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DAILY AND SEASONAL PATTERNS OF ACTIVITY AND ENERGETICS IN A HETEROMYID RODENT COMMUNITY[1]

G. J. KENAGY

Department of Biology, University of California, Los Angeles, California 90024

Abstract. *Dipodomys microps, D. merriami,* and *Perognathus longimembris* spend most of their lives solitarily and in the ground, coming out onto the surface only at night and foraging for as little as an hour. However, they are active within their burrows throughout the day, seldom remaining motionless for more than half an hour at a time during the warmer parts of the year. All three species rest at positions in their burrows which are generally at the nearest of available temperatures to the lower end of thermal neutrality, but not warmer than 30° C. To do this, they occupy different depths at different seasons and in some cases different times of day. Daily vertical movements are most common in *P. longimembris*, because it maintains tunnels as near as 1 cm from the surface, where daily fluctuations in temperature are profound. In late fall, winter, and early spring all three species occupy nests, which serve to reduce metabolic expenditure.

Energetic strategies differ interspecifically in relation to differences in body weight among the species: *D. microps* (56 g), *D. merriami* (35 g), and *P. longimembris* (7 g). The amount of surface activity in the populations and the frequency of movement measured in individuals decrease during colder parts of the year. This decrease is most apparent in the smaller species, and is related to the decreasing success at foraging later in the season and the increasing costs of metabolism at colder temperatures. Surface activity in *D. microps* and *D. merriami* continues throughout the year, at temperatures measured as low as −19° C. However, for *P. longimembris* the costs of foraging in winter usually far outweigh the yield, and the mice become continuously fossorial for up to 5 months of the year, living on seeds that they have cached in their burrows, and spending a great deal of time in dormancy.

Seasonal cycles of body weight and reproduction are not synchronous in *D. microps* and *D. merriami*, because of differences in diet and foraging behavior. *Dipodomys merriami,* which is primarily a seed eater, requires the green vegetation of annual plants to reproduce, and therefore this species increases body weight and reproduces at sporadic intervals according to the unpredictable availability of annuals. *Dipodomys microps*, however, reproduces in a brief, annually consistent period because leaves of perennial shrubs are its primary year-round food and water resource. This larger kangaroo rat forages over a smaller area for leaves than *D. merriami* does for seeds; but *D. merriami* runs 50% faster, which should compensate for the cost of moving greater distances. *Dipodomys microps* is most active during the first part of the night, but *D. merriami* becomes more active during the course of the night as the activity of *D. microps* decreases. Height and breadth of burrow hillocks and height of shrubs on hillocks were significantly larger for *D. microps* than the other species, but height of burrow hillocks and shrubs on them did not differ between *D. merriami* and *P. longimembris*. *Perognathus longimembris* resembles *D. merriami* more than it does *D. microps* in diet and reproductive pattern, but in winters of great food scarcity competition between *P. longimembris* and *D. merriami* is reduced by the total absence of *P. longimembris* from the surface.

INTRODUCTION

Desert rodents, such as the Heteromyidae (kangaroo rats and pocket mice) of western North America, are highly specialized at acquiring the sparse and ephemeral food resources available in their arid habitats. They may spend less than an hour on the surface at night and therefore live most of their lives in subterranean burrow systems.

The present paper presents behavioral and physiological aspects of the ecology of two kangaroo rats and one pocket mouse in relation to the acquisition and expenditure of energy. The nature of burrow systems and the seasonal and daily changes in behavior of the animals within them are examined. Activity on the surface is analyzed on a daily and seasonal basis. Ecological differences among the three species are pointed out, thus accounting for the basis of coexistence in the community.

SPECIES STUDIED

Three species of heteromyid rodents, sympatric in the Owens Valley of eastern California, were studied: (1) *Dipodomys microps* (the Great Basin or chisel-toothed kangaroo rat), which occurs in the Great Basin of Nevada and the surrounding states,

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(2) *D. merriami* (Merriam's kangaroo rat), which occurs from northern Nevada across the deserts of the southwestern United States to the central plateau of Mexico, and (3) *Perognathus longimembris* (the little pocket mouse), which occurs from southeastern Oregon, across Nevada and parts of eastern California and adjacent states, into northern Mexico (Hall and Kelson 1959). All three are typical of arid scrub habitats, are fossorial, and are active on the surface only at night.

Field Site

Field studies were conducted in 1969–1972 on the east side of the Owens Valley (elevation 1,220 m) near Big Pine, Inyo Co., California. The three heteromyid rodents under study were virtually the sole constituents of the nocturnal rodent fauna. Southern grasshopper mice (*Onychomys torridus*) and deer mice (*Peromyscus maniculatus*) were captured on rare occasions, and a juvenile desert woodrat (*Neotoma lepida*) was captured once. The day-active antelope ground squirrel (*Ammospermophilus leucurus*) was often seen on the site.

The Owens Valley is in the rain shadow of the Sierra Nevada, and the annual precipitation is only 10–15 cm. It lies between the Mojave Desert and the Great Basin, and has the hot summers of the former and the cold winters of the latter. Snow may lie on the valley floor for short periods several times during the winter.

Vegetation at the study site is Great Basin scrub. The most abundant shrubs are spiny saltbush (*Atriplex confertifolia*) and greasewood (*Sarcobatus vermiculatus*). The alkaline soil supports 10 other shrub species, in lesser abundance, but there are few annuals. The buckwheat *Eriogonum deflexum* and the common tumbleweed, *Salsola kali*, are the most conspicuous annuals. There are occasional tussocks of the perennial grass *Oryzopsis hymenoides*.

Methods

Environmental measurements

Ambient temperatures were measured with a Yellow Springs thermistor telethermometer. Air temperature and relative humidity within 10 cm of the surface were also measured with a recording hygrothermograph. Profiles of soil temperature were measured with calibrated Fenwal 2,000-ohm thermistors embedded in the wall of tapered fiberglass rods (fishing pole stock), which were forced into the ground. Temperatures were read about every 3 hours during a 24-h period to record daily fluctuations. Data on precipitation are from the U. S. Weather Bureau station at the Bishop Municipal Airport (elevation 1,250 m), 25 km north of the study area.

Surface activity

Mark-and-recapture live-trapping was used to provide a record of relative activity throughout the year. Trapping was conducted monthly at or within several days of full moon. Traps were provided with a ball of cotton in winter. Externally apparent reproductive conditions were noted for all animals, and kangaroo rats were weighed to the nearest gram with a portable spring balance.

In order to assess the activity at different times of night, we set traps during successive quarters of the night. Four separate quadrats (62.5 m × 62.5 m) of 36 trapping stations each (6 × 6 traps, 12.5 m apart) were set up in a row, with unused quadrats of the same size alternating between the trapping grids. Nights were divided into four equal quarters, ranging from about 2 h 15 min in summer to 3 h in winter, and one quadrat of traps was baited (1 g bird seed per trap) at the beginning of each successive period. At the end of each period, any open traps were closed, thus providing a discrete sample of activity for the given period of the night. Animals were then examined and released.

Most animals were captured within the 1st hour after baiting. Thus the variations in length of sampling periods due to seasonal changes in length of night are probably of minor importance in this study. In any event, trapping periods were not greater than 3 h, even though quarters of the night were 3½ h long in winter. Sampling periods in summer therefore followed one another immediately, but there was a half-hour interval between sampling periods in winter.

Subterranean activity and soil temperature

Details of the method of locating animals in their burrows and determining the temperature of the soil at the resting location are presented elsewhere (Kenagy and Smith 1973). Animals were tagged with radioactive gold wires (1 cm long, 40 mg weight). At the burrow, gamma-ray emission of gold-198 was measured through the soil with a Geiger-Müller survey meter (Eberline E-510), corrections for decay and background were applied, and the depth at which each animal was located was determined from a calibration curve. Animals did not receive heavy radiation doses because of the short half-life of ^{198}Au (2.7 days), which leads to decay of the isotope to background within 3 weeks. We inspected the burrow sites of located animals periodically (at ½–3 h intervals during the daytime and less frequently during the night) to determine typical resting locations. Spray paint was applied on the surface to mark the resting locations of animals. Profiles of soil temperature were measured

in the burrow to determine the microenvironmental temperature at the location of the animal.

The activity of tagged animals was also monitored by continuous automatic recording in the field. A 2-inch NaI gamma scintillation detector was placed at the burrow and the output of the detector fed to a Nuclear Chicago rate meter with a regulated power supply. Output of the rate meter was recorded on a strip chart recorder. The recorder and rate meter were powered with a 300-W motor generator, located about 50 m away.

Laboratory measurements of metabolism

Oxygen consumption was measured in an open-flow system at 5° C(± 0.3) for animals isolated in glass chambers and for the same animals in the same chambers occupying natural nests collected in the field. Absorbants removed water and CO_2 from the air before and after passage through the chamber, and the air was analyzed in a Beckman G-2 recording paramagnetic oxygen analyzer. The metabolic chambers were Erlenmeyer flasks fitted with rubber stoppers and glass tubing. Flow rate was 1,000 cc/min and flask size was 2,000 ml for *D. microps*. Flow rate was 500 cc/min and flask size was 1,000 ml for *D. merriami*. The experiments were performed in February 1971 on freshly captured animals kept in the laboratory at 15° C. All measurements were made between 0800 and 1600 h, and animals were deprived of food 2 h before being placed in chambers. After 1 h for equilibration, the three lowest consecutive readings at 12-min intervals during the next 2 h were averaged to represent oxygen consumption at rest. We weighed animals before and after measurements, and used the average weight to calculate weight specific oxygen consumption. All oxygen volumes are converted to STP.

