaroo rats to drink directly from pools of water. Individuals drank a little and then pushed their noses into dry sand. When water was made available to kangaroo rats through glass tubing, they not only licked the end of the tube, but also grasped at the end of the tube with their forepaws. Many times this caused extra drops to come out of the tube and these were licked from the manus.

They readily ate snow in the laboratory. A snowball was placed in the cage and individuals pulled pieces of snow off with the manus and ate them. Sometimes both forepaws were placed on the snowball and the snow was eaten directly with the teeth and mouth.

DISCUSSION

Lack of cover, extremes in temperature, limited available water, and scarcity of food during rainless periods in arid climates place certain strenuous demands upon mammals. This study has dealt with the adaptations for securing food under the above-mentioned conditions. It cannot be considered mere coincidence that bipedal, saltatorial mammals of various unrelated groups are found mainly in the major desert and semi-desert areas of the world. The various groups which illustrate this type of convergent evolution are well summarized by Hatt (1932:619).

Assuming that the microclimatic conditions in the burrows are adequate to sustain moisture, perhaps the greatest critical factor in nature is finding food. The burrows provide Dipodomys with protection from the temperatures of deserts as well as from many of their natural enemies (Schmidt-Nielsen, 1950). Field observations indicate that much of the time spent outside of the burrow is used to forage for food and that the predominant food consists of seeds, although green material is sometimes harvested when available (Dale, 1939; Grinnell, 1932; Shaw, 1934; Tappe, 1941; Vorhies and Taylor, 1922). With the exception of that taken from the standing vegetation, most of the food collected is picked up from the desert floor. Vast quantities of food are stored either in the den or buried near it in several small caches just beneath the surface (Shaw, 1934). Vorhies and Taylor (1922:19) found that D. spectabilis stored relatively large amounts of food; the largest single lot, from New Mexico weighed 5750 grams (12.67 lbs.). They also stated that spectabilis in south-eastern Arizona, at least, relies largely upon stored materials, except during harvesting seasons. Tappe (1941:124) found that D. heermanni tularensis stored some caches containing 33 grams about 20 inches below the surface. He also noted that seeds of one kind were generally stored together, as did Vorhies and Taylor (op.cit.). D. merriami stores food in several small caches, and no large stores have ever been found in their burrows. Thus, it appears that although there are differences in the manner in which food is stored, kangaroo rats apparently store most of the food which they are able to find on their sojourns outside the den.

In the laboratory the senses of smell, sight, hearing and touch were used while feeding. Although sight and hearing are not thought to play a major role in food finding in the wild, individuals learned quickly to recognize the sounds and activity of the observer while they were being fed. Certainly, vision could be used in the wild to locate stands of vegetation. Nevertheless, kangaroo rats are not able to see objects on the ground beneath the nose and mouth where olfaction and touch must be used almost exclusively. The results of observations made in the laboratory indicated that olfaction was used primarily in locating food. However, touch may be used as evidenced by those individuals which picked up pieces of cardboard and cotton in the sand-seed test. Both were sampled after being touched with the manus. On the other hand, the possibility exists that some odor from the cardboard and cotton may have prompted the animals to pick them up. All the animals tested rejected the food pellet, and many of them rejected it with little or no sampling. This seems to indicate that the odor of the pellet was sufficient for the individual to make a decision. Thus, it would appear that olfaction serves to find a spot where food is located, and that the amount of sampling and manipulating needed depends upon the ease with which organic matter is identified as food. Under extremely arid conditions it would seem that kangaroo rats would encounter more difficulty in distinguishing food. In the Arizona desert the diurnal relative humidity varied from 3 to 28 percent at the surface of the ground (Schmidt-Nielsen, 1950:78). Under similar conditions in the laboratory _D. merriami_ and _D. deserti_ were not able to locate with the sense of smell seeds buried ten to fifteen millimeters beneath the surface of fine sand. However, a few individuals were tested later during the summer when the relative was 50 to 85 percent; they were then able to locate some of the buried seeds by smelling. Thus, the relative dependency upon the senses of smell and touch would seem to depend primarily upon the ability of the individual to find objects by smell. Under drier conditions the kangaroo rat would depend more upon the sense of touch.

Individuals were unable to locate seeds buried in dry sand. Thus the possible selective advantage of covering the food becomes more apparent when placed in small covered surface caches. This habit might tend to prevent other animals from raiding the surface food stores outside the den. There is still the problem as to how an individual finds his own seeds. Shaw (1934:281, 282, 285) reported that the giant kangaroo rat (D. ingens) stores food in many small caches about the entrance of the den. When the caches were uncovered by the observers, the material was not again covered with soil, but carried into the den by the kangaroo rat. Possibly it was not able to find the stores except by random sifting as in the sand-seed test, or that during the winter, it was able to locate the stores by the sense of smell since the relative humidity might be higher at that time.

Frequently the pouches of individuals which were snap trapped, held many small pieces of organic material not suitable for consumption. This material could possibly be there as a result of an inability of the animal to discriminate during the short intervals spent outside of the burrow. The adaptive advantage of collecting food-like material outside the burrow and later discriminating more precisely in the den is obvious. The results of the bead-seed test suggest that the tactile senses were used as the primary mechanisms for discrimination when material was collected for the first time. There was a preference for beads similar in shape and size to the seeds chosen. At least under those conditions the shape and size and perhaps weight of the particles were used as cues when picking up food. Sometimes beads were not rejected until several attempts were made to hull or bite them. It is well known that the seeds of some desert plants are so hard and impermeable that they do not germinate until after the abrasive action of the soil has ground off some of the outside of the seed coat during flooding (Went, 1956:72). Therefore, the seeds found in the dry washes and probably many others may be so hard that a great deal of sampling is necessary before kangaroo rats and other rodents can determine whether such objects are edible.