Experimental exposure to low ambient temperatures

Animals were exposed to air temperature of –25° C in a lighted walk-in cold box. They were placed in small wire cages with cardboard bottoms and without food for periods as long as 1 h. Rectal temperatures were taken at intervals with a calibrated Yellow Springs thermistor.

Experimental field enclosures for P. longimembris

The winter habits of *P. longimembris* were studied by means of small enclosures at the field site. Six pits were dug in the ground, and a cylindrical enclosure of hardware-cloth wire (75 cm diameter × 90 cm height) with a bottom was placed in each to a depth of 80 cm. Soil was replaced and compacted, and a top was fastened onto the cylinder.

Animals were placed in the enclosures and provided with weighed rations of bird seed (65% millet, 25% canary grass seed, and 10% oat groats). A wooden sunshade (30 × 40 cm) was placed on the top of each enclosure. Profiles of soil temperature were obtained at a location central to the six enclosures. The enclosures were observed at intervals throughout the autumn and winter. Each enclosure was eventually excavated and its contents removed. Average body weight of each animal was calculated from weight at beginning and end of the period.

Food consumption and torpidity in P. longimembris

The seed consumption of 11 captive animals at normal body temperature was measured during the fall of 1971 at ambient temperatures of 25, 15, and 5° C on a photoperiod of 10 h (0700–1700 h, at light intensity of 50–750 lux) alternating with 14 h of total darkness. Animals were maintained at each successive temperature for 1 week prior to the 1-week period of measurement. A single, measured, excess ration was provided at the beginning of each week, and seed consumption was determined by weighing the remaining seed and hulls at the end of the week. Data were discarded for any individuals observed to be torpid at any time during the week. Animals were maintained in fiberglass cages 20 × 18 × 15 cm with about 2 cm sand in the bottom.

Patterns of torpidity and seed consumption at 6.5° C(± 0.3) were observed during a 77-day period in the spring of 1972 in animals in the same cages described above and in an isolated walk-in constant-temperature cabinet. Initially the animals were on a 10-h photoperiod (1000–2000 h at light intensity 60–80 lux) alternating with 14 h of total darkness, but after 15 days they received constant total darkness. Small amounts of seed were supplied at short intervals during days 1–18. Animals were inspected at random times during the day for the initial 18 days and torpor was observed. During darkness a flashlight with a dim red beam was used to observe the animals briefly. On day 19 a single large ration of 80 g was provided, each animal receiving a total of 132 g whole seed (= 117 g edible seed, discounting chaff). From day 19–77 animals were observed once daily between 0700–0900 h and recorded as either torpid or active. A few pieces of chaff were placed on the backs of torpid individuals, and therefore by observing the presence or absence of the chaff on the next day it was possible to know if the animal had remained torpid during the whole day. The seed supplies of animals were observed and when several animals had used all the seed in their cages before the end of 77 days they were weighed and removed from the experiment. Average body weight was calculated from weight at beginning and end of the observation period of each animal.

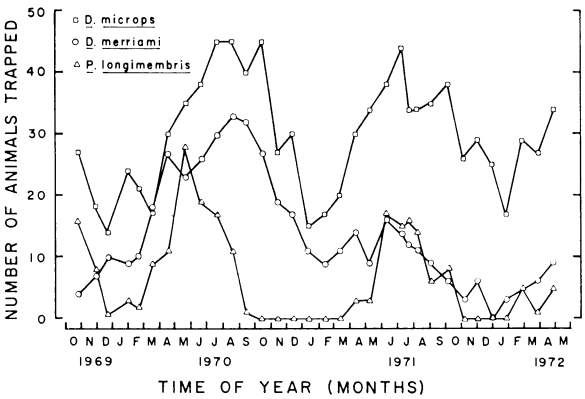

FIG. 1. Total number of *D. microps, D. merriami,* and *P. longimembris* trapped during each of 33 nights over a 31-month period.

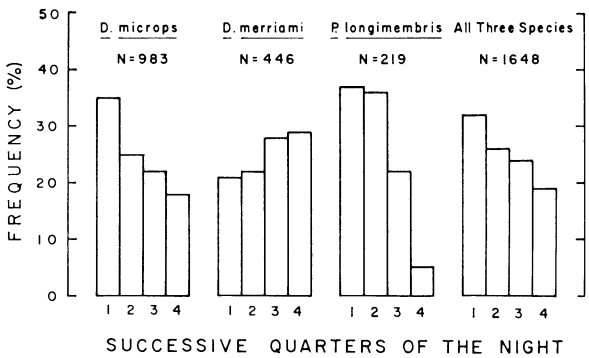

FIG. 2. Frequency histograms of activity in the 4 successive quarters of the night, taken from the data of Fig. 1.

ABOVE-GROUND ACTIVITY

Variation with season

D. microps and *D. merriami* were active every month of the year (Fig. 1). *P. longimembris* was trapped throughout the winter of 1969–70, but was not trapped during the following two winters. In addition to the variation in the intensity of activity during the year in all three species, there was also a conspicuous decline in the number of *D. merriami* and *P. longimembris* in the area during the course of the study.

Variation within the night

Activity for the community as a whole decreased gradually through the night (Fig. 2). The temperature of the air and the soil surface also fell gradually during the night at all times of the year. *P. longimembris* showed a strong tendency for inactivity in the last part of the night.

The divergence, however, of *D. merriami* in its nightly activity pattern from the other two heteromyids is striking (Fig. 2). With such an activity pattern, *D. merriami* was faced with the lower temperatures that occurred later in the night. Social interactions between *D. merriami* and *D. microps* may play an important role in establishing this observed activity pattern. *D. microps* repeatedly chased intruding *D. merriami* from the areas surrounding their home burrows, but *D. merriami* was never observed making an aggressive display toward *D. microps*. It thus appears that *D. merriami* may have been able to avail itself of the bait in traps with greater facility as the night progressed because of the decrease in the activity level of *D. microps*. It follows that the social interactions of *D. merriami* and *D. microps* in this habitat should similarly influence the foraging activity for natural food resources.

Distances moved and running speeds

D. merriami moved over greater distances during the night than the other two species. On 28 occasions individual *D. merriami* (five males and six females) were trapped on two different quadrats on the same night. The minimum distances moved by these *D. merriami* were between 65 and 125 m. One male was captured once in three quadrats on the same night, representing a minimum distance of 190 m.

Although some *D. microps* moved permanently from one quadrat to another over longer periods of time, this species was trapped on two different quadrats in the same night on only one occasion. The nightly maximum distance traveled by *D. microps* was about 50 m or less, because the quadrats were 62.5 m apart and an animal living in between two quadrats would have to move only about 30 m in either direction to come upon a trap.

Individual *P. longimembris* were never caught on more than one quadrat at any time during the study. The maximum distance moved during the night by this little mouse was undoubtedly much less than 50 m. *P. longimembris* was only rarely seen in the open areas, but rather spent most of its time in or very near to bushes.

An interesting correlate of the greater range of nightly movement in *D. merriami* as compared with *D. microps* is that *D. merriami* runs about 50% faster than *D. microps*. Maximum speeds of 32 km/h for *D. merriami* and 21 km/h for *D. microps* were recorded by timing at least 12 animals of each species following their release from traps.

Effects of weather and temperature

The pocket mouse and kangaroo rats were active throughout all four quarters of the night of 5–6 May 1971, when a moderate rain fell almost continuously. However, fewer *D. merriami* were caught on this night than on a night 1 month before (Fig. 1).

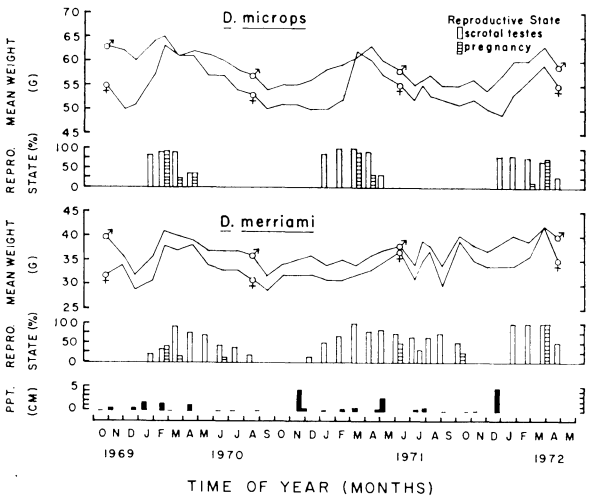

FIG. 3. Mean body weight and the reproductive condition of *D. microps* and *D. merriami* in relation to time of year and monthly precipitation. Sample sizes shown in Fig. 1. Total monthly precipitation is plotted at the date of greatest precipitation for each month; no mark is shown for months of zero or trace precipitation.

Both kangaroo rats continued their activity on the surface during a light snowfall of 3 cm between 0200 and 0600 h on 21 December 1970. Tracks were common in the powdery snow, and signs of digging through the snow and into the loose sand below were apparent.

The lowest levels of activity in winter were on nights following storms, when the surface was already wet and then became frozen hard at night. Such nights were not necessarily the coldest nights of winter.

Dipodomys microps and *D. merriami* were both active at temperatures as low as −19° C (the lowest recorded), when the soil was dry and loose. On one occasion two *D. microps*, following their release from traps, sand-bathed in soil that was −15° C. *P. longimembris* was active at temperatures as low as −10° C.

All three species were active in summer at temperatures as high as 30° C (the highest recorded during activity period), at which the relative humidity was only 15%.

Effects of a flood

The effects on the animals of a small flash flood were studied by the usual trapping routine on 22 July 1971 (Fig. 1), 5 days after a cloudburst in nearby mountains brought torrents of water as deep as 50 cm through the study area. As much as 30 cm of new sediment were deposited in places, and small pools of water remained for a week following the flood. The aggregations of the seed-bearing bracts of *Atriplex* that had accumulated in pockets at the edges of hillocks were virtually all washed away or covered. Many burrows were heavily damaged.

The carcass of one of the marked *P. longimembris* was found washed into a shrub at 40 cm above the ground. At 1000 h on the morning following the flood a *D. microps* was seen hopping around a large hillock that was partially surrounded by water.

The greatest apparent immediate effect of the flood was the 23% reduction in the number of *D. microps* trapped as compared with the number trapped 9 days before the flood (Fig. 1). However, the numbers of *D. merriami* and *P. longimembris* trapped did not change much from the previous trapping period. Because trapping success is a function of both the size of the population and the amount of activity of its individuals, one should expect that these two factors would have opposite effects on trapping success under the conditions of this environmental perturbation. Thus the immediate mortality from the flood could not be determined precisely. It is noteworthy, however, that in spite of the great destruction in the habitat, so many animals actually did survive.

TABLE 1. Mean body weight of *D. microps* (n = 896, representing 157 individuals) and *D. merriami* (n = 392, representing 74 individuals) for measurements over a 31-month period

	Mean weight (g)	SE
D. microps		
both sexes	56	0.42
males	58	0.25
females	54	0.27
D. merriami		
both sexes	35	0.20
males	36	0.22
females	33	0.32

BODY WEIGHT AND REPRODUCTION

Dipodomys microps *and* D. merriami

The body weight of *D. microps* is about 1.6 times that of *D. merriami* (Table 1). The males were significantly heavier than the females in both species ($p < .001$). Mean body weight for the populations of *D. microps* and *D. merriami* fluctuated considerably throughout the year (Fig. 3). Peaks in body weight of both males and females occurred at the times of greatest reproductive activity. Body weights of males and females differed least when females were pregnant.

Cycles of body weight and reproduction were often asynchronous in the two species. For example, in the spring of 1971 *D. microps* had passed its reproductive peak and begun to decline in body weight by May 5, but *D. merriami* had not yet reproduced and was still increasing in body weight (Fig. 3). Following rains of about 2.5 cm in the 1st week of

May (Fig. 3), there was a great proliferation of previously germinated annual plants and also considerable new germination. By the beginning of June the body weight of *D. merriami* had increased further and some of the females were pregnant. This pattern of body weight and reproduction in *D. merriami* appears to be related to the increased productivity of annual plants resulting from the late rain.

It has been pointed out that green vegetation is a requirement for reproduction in desert heteromyids (Beatley 1969, Bradley and Mauer 1971). The source of green vegetation for *D. microps* is the leaves of perennial shrubs (Kenagy 1972, 1973); for *D. merriami* it is annual herbs. Cycles of reproduction and body weight in *D. microps* and *D. merriami* reflected the cycles of these two different sources of green food. The leafing-out of existing shrubs in late winter and early spring is far more regular and predictable from year to year than the germination and growth of annual forbs. The reproductive period of *D. microps* was short, well defined, and consistent from year to year, whereas that of *D. merriami* was attenuated and "on standby," and responded rapidly to the erratic occurrence of favorable conditions at any time from late winter through early autumn.

The reproductive readiness of both *D. microps* and *D. merriami* in late December or January favors the possibility that under optimum conditions the females can become pregnant by mid- or late winter, and therefore that the juveniles can appear on the surface by spring and complete their maturation before the severity of summer weather reduces the quality and quantity of non-seed items of food required for growth.

Some of the changes in mean monthly body weight of *D. microps* and *D. merriami* (Fig. 3) can be attributed to changes in population structure. However, marked changes did occur in all individuals as well (Fig. 4). Therefore the changes of weight in individuals were largely responsible for the seasonal fluctuations in body weight measured for the population as a whole.

Perognathus longimembris

Body weight of 22 *P. longimembris* captured near the study quadrats in spring and summer ranged from 6.3 to 8.0 g (mean 7.1, SE 0.11). Males and females did not differ significantly ($p > .05$).

Although the determination of reproductive status of live *P. longimembris* by external examination was difficult, some general observations can be made. Males appeared earlier than females in the spring, and testicular enlargement was apparent within several weeks of emergence. Females showed signs of vaginal activity (opening, swelling, bleeding) from shortly after the onset of activity in spring until September or October. Thus the reproductive pattern of this species resembles that of *D. merriami,* rather than *D. microps.*

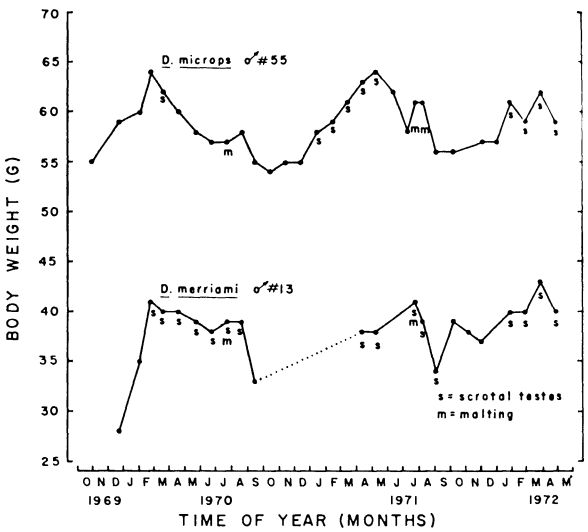

FIG. 4. Body weight, reproductive state, and molt in an individual, free-ranging, male *D. microps* and *D. merriami* captured at intervals over a 31-month period.

Molt cycle

All three heteromyids molted in July and August, as exemplified by two male kangaroo rats shown in Fig. 4. The energetic requirement for molt is undoubtedly less than that of reproduction, but slight increases in body weight appear to correlate with the molting process as well (Fig. 4). The synchrony of molting time from year to year and among the three species suggests that this process may operate largely under photoperiodic control with little modification by other environmental factors.

BURROW SYSTEMS

The burrows of 25 *D. microps*, 15 *D. merriami,* and 20 *P. longimembris* were located after animals had been tagged with radioactive gold wires. The behavior of these animals in their burrows was followed for at least a week in most cases, in May–August 1970, December 1970, and January, April, and September 1971. Burrow systems were usually excavated at the end of an observation period, but some burrows were left intact, allowing the observation of five *D. microps* and three *D. merriami* in their original burrows at a later season.

Occupation of burrow sites

Most of the few animals released in the morning did not enter their normal burrows; instead, they

TABLE 2. Physiognomic characteristics of the burrow sites of *D. microps*, *D. merriami* and *P. longimembris*. Average breadth of each hillock was calculated as the diameter of a circle with area equal to the product of the maximum and minimum horizontal dimensions of the hillock

	D. microps		*D. merriami*		*P. longimembris*	
	Mean	SE	Mean	SE	Mean	SE
Mean height of hillock	67cm	(5)	40cm	(3)	33cm	(2)
Mean breadth of hillock	2.5m	(0.1)	1.8m	(0.1)	1.1m	(0.1)
Mean maximum shrub height	85cm	(5)	56cm	(8)	42cm	(7)
Number measured	25		15		19	

often remained during the whole day in the first available tunnel into which they could escape. Their true home burrow could be determined only on a subsequent day. Therefore, the usual procedure was to tag and release the animals by midnight on the night of capture, and then to search for them the next morning. Under such circumstances the burrow occupied on the following morning always turned out to be a home burrow of the tagged individual. None of the burrow systems examined contained more than one adult animal.

In summer and early fall some individuals, both male and female, of each species occupied as many as two or occasionally three separate home burrows, within about 10–20 m of each other. Some of these individuals, which were observed for up to 3 weeks, spent 1 to 3 days in one burrow and then shifted to another. None of the individuals ever used more than three separate burrow systems. The *D. microps* and *D. merriami* observed in late fall, winter, and spring each occupied only one burrow system, in which a nest was constructed.

Physiognomy of burrow sites

Differences in height and breadth of burrow hillocks and maximum shrub height on the hillocks were tested (at $p < .05$) among the three species of rodents (Table 2). The three parameters were largest for *D. microps* and smallest for *P. longimembris*. One *P. longimembris* occupied a burrow lacking any shrub cover. *Dipodomys microps* differed significantly from both *D. merriami* and *P. longimembris* in all three burrow site parameters. The differences in both height of hillocks and height of the shrubs were not significant between *D. merriami* and *P. longimembris*, but the difference in horizontal expanse of the burrow system was significant.

The dominant shrub species on 76% of the hillocks of *D. microps* was *Sarcobatus vermiculatus*. *Atriplex confertifolia* was the dominant shrub on 54% of the hillocks of *D. merriami* and 58% of the hillocks of *P. longimembris*. No other shrub species were dominant on more than 15% of the hillocks of any of the three rodent species. That *Sarcobatus* was the most common shrub on the hillocks of *D. microps* reflects the fact that larger hillocks are formed at the bases of *Sarcobatus* than of any other shrub species at the study area.

Tunnels and resting areas

Tunnel diameters vary throughout the burrow systems. Tunnels may become enlarged through wear or general deterioration, but the animals also enlarge certain areas—"resting chambers"—up to twice or three times the diameter of adjacent sections of tunnel. Several resting chambers were located in all burrow systems and corresponded to the positions at which animals were determined by radioisotopic tracking to locate themselves most often in spring, summer, and early fall.

The tunnels of *D. microps* were mostly 6–8 cm diameter, but occasionally as narrow as 5 cm, in firm, moist soil. Most *D. merriami* tunnels were 4.5–6 cm diameter, but some were as narrow as 3.5 cm. *Perognathus longimembris* had tunnels about 2 cm diameter, occasionally as narrow as 1.5 cm.