The results of the bead-seed test revealed that kangaroo rats are capable of making a decision at some level after a limited amount of sampling. When they were presented with both beads and seeds, individuals which first chanced to select a few seeds, placed all remaining objects of similar shape including glass beads into the cheek pouches without sampling each one. Since beads which are odorless as well as seeds were placed in the pouches, only the tactile senses must have been used when the former were picked up. The amount of time saved by limiting the sampling to a few objects would have selective advantage by greatly shortening the periods spent outside of the burrow.

So far we have been concerned with food finding as distinct from food handling and the amount of discrimination used in conjunction with the former. The various steps in food handling will be treated separately, although both food finding and discrimination necessitate handling of food. The posture, manipulatory ability, sorting methods and handling speed are all closely associated with the presence and use of the external, lateral cheek pouches. Without a place to put the material immediately after finding it, the rapid handling behavior would be of little consequence. It is suggested here that the relative positions of the nose, mouth, vibrissae, manus and pouches are an adaptation for foraging in loose soil.

The external nares are located at least 10 millimeters anterior to the mouth. Thus an object that had been picked up and brought to the mouth is probably out of the range of the olfactory senses. The photographs taken from beneath the animals revealed that individuals picked up seeds which were located directly beneath the external nares. Therefore, while one seed was being sampled or placed inside the cheek pouch another one could be located. When seeds were on the surface the animals reached out and picked them up with accuracy and were never observed to feel with the manus for objects.

The family Heteromyidae represents a unique group in that it is specialized for gleaning food from the desert floor. The morphology of the manus must be considered as specialized for manipulating and sorting small particles from the soil. The tools needed to perform such a task would resemble some sort of rake or sieve. As was observed in the sand-seed test, the claws of the manus served as a rake. Secondly, the rake must be manipulatory. The results of those observations indicated that the small merriami is quite capable of manipulating millets with diameters as small as one to two millimeters.

Three genera, Peromyscus, Onychomys and Neotoma which are more generalized rodents than the heteromyids and are quadrupedal, picked up objects from the ground with their incisors. Such objects were sampled on the spot or taken to a corner of the cage. The observed members of these three genera were able to pick up objects with the incisors only after they had brought the material to the surface by digging. The heteromyids save one step in this process since the digging out and picking up of an object are combined into one operation. Furthermore, the generalized rodents sampled each object which was picked up. Thus, the kangaroo rats were able to save further time since they sampled less, and this also enabled them to handle food on a mass production basis. Peromyscus and Onychomys were observed to pick up beads with their teeth and sample them much as did Dipodomys. Such limited data suggests that most desert rodents would have difficulty in distinguishing seeds from similar objects on the desert floor. The advantages resulting from the method used by the kangaroo rats become obvious when one notes that the more laborious task of discrimination can be done in the safety of the burrow.

On the basis of the ability of kangaroo rats to gather food on dry soil, they may be considered as best adapted for seed gathering from the desert floor. There are other sources of food but the seeds of the desert floor represent a definite niche, which if exploited could yield a vast amount of potential food. One needs only to observe the desert after sufficient rainfall to note the great numbers of growing plants whose seeds may have been dormant in the soil for years. Thus it would seem that under the severest drought conditions, the heteromyids would have a selective advantage.

Trapping results, tracks, and burrows suggest that the heteromyids are the most numerous rodents in the desert regions of Southern California. Their success is further supported by the fact that the kangaroo rats sustain their large population with a low reproductive rate (two to three per litter). Thus the ability to live in a severe climate and to elude capture by natural enemies make them well suited to the rigors of the deserts.

SUMMARY AND CONCLUSIONS

1. Foraging in four species of *Dipodomys* was studied by means of highspeed flash photographs, slow-motion moving pictures, and direct observations.
2. When finding food animals used the sense of smell primarily, but depended relatively more upon the tactile senses when searching for less odoriferous food.
3. Kangaroo rats were able to sift and pick up objects from the soil with the manus.
4. Individuals were unable to locate buried seeds under dry conditions but could do so when the relative humidity was above 50 percent.
5. More critical discrimination was accomplished by manipulating with the manus and nibbling with the incisors. When glass beads were mixed with food, kangaroo rats were not able to distinguish between beads and seeds until they had been sampled by use of the incisors and manus.
6. They exhibited an ability to make a decision about material after sampling a portion of it.
7. Individuals were able to place seeds in their pouches at a rate of one seed in 0.2 second.
8. Kangaroo rats exhibited the ability to manipulate seeds by means of their claws. Either the claws could be used separately or in combination with the palmar pad.

9. During hulling operations the claws were used to pull away the loosened hull. Discarded material was thrown with the manus backward between the hindlimbs or sometimes to the side.
10. Seeds were sorted after collecting by emptying the pouches and selecting a certain type which was carried to a different area.
11. Individuals covered the emptied contents of their pouches with loose soil when the material was stored.
12. The possible evolutionary and distributional implications of the animals' foraging adaptations and related behavior are discussed.

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