Tunnels and chambers of the smaller species were nearer to the surface than those of the larger species. The minimum thickness of soil above resting areas was about 8 cm for *D. microps*, 5 cm for *D. merriami*, and only 1 cm for *P. longimembris*. This pattern is in part determined by the greater friability of the soil at shallower depths and the greater probability that a smaller tunnel can be maintained under the given conditions for a longer time without being caved in.

Fresh soil was commonly brought to the surface by the rodents following rains and snows—rarely at other times. It appears that the firmness of the moist soil would optimize the permanency of new tunnels constructed at that time, partly because each species can construct narrower tunnels in firmer soil. By the end of summer, when the soil was driest, some of the shallowest surface tunnels of *P. longimembris* had usually caved in.

Despite the loose sandy soil in which they were dug, most burrow systems—especially those of kangaroo rats—were probably somewhat older than their occupants. In the deeper parts of burrows, abandoned nest chambers, with dust and in some

FIG. 5. Nest of *D. microps* at 40 cm depth, seen in a partial excavation of the burrow, showing the tunnel leading to the single entrance. Nest is 16 cm wide.

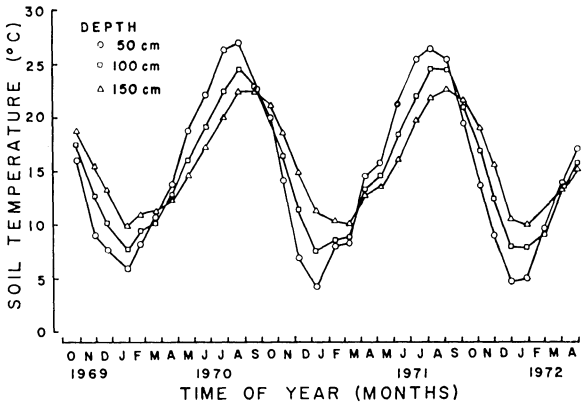

FIG. 6. Soil temperatures near Big Pine, California, recorded over a 31-month period.

cases deposited sediment mixed in with old litter, were found near to currently used chambers or storage areas.

Dipodomys microps had caches of *A. confertifolia* leaves as large as 150 g in storage chambers (Kenagy 1973). However, major caches of seeds were not found in the burrows of any of the three species.

Nests

All *D. microps* tagged in the winter of 1970 were located and found to occupy neatly constructed nests. Mean depth of the nine nests (to middle of the nest) was 40 cm (range, 24–45).

Only four of 12 tagged *D. merriami* were located, and each of these animals occupied a nest. The depths of these nests were highly variable: 26, 50, 140, and 175 cm (mean 98). The two deepest nesters were located only by chance when they happened to be near the surface; the gamma-ray emission of their tags was beyond the range of detection when these two animals were in their nests. The failure to detect eight of the tagged *D. merriami* indicates that the nests of most of these individuals were deeper than 1 m.

The globular nests of the kangaroo rats fit snugly into the nesting chambers, and there was only one entrance to each nest (Fig. 5). Animals rested in the middle of the nests. Nests of *D. microps* were almost exclusively constructed of the ricegrass *Oryzopsis hymenoides*, the only common grass in the area. This was also the predominant structural constituent of the nests of *D. merriami*, but they also contained a great variety of smaller material packed in between the grass blades, such as the woolly flower parts of *Eurotia lanata* and *Tetradymia axillaris*. The nest of one *D. merriami* contained about 100 feathers.

Variation in nest dimensions among individuals of the same species was within the range of 1 cm. The nest of *D. merriami* filled the entire nest chamber (10 cm wide × 9 cm high), except for a small amount of litter in the bottom. The nest proper of *D. microps* filled approximately the top 13 cm of the 17-cm-high cavity, and was 16 cm wide. The bottom portion of the chamber was stuffed with the discarded surface tissue of *A. confertifolia* leaves in amounts as great as half a kilogram (Kenagy 1973); consequently, the nest chamber of *D. microps* was higher than it was wide. All nests were fresh smelling and contained little or no urine and feces. The nests of *D. microps* weighed from 59 to 75 g (mean 65) and those of *D. merriami* were 37–53 g (mean 44).

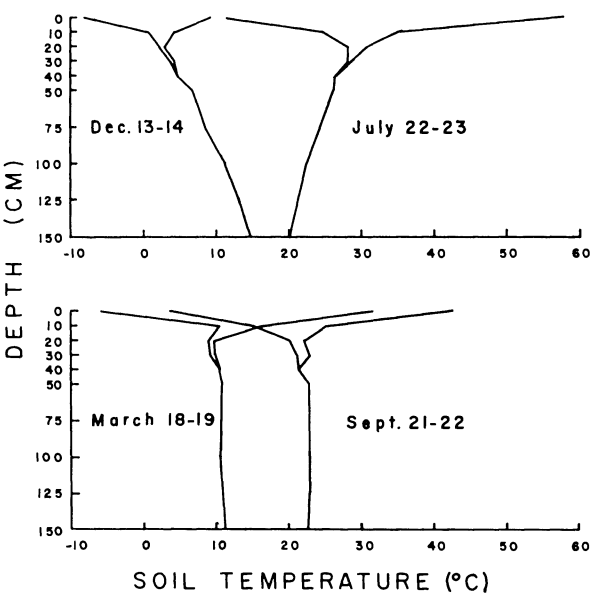

FIG. 7. Profiles of soil temperature near Big Pine, California, during four selected 24-hour periods in 1970. Pairs of lines enclose the range of 24-hour fluctuation in temperatures near the surface. Lines connect temperatures measured at each of the depths indicated on the vertical axis.

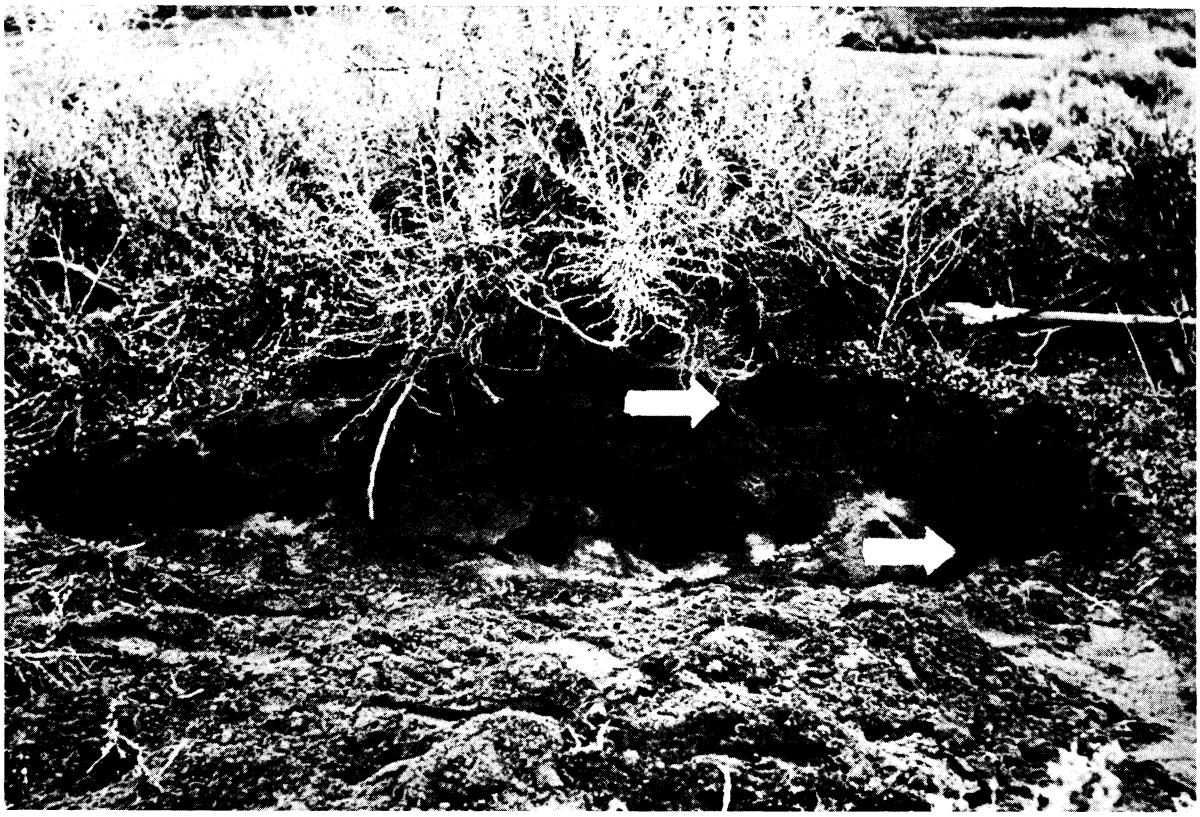

FIG. 8. A cross section of the dissected burrow system of a male *D. microps* whose behavior was observed in the same burrow system in both late spring and winter. The usual resting chamber occupied by the animal in May is indicated by the upper arrow. The location of the animal in its nest (behind several centimeters of sand) during the course of the excavation in December is indicated by the lower arrow, directly below the Geiger-Müller tube.

Two abandoned nest cavities of *P. longimembris* at 52 and 65 cm depth were located in the summer as part of other excavations. Each of these two unoccupied chambers were 8 cm wide and 5 cm high, and contained a loose bed mainly of dry roots and leaves.

SUBTERRANEAN BEHAVIOR IN RELATION TO SOIL TEMPERATURE

The location of rodents in their burrows was associated with three kinds of changes in the temperature of the soil: (1) seasonal changes, (2) daily changes in the vertical profile of temperatures, and (3) daily changes in the horizontal pattern of temperatures.

Daily and seasonal thermal regimes

Seasonal changes in soil temperature were profound (Fig. 6). Annual amplitude of temperature change decreased with depth, but was still as great as 13.6° C at 150 cm. Soil temperatures were vertically uniform twice a year, and also reached maximum gradients—each of opposite direction—twice per year (Fig. 7). Vertical uniformity of soil temperature was reached at about the time of the equinoxes, but the temperatures of these thermally uniform columns of soil differed by more than 10° C in spring and fall (Fig. 7). The steepest gradient of winter occurred before the coldest temperatures of winter, and the steepest gradient of summer occurred before the warmest temperatures of summer. Finally, the daily range of temperatures decreased with depth, generally being less than 1° C at depths greater than 40 cm (Table 3).

The daily maxima (Fig. 7) did not occur at the same time at each depth, nor did the daily minima. For example, in summer the daily maximum at 10 cm usually occurred at or before sunset, whereas the daily maximum at 20 cm often occurred 2–3 h after sunset.

In winter the heat flux per unit area into the south-facing slope of a hillock was much greater than into a nearby flat surface, because of the angle of incident radiation. In summer the heat flux per unit area into the slope was slightly less than in the flat, because of the angle of incident radiation and the

TABLE 3. Magnitude of daily fluctuations in temperature in the upper 50 cm of soil. Values are based on 45 24-hour periods over a 31-month period

Depth	Maximum ° C	Minimum ° C
surface	51.6	5.0
10 cm	15.3	< 1
20 cm	3.3	< 1
30 cm	2.6	< 1
40 cm	1.2	< 1
50 cm	< 1	< 1

shading by shrubs on the hillock. This phenomenon was observed by simultaneous measurements of profiles of soil temperature on the south-facing slope (45°) of a hillock and on a flat for a 24-h period in late January and again at the same locations in late July of 1971. In winter the maximum temperatures at 10 cm were 12.0° C on the hillock but only 32.2° C in the flat. In summer the maxima at 10 cm were 30.0° C on the hillock and 32.2° C in the flat.

Summer behavior

The depths occupied by all three species were more similar to each other in summer than at any other time. In late June, July, August, and mid-September, the resting depths of all three species were generally 20–30 cm, at locations where the temperatures were 26–30° C. Temperatures at 10 cm reached 40° C. An unusual hot spell made soil temperatures in mid-September 1971 not much different from those of the earlier summer. Animals rested at about 20 cm at the beginning of summer, and as the surface temperatures rose during the course of summer, the animals rested nearer to 30 cm. They did not rest in soil warmer than 30° C. Out of 50 or more measurements at each burrow, the animals were usually found at only one or two typical positions. These were the "resting chambers" or widened spots in the tunnels.

Perognathus longimembris almost always plugged tunnel entrances, *D. merriami* did so fairly often, and *D. microps* less often. A kangaroo rat was more apt to plug an entrance if it was near a favorite resting chamber.

Virtually all of the animals tagged in summer were found; at no time did any of the summer or spring animals retreat to great depths either when disturbed in their intact burrow or when the burrow was being excavated.

Winter behavior

Kangaroo rats were deeper in the soil in winter than at any other time of year (Fig. 8). Their behavior in burrows is more amenable to discrete analysis in winter because they generally rested in a single fixed position, the nest. Most nests of kangaroo rats were located on the southern exposures of hillocks; no nests were on the north sides. Nests were probably constructed in the first half of autumn, and were occupied through early spring. By April the nests of both male and female kangaroo rats had been reduced to a flat bed of trampled grass. Intact nests were therefore probably used for about 5 months.

Soil temperatures next to the nests of *D. microps* examined in December were between 4° and 6° C. Temperature at 40 cm (the average depth of the nine nests examined) was never recorded below 4° C during the winter of 1970–1971, but was recorded at 2° C the next winter. *Dipodomys merriami* were located in nests in late January 1971, when deep soil temperatures were at their winter minimum. Temperature of the soil next to the deepest nest (175 cm) was 11° C; at the shallowest nest (26 cm) it was 3° C. On some occasions in the following winters, temperatures at that depth dropped to nearly 0° C. However, the nests of most *D. merriami* in the area were probably located at greater depths and therefore warmer temperatures than those of most *D. microps*.

Diurnal vertical movements

A striking relationship between subterranean behavior and profound daily fluctuations in temperature near the surface was observed in three of the four *D. merriami* studied in winter, during several days of very warm weather. At about noon on 28, 29, and 30 January 1971 each of the three animals left its nest and spent the rest of the day in resting chambers 7–10 cm below the surface on south-facing slopes of their burrow hillocks. (In fact, we had not previously detected the burrows of the two rats with the deepest nests until these daily vertical movements occurred. The gamma-ray emissions of the tags on these two animals were never detected before 1100 h on any of the 3 days mentioned.) During this warm spell, daytime air temperatures rose to 20–25° C, temperatures of the soil surface on the south slopes of hillocks were as great as 30° C, while temperatures at 10 cm depth were as great as 17° C. Minimum daily temperatures of the air and the soil surface were about −10° C, and the temperatures at 10 cm depth fell to about 3° C. Therefore the daily fluctuation in temperature at 10 cm was about 14° C, which is nearly the maximum recorded for that depth (Table 3). By moving from their nests to the subsurface resting chambers at the appropriate time, the three animals experienced increases as great as 8° C in ambient temperature.

In early spring, diurnal vertical movements were particularly common in *P. longimembris*. Animals resting in early morning at 30–40 cm, where tem-

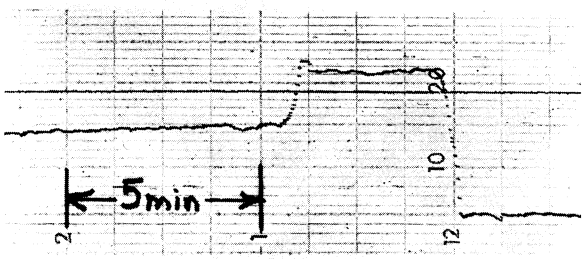

FIG. 9. Photograph of a strip-chart record of the gamma-ray emission of a radioisotopic tag on an animal. The abruptness of the changes in counting rate indicates that animals moved quickly from one discrete point to another, both in the burrow and on the surface. The changes in counting rate mark the beginning and end of "activity bouts."

peratures were 12–14° C, moved to within 1 cm of the surface by midmorning. Temperatures at the location of these animals just below the surface reached 29° C by midday, although they had been as low as 4° C in early morning.

Spring behavior

In April 1971, following the time of vertical uniformity of soil temperature in late March, all three species were the nearest to the surface of any time of the year measured. The temperatures near the surface were gradually becoming warmer for the major part of the day than temperatures at greater depths. Some individuals of each species got as close to the surface as possible during the warmest part of the day. But because the minimum depth of the tunnels or resting chambers of each species differed, the minimum resting depth of each species differed accordingly.

During the day *P. longimembris* were commonly found near 10 cm depth, where temperatures were 20–25° C. However, some individuals came as close as 1 cm to the surface.

Usually *D. merriami* were located at 10–20 cm, but some individuals were as near to the surface as 5 cm in the warmer parts of the day. *Dipodomys microps* were slightly deeper, mostly 15–30 cm, but one individual occasionally rested at 8 cm. A female *D. microps* with two young stayed mostly in the nest chamber, at 39 cm. Because the profile of soil temperature was just passing the springtime period of vertical uniformity, the temperature varied little with depth, except that the soil in the top 10 cm became significantly warmer in the daytime (e.g., Fig. 7, March 1970). Some individual *D. merriami* and *D. microps* had shallow enough tunnels and resting chambers to occupy soil that reached these warmer temperatures during parts of the day.

TABLE 4. Activity of an individual, non-breeding, male *D. microps* as registered on an automatic recording system at the same burrow in June and December 1970. A bout of activity is the time for which an animal remains in one location before changing to another (Fig. 9). Days and nights are arbitrarily divided at sunrise and sunset. These records consist of uninterrupted recordings for whole days and nights

	Daytime activity	Nighttime activity
	average bouts/h	average bouts/h
June 5	—	10.7
June 6	3.8	8.8
June 7	2.5	12.5
June 8	4.9	—
MEAN	3.7	10.7
December 17	2.4	—
December 18	1.4	4.3
December 19	2.1	4.3
December 20	1.2	4.5
December 21	—	4.9
MEAN	1.8	4.5

Diurnal horizontal movements

Some *P. longimembris* in spring showed daily patterns of horizontal movement associated with diurnal changes in the horizontal pattern of soil temperature. Two animals occupied resting chambers within 5 cm of the surface on the east sides of shrubs in late morning on 4 consecutive days. By midafternoon, when the sun's radiation was directed at the soil at the west base of the shrubs, and the original resting location of the morning had become shaded, the animals moved to the west sides of the shrubs for the rest of the day.

CONTINUOUS AUTOMATIC RECORDING OF THE AMOUNT OF DAILY ACTIVITY IN INDIVIDUALS

Although individual rodents were found at several typical locations (resting chambers or a nest) when their position was observed at intervals throughout the day, continuous automatic recordings showed that the animals made many short excursions around the burrow system during the daytime. By associating particular readings on the strip chart record with the major resting sites, and then correcting the record for radioisotopic decay over the course of the observations, I could measure the frequency of individual bouts of movements (1) within the burrow in the day and (2) both within the burrow and on the surface in combination at night. Surface and subsurface records were combined for the nighttime, because it was not possible to tell from the record whether an animal was on the surface or in the burrow. The frequent and abrupt changes in readings on the ratemeter during both day and night

(Fig. 9) were used to compile a record of the number of bouts of activity for the animals.

Nighttime activity (number of times an animal changed locations, either on the surface or in the burrow) was 2½–3 times as intense as daytime activity for a single *D. microps* studied in the same burrow in June and December (Table 4). Activity as a whole in June was 2–2½ times as intense as activity in December. Amount of activity was more variable in the day than at night. On the night of greatest activity in winter (21 December) 3 cm of snow fell between 0200 and 0600 h, during which the animal visited the surface often, as shown by many fresh tracks in the snow. As previously mentioned, other kangaroo rats were active in the snow that night as well.

Records for *D. merriami* and *P. longimembris* in May and June 1970 showed the same threefold increase in the frequency of movement at night, but activity of some individual *D. merriami* and *P. longimembris* was as much as 50% higher than for *D. microps*. In the recordings in May and June none of the three species remained motionless in its burrow for greater than half an hour at a time.

In December the maximum time that a *D. microps* (Table 4) remained motionless in its nest was 92 min, between 0700 and 0900 h on 20 December. A *D. merriami* studied on 28–30 January 1971 showed a maximum resting time of 2 h 40 min, between 0600 and 1000 h on 29 January. This *D. merriami*, a female occupying a nest at 26 cm depth where soil temperature was 3° C, showed activity levels otherwise similar to those of the *D. microps*.

Metabolism at Cold Temperatures

Insulation by nests

At 5° C in the laboratory, the metabolic rates of *D. microps* and *D. merriami* were significantly lower when they occupied nests than when they did not ($p < .01$) (Table 5). Oxygen consumption of *D. microps* was reduced 21% and *D. merriami* by 14% when animals occupied nests. Similar energy savings should accrue to free-ranging animals, whose nests are situated in soil that may drop to 5° C or a few degrees lower in the coldest part of winter.

Tolerance of animals to cold temperature

When exposed to cold air at –25° C in the laboratory, none of the three species maintained body temperature. *D. microps* were exposed for 1 h, *D. merriami* for 40 min, and *P. longimembris* for 20 min. The tails of the animals froze. Average decreases in body temperature for six animals of each species, expressed as a rate per minute, were *D. microps* 0.11° C/min (range, 0.07–0.16); *D. merriami* 0.3° C/min (0.2–0.4); and *P. longimembris* 0.9° C/min (0.5–1.2).

TABLE 5. Resting metabolism of *D. microps* and *D. merriami* in the laboratory at 5° C with and without natural nests

	Oxygen consumption ($ccO_2/g \cdot h$)			
	Without nest		With nest	
	Mean	SE	Mean	SE
D. microps (n = 6)	3.08	0.12	2.44	0.11
D. merriami (n = 6)	3.76	0.11	3.24	0.12

In the field *P. longimembris* was not active on the surface at temperatures below –10° C. The activity of *D. microps* and *D. merriami* never became totally inhibited throughout the range of measured temperatures down to the minimum of –19° C. Kangaroo rats should be able to forage on the surface at –25° C or lower, as long as they are on the surface for only a few minutes at a time.

Winter Inactivity and Torpidity in *P. longimembris*

The extent of winter activity in the population of *P. longimembris* was different in each of the three winters, ranging from zero to 5 months of inactivity (Fig. 1); but the lowest level of activity in the winter of 1969–70 and the midpoint of inactivity in the following two winters corresponded roughly to the winter solstice. At all times of year, activity was very low in the last quarter of the night (Fig. 2); and during the coldest times of the year at which pocket mice were active, none at all were trapped in the last quarter of the night.

The success of the population at surviving through the winter diminished in each of the 3 succeeding years. For this determination the starting population level included all animals caught during the last 2 months prior to minimal activity in 1969 and prior to inactivity in the next two winters. The numbers of animals surviving in spring were 82%, 56%, and 36% the original autumn populations for each of the 3 years. The original numbers of animals for each of the 3 years were 27, 25, and 11. Therefore percentage overwintering success was directly related to the absolute size of the population.

During 1969–70, the year of greatest survival (82%) and of largest population (27) *P. longimembris* were active all winter (Fig. 1). That winter the food supply was greater than during the following two winters. Precipitation during the season prior to the first winter was three times normal, and plants produced a prolific crop of seeds, which was

available in abundance throughout the winter. The most abundant annual in 1969, *Eriogonum deflexum,* virtually did not germinate in 1970 and was uncommon in 1971. In these latter 2 years rainfall was 60% normal. Therefore the amount of food available to *P. longimembris* was directly related to (1) the size of the population, (2) the extent of activity in winter, and (3) the percentage of the population surviving through the winter.

Winter habits

The winter behavior of pocket mice was observed in small field enclosures since natural winter burrows of the animals had not been located in the earlier studies. On 29 August 1971 six *P. longimembris* were captured about 1 km from the study site, kept in a nearby house in laboratory cages during the following daytime, and provided with 10 g bird seed. On the following evening the animals were introduced into the individual wire-mesh enclosures (see methods) at the study site, along with the seed remaining in their cages and an additional 10 g ration. By the next morning three animals had disappeared below the surface and had removed all seed from the surface. The other three animals, which were still on the surface, were returned to the house in cages along with the seeds that remained on the surface. On the second evening the latter three animals and their food were again taken to the enclosures after a small tunnel was prepared with an auger in each enclosure. An additional 10 g seed was provided at 2200 h to all six animals. By the following morning all animals remained in tunnels in the ground during the day. Three animals had left some seeds of the surface, but the soil around their enclosures was sprayed with a commercial insect spray to restrain ants from removing seeds until the mice subsequently cached them in their burrows.

Within the first several days of the introduction of the animals into the enclosures, mounds of soil appeared at the surface, indicating extensive burrowing activity. By 22 September, 130 g of whole seed had been provided to each mouse, and the mice had removed all the seed from the surface. On that date animals 1, 2, and 3 were given 40 g dry grass stems (*Oryzopsis hymenoides*) as nesting material.

Five of the six mice behaved similarly throughout the winter. They remained underground continuously for 4–4½ months, and eventually returned to the surface between 2 and 16 March. After an additional 65 g seed was placed in each enclosure on 4 November, it remained on the surface in the enclosures of these five animals until the spring emergence, and there were no breaks or other disturbances in the soil surface during the interim.

One of the six mice (number 1) differed from the others in its behavior. It removed the 65 g seed provided in November as well as an additional 80 g provided on 1 December. However, by 30 January 1972 it had not removed an additional 5 g provided on 20 December, and the soil surface had become weathered and appeared undisturbed. The entire enclosure of animal number 1 was excavated and the live animal and other contents of the burrow were removed on 30 January. This animal had been exclusively underground for only about 6 weeks.

All six animals constructed nests, mainly out of old roots and leaf mulch gleaned from the soil within the enclosures. Five of the six mice constructed their nests within 5 cm of the bottom of their enclosures, i.e., at about 75 cm depth. Animal number 1 constructed its nest only 8 cm below the surface, and had no tunnels deeper than 40 cm. The nest of animal number 1 was also exceptional in that it was principally made from ricegrass, whereas the other five nests—including those of animals 2 and 3 which were also provided with ricegrass—essentially lacked grasses.

The nests were globular and filled the nest chambers, which were about 8 cm wide and 5 cm high (corresponding to the dimensions of the two natural nest chambers discovered in previously mentioned excavations). There was a small amount of litter—hulls and a few seeds—at the bottom of each nest. Each of the five deep nests contained a few of some of the common nest parasites of the local heteromyids (flies, crickets, beetles—including larvae—and scorpions), even though the burrow systems were nonexistent before September. A noteworthy characteristic of some of the deeper tunnels, at 30–60 cm, is that they were nearly vertically oriented in some places, for lengths as great as 20 cm, over which the diameter of the tunnel was only 1.5 cm. Disturbances in these areas of the burrow system, as would naturally be made by some predators, result in immediate filling in of the tunnels with soil.

The voluntary emergence of animals 2–6 in March was apparent from the sudden and total disappearance of the 65 g ration of seeds, which had remained on the surface since 4 November. Within the first 2 days of emergence, fresh soil was pushed out from newly constructed tunnels near the surface, and a well-worn pathway appeared on the surface around the rim of the enclosure. The entire contents of enclosures 2–6 were excavated within several days of the emergence of each mouse. Only 50–60 g of seed were recovered from each enclosure. This was obviously primarily the remains of the 65 g seed that had stayed on the surface between 4 November and the date of emergence, at which time the mice had removed it to their burrows. This observation indicates that all or almost all of the useful winter

TABLE 6. Seed consumption of *P. longimembris* in field enclosures near Big Pine, California. Predicted seed consumption is derived by integrating Equation (1) over the soil temperatures available to the animals. Body weight is an average of weight at beginning and end of experiment. See text

Animal number	1	2	3	4	5	6
Sex	M	M	F	M	M	F
Body weight	7.5g	7.5g	7.7g	7.8g	7.3g	7.3g
Days (30 August through date of emergence)	154	190 ± 2	197 ± 2	185	185	197 ± 2
Actual seed consumption (mg/g·day)	197	81	76	80	85	80
Predicted seed consumption for normothermia (mg/g·day)	314	288	289	287	287	289
Percentage of normothermic requirement used	63	28	26	28	30	28

seed supply had been exhausted by the date of emergence of each animal. The useful winter seed supply was therefore 130 g, which does not include the 65 g that remained on the surface during the winter. For purposes of the calculations presented in the following section, the seed consumption by each of animals 2–6 between 30 August 1971 and the date of emergence in March 1972 was therefore 115 g (that is, the original 130 g seed, less 15 g chaff).

Seed consumption and torpidity

Laboratory measurements provided for further interpretation of the field data. The seed consumption as a function of ambient temperature for *P. longimembris* existing at normal body temperatures in the laboratory is described by

$$S = -9.37T + 408 \qquad (1)$$

where S is seed consumption in milligrams per gram of body weight per day and T is the ambient temperature in ° C. This equation was derived by a least squares linear regression ($r = 0.95$) of seed consumption on ambient temperature for at least eight normothermic animals each at 5° C, 15° C, and 25° C.

The seed required to maintain normal body temperature was calculated for each of the six mice in field enclosures on the basis of their average body weight by integrating Equation (1) over the soil temperatures in the field enclosures from September through the time of the emergence of each animal. It was assumed that animals 2–6 existed at the warmest available ambient temperatures throughout the study, but that animal 1 existed at the colder temperatures associated with its shallow nest. The amount of seed actually consumed was compared with the calculated normothermic requirement (Table 6). The animals ate much less seed than was required to maintain normothermy. This suggests extensive use of hypothermia as an energy-conserving mechanism. The percentage of the normothermic seed requirement actually used (Table 6) offers an index to the amount of time spent in torpor by the animals. The true normothermic values of seed consumption for animals in the field enclosure should probably be higher than those derived from Equation (1), because the mice in the enclosures spent considerable energy on maintenance functions such as building tunnels and nests. Therefore the actual seed consumption was probably even a lower percentage of the true normothermic seed requirement than of the calculated requirement. The rates of seed consumption in Table 6 are averages for periods slightly greater than 6 months, except that that of animal 1 is for 5 months. Because maintenance activity was greater and the use of torpor probably less frequent and less profound during the first 1–2 months, it is certain that the minimal daily rates of seed consumption for the middle of winter were considerably below the average values shown in Table 6.

P. longimembris in the laboratory also ate less seed than was required to maintain normothermy, but the use of torpor varied greatly (Tables 7 and 8). Although most of the pocket mice in the laboratory did not save as much over the normothermic rate as did the mice in field enclosures, one laboratory animal (Table 7) used only 6% of its normothermic requirement, which was the greatest savings of any animal in either the field enclosures or the laboratory. This animal was torpid every day during 59 days of observation, and its bouts of torpor most frequently spanned 3 days (Table 8).

The laboratory mice varied considerably in the length of individual bouts of torpor (Table 8). Six of the ten were observed at least once in the same bout of torpor for 4 consecutive days, and two of the ten were never observed in torpidity while food was available. There was no direct relationship between individual, modal lengths of bouts and total energy saving. Animal number 4, which showed the greatest frequency of 4-day torpor bouts (Table 8), was outranked in total energy saving by three other animals (Table 7) that more frequently employed bouts of torpor lasting 3 days or less. The mouse with the greatest energy saving (Table 7) was among those which most frequently employed 3-day (i.e.,

TABLE 7. Seed consumption of *P. longimembris* in the laboratory at 6.5° C. Animals are ranked according to percentage of normothermic seed requirement used. Predicted seed consumption for normothermia at 6.5° C [from Equation (1)] is 347 mg/g·day. All animals received a total of 117 grams of edible seed, consisting of small amounts provided at short intervals over the first 19 days, and a final single ration of 71 grams. Some animals consumed all of the seed in less than 77 days; others had a surplus at the end of 77 days. Animals were removed and weighed when they had consumed their seed ration. Animals were in constant darkness from day 16 through the end of the experiment. Text gives further details

Animal number	Days on seed ration	Seed consumption (mg/g·day)	Percentage of normothermic requirement used
1	77	20	6
2	77	67	19
3	77	109	31
4	77	131	38
5	77	138	40
6	77	199	57
7	74	208	60
8	75	218	63
9	47	286	82
10	48	316	91

48–72 h) bouts of torpor (Table 8). Although it is now known that *P. longimembris*, as well as several other small heteromyids (Brown and Bartholomew 1969, Brower and Cade 1971), employ bouts of torpor longer than 24 h, the regulation of the length of these periods in terms of optimizing energy expenditure is not well understood.

TABLE 8. Frequency of torpor bouts of 1, 2, 3, and 4 continuous days in *P. longimembris* in the laboratory. Data are from the 10 animals shown in Table 7. The observations include only days 19–77; on day 19 the final single ration of 71 g seed was given to each animal. Some animals consumed the ration before the end of the observation period, as indicated by footnotes. Table 7 and text give further details

Animal number	Duration of torpor (days)				Total days of torpor
	1	2	3	4	
1	5	7	12	1	59
2	14	9	5	1	51
3	14	19	4	1	50
4	4	1	2	6	36
5	6	5	5	3	43
6	7	3	2	2	27
7	29	4	0	0	37 (56)[a]
8	14	4	1	0	25 (57)[a]
9	0	0	0	0	0 (29)[a]
10	0	0	0	0	0 (30)[a]

[a] Indicates total days of observation, when less than 59.

GENERAL DISCUSSION

The energy metabolism of rodents under laboratory conditions has been extensively studied, but how rodents regulate the acquisition and expenditure of energy under natural conditions has received relatively little attention. To understand the energy relations of a species one must know the magnitude and duration of displacements in the metabolic rate from the minimal resting rate. The magnitude of the change is related to body weight and ambient temperature, and its duration is related to the activity pattern of the species.

Pocket mice and kangaroo rats spend most of their lives in the ground. Although temperature extremes in the soil are not as great as those on the surface, they still offer a broad range of conditions, some of which cannot be tolerated by the soil-inhabiting rodents. *D. microps*, *D. merriami*, and *P. longimembris* occupy positions in the soil which are generally at the nearest of available temperatures to the lower end of thermal neutrality. In midsummer, when daytime temperatures in the upper tunnels reached 40°–50° C, the animals occupy deeper tunnels during the daytime, avoiding parts of their burrows above 30° C. It is known that the physiological capacity of heteromyid rodents to withstand temperatures above thermoneutrality is not great (Dawson 1955, Carpenter 1966, Chew et al. 1967). The use of nests for as much as 5 months, during the colder part of the year, serves to minimize the obligate increase in metabolic expenditure at lower ambient temperature. The duration of the nesting season, size of nests, and depth of the nests in the ground—among other aspects of thermoregulatory behavior—may vary over geographic and climatic gradients.

The correlation in the present study between soil temperature and the location of animals demonstrates the operation under natural conditions of a precise selective capacity. The laboratory studies of Herter (1936) first showed that rodents select a preferred resting temperature when offered a wide spectrum of available temperatures. Rodents sense heat primarily through the feet (Smith and Fisher 1956), and thus these animals have immediate sensory input of environmental temperature as they move through their burrow systems. The temperature-selection behavior of rodents has obvious value in minimizing excursions of the metabolic rate beyond the minimal rate at thermoneutrality.

The response of heteromyid rodents to the physical conditions of their burrows should not be considered a unique adaptation to the desert. In fact, the regime of temperature and humidity to which these burrow-dwelling desert rodents are subjected is similar to that of mesic habitats. Thus the "harshness" of the desert environment lies not in the direct effects of heat and aridity on the bodies of nocturnal, burrowing rodents, but in correlates of heat and aridity which are less proximate to the animals—namely the temporal and spatial scarcity of plant life, the

primary food source. Ecological specializations for sequestering sparse and ephemeral food resources, and thus for minimizing the time spent out of the burrow, have therefore been a major avenue of adaptation for rodents inhabiting the deserts.

The energetic cost of acquiring more energy varies throughout the year with changes in such factors as the amount of food available and the ambient temperature at which animals must forage on the surface and rest within their burrows. The relative effects of cold weather are more profound for smaller species in this regard. For example, in the species studied the weight-specific resting metabolism is greater at 5° C than at thermoneutrality by the following factors: *D. microps* 2.7 times, *D. merriami* 3.1 times, and *P. longimembris* 4.6 times. [These factors are derived from the available metabolic data on *P. longimembris* (Chew et al. 1967), *D. merriami* (Carpenter 1966), and *D. microps* (Carpenter's data for *D. agilis*, which is similar in weight to *D. microps*).] Thus the total resting metabolism of *P. longimembris* at thermoneutrality is one-fourth that of *D. microps*, even though body weight is only one-eighth; but at 5° C the total resting metabolism of the little mouse becomes half that of the kangaroo rat, which weighs eight times as much. Therefore in winter, as costs of maintenance increase and availability of food decreases, the cost-benefit ratio of foraging increases for heteromyids, most profoundly for *P. longimembris*. This rationale can be used to explain the winter decrease in activity in all three species studied, epitomized by the total inactivity of *P. longimembris* during two out of three winters and the accompanying use of physiological dormancy as an energy-conserving strategy. It has been observed that *P. formosus* in Nevada are less active in winter than in summer (French et al. 1966), but it was not shown whether this species becomes continuously fossorial.

Decreases in activity are associated with decreases in temperature on not only a seasonal (Fig. 1) but also a daily (Fig. 2) basis. *D. merriami* is an exception to the pattern of decreased activity with decreasing temperature during the course of the night (Fig. 2); this species thereby avoids aggressive encounters early in the evening with *D. microps*, which is strongly active at that time and is socially dominant over *D. merriami*. With regard to cold-weather activity in general, the laboratory measurements of temperature tolerance suggest that kangaroo rats, particularly larger species, should be able to forage at –25° C or lower, as long as they are on the surface for only a few minutes at a time. Thus a homeostasis of body temperature can be maintained under a wide range of macroenvironmental conditions, simply by limiting the time of exposure to an environment in which steady-state maintenance is impossible.

Seasonal fluctuations should be expected in the baseline of metabolic expenditure in each species; this is suggested in part by the large seasonal fluctuations in body weight of kangaroo rats (Fig. 3 and 4). It is not understood to what extent these fluctuations are associated with reproductive output and to what extent with seasonal acclimatization. It is well known that daily fluctuations also occur in the metabolism of animals (Aschoff and Pohl 1970).

The ecological context in which animals behave is an important determinant of the amount of their activity. No broadly acceptable generalization has been made regarding amount of "activity" measured in the laboratory as a function of ambient temperature. Some species show greater activity at lower temperatures; other species show less (Aschoff 1962, Hart 1971). Pohl (1968) has presented data that show different activity patterns in dormice (*Glis glis*) according to the type of "activity" outlet available in a cage. Animals with running wheels increased activity with decreasing ambient temperature, but half of the animals in spring-suspended cages without running wheels decreased activity with decreasing ambient temperature, and furthermore became torpid. "Activity," as studied in the laboratory, is a function of many artifacts, including ad libitum food supply, and therefore ecological interpretations are generally impossible. Under laboratory conditions animals do not regulate their activity on the basis of the cost-benefit analysis that occurs in nature, where both the availability of food and the physical conditions for foraging are taken into account.

In a field study of a rodent community in California coastal scrub where rainfall and thus productivity were greater and climate was milder than in the Owens Valley area of the present study, MacMillen (1964) found that activity was greater in winter than in summer. This is the opposite of my findings, and exemplifies reversed seasonal trends in activity in two different habitats as a function of different regimes of climate and productivity. Thus, in an ecological context, there is not necessarily a uniform seasonal response for rodents in general to the lower temperatures of winter.

Kangaroo rats and pocket mice are fairly sedentary animals and do not run or walk for sustained periods of time. They move abruptly from one location to another (Fig. 9), both on the surface and in their burrows. The running speeds of kangaroo rats measured in the present study are an order of magnitude greater than those measured in laboratory studies (Taylor et al. 1970, Yousef et al. 1970). Bipedal lizards can also run at speeds near 30 km/h (Belkin 1961). Kangaroo rats and pocket mice may walk on

all four feet, but faster movement is bipedal in kangaroo rats (Bartholomew and Caswell 1951, Bartholomew and Cary 1954). Movement in underground tunnels is probably largely quadrupedal, but small kangaroo rat species, such as *D. merriami*, could employ slow bipedal hopping. Assuming a locomotion time of 5 sec for each time an animal changes position both on the surface and within the burrow, a single *D. microps* (Table 4) spent an average of 13 min moving around per day in June, but only 7 min per day in December. The time spent running and walking is therefore probably no greater than 15 min per day, which means that the increase of resting metabolic rate to the locomoting rate generally occurs over less than 1% of the day. No estimate is presently available of the energetic expenditures for extracting and processing food and for digging in the burrow.

A fourfold increase was measured in the metabolism of running *D. spectabilis* (mean weight = 100 g) over the resting metabolic rate (Taylor et al. 1970); for *D. merriami* the increase was as great as eightfold (Yousef et al. 1970). The metabolic rate of *P. longimembris* at 5° C was 4.6 times the minimal rate (Chew et al. 1967), but data on the metabolic increase of this species while running are not available. Scopes of metabolic rate as great as 8 times the resting metabolism are known in other rodent taxa (Wunder 1970, Hart 1971). The relationship between the metabolic expenditures for activity and for thermoregulation at cold temperatures are not clear for small mammals (Wunder 1970, Yousef et al. 1970, Hart 1971). However, because the total daily time locomoting is brief in heteromyids, the total energetic cost of locomotion is low relative to other expenditures. This contrasts with larger and more mobile animals that locomote for sustained periods of time and therefore undergo greater daily costs for locomotion relative to their total energy expenditure (Tucker 1970).

Energy conservation through dormancy

The strategies of energy expenditure discussed so far have involved regulation of the displacements in metabolism above the resting level. But an important strategy of energy conservation used by *P. longimembris* is that of physiological dormancy, or torpidity (Bartholomew and Cade 1957), in which metabolic rate may drop to 3% of the resting rate (Chew et al. 1967). Moderate hypothermia has been induced in kangaroo rats in the laboratory by removing food (Dawson 1955, Carpenter 1966, Yousef and Dill 1971, Breyen et al. 1973), but it does not occur in other than starving individuals. The present study showed that two kangaroo rats had maximum continuous rest periods in winter (*D. microps*, 1 h 32 min; *D. merriami*, 2 h 40 min) that were longer than those in summer (about 30 min). It is possible that during such a rest period the labile body temperature could drift downward slightly; however, there was no evidence for prolonged dormancy. It must be pointed out that the existence of this phenomenon in kangaroo rats in an ecological context, as well as the physiological and behavioral regulation of such a process, remains unknown.

The present study shows that the disappearance of *P. longimembris* from the surface in winter corresponds to their remaining beneath the surface continuously for as long as 5 months (Fig. 1). Presumably taking in a cache of seeds in the fall, the mice spend the winter in the complete absence of external environmental conditions and of the daily photoperiod. They occupy nests of leaf mulch and roots, and spend a great deal of time in torpor (Tables 6, 7, and 8). Laboratory data suggest that 3-day bouts of torpor (i.e., greater than 48 but less than 72 h duration) may be the most frequently used by individuals minimizing energy expenditure (Tables 7 and 8). Some *P. longimembris* can remain torpid for more than 72 (but less than 96) h at a time.

Perognathus longimembris undoubtedly construct nests deeper than 75 cm (the depth of the enclosures in which they were studied). Scheffer (1938) found nests of *P. parvus* as deep as 193 cm. Animals locating their nests at great depths should minimize the metabolic cost of maintaining normothermic body temperatures. However, as suggested by studies of torpor in the 10–14 g heteromyid *Microdipodops pallidus* (Brown and Bartholomew 1969), lower ambient temperature should result in more profound and prolonged bouts of torpor. Therefore, a shallow nest and the corresponding, cold ambient temperatures should minimize the metabolic costs of dormant animals. Thus the regulation of the depth of the nest may also be important in the annual energetic strategy of *P. longimembris*.

The food supply available to *P. longimembris* appears to be more important than temperature and photoperiod in determining the annual period of inactivity on the surface. The period of inactivity was different in each of three winters (Fig. 1), and so was the seed crop; whereas thermal regime (Fig. 6) and photoperiod followed the same yearly pattern. The onset of inactivity in winter and the use of torpidity is an interesting problem in physiological and behavioral regulation in an ecological context. Presumably there should be a negative feedback during an autumn of seed scarcity, which eventually leads to a prolonged period of holing up. In a year of great productivity, foraging on the surface should continue through the winter. The strategy of remaining active during the winter and foraging on

the surface appears to be optimal for survival of the population, since overwintering success was greatest in the winter of continuous activity on the surface (1969–70). Extensive use of torpidity by a population should therefore be advantageous only when food is scarce. There was no evidence for estivation, or summer dormancy, in the pocket mouse population.

A food resource not previously considered for pocket mice is the burrow parasites. The ready dispersal of these insects and scorpions into the winter nest, and in some cases their production of larvae, may represent a potential food source that should be considered in further studies.

Laboratory observations on torpidity in *P. californicus* (Tucker 1966) corroborate my suggestions that food availability determines the period of inactivity and the use of torpor during the winter. Tucker found that smaller rations of seed produced more prolonged and profound bouts of torpor. He also observed that periods of daily torpor began in the nighttime. This has also been observed in small rodents of other taxa which become torpid: *Baiomys taylori* (Hudson 1965) and *Sicista betulina* (Johansen and Krog 1959). The daily pattern of activity in *P. longimembris*, which shows a marked drop in activity in the last part of the night (Fig. 2), correlates well with the observation that torpor bouts may begin in the latter part of the night. Thus the activity pattern of these other species in nature may resemble that of *P. longimembris*.

Ecological differences among the species

Dipodomys microps, D. merriami, and *P. longimembris* differ ecologically in certain respects within the following categories: diet and foraging behavior, foraging area, running speed, annual cycles of body weight, reproductive cycles, daily and seasonal activity periods, and physiognomy of burrow sites.

Cycles in the regulation of body weight and reproductive state do not coincide in the two species of *Dipodomys* (Fig. 3). The differences may be attributed to the reliance of each of these species on different green food resources critical for reproduction, which differ in seasonal availability (Kenagy 1973). In *D. merriami* the prolonged potential period for reproduction and the sporadic occurrence of reproduction within that period are associated with its dependence on ephemeral annual herbs, which germinate only under special conditions of precipitation and temperature. The short and annually consistent reproductive period of *D. microps* is associated with its independence of such vegetation and its use instead of the leaves of perennial shrubs.

A single, short reproductive period early in the year may be characteristic of *D. microps* over much of its geographic range. A report on the breeding season of "*D. microps* and *D. ordii*" (Duke 1944), which states that these species show reproductive activity in September, is inconclusive, because the author failed to identify the females by species. Extended reproductive periods have been observed in *D. merriami* in various parts of its range (Reynolds 1960, Bradley and Mauer 1971).

Dipodomys merriami (mean weight = 35 g), which is primarily a seed eater, forages over larger areas than *D. microps* (mean weight = 56 g), which is primarily a leaf eater. However, *D. merriami* can run 50% faster than *D. microps*. It is well known that the energetic cost of moving a given distance decreases with increasing speed, and this has recently been demonstrated for a variety of mammals (Taylor et al. 1970). Thus it appears that *D. merriami* may offset the potential energetic costs of moving larger distances than *D. microps* by running faster. The nightly activity periods of the two species are complementary, in that *D. microps* is strongly active in the first part and *D. merriami* in the last part of the night. The basis of this relationship appears to be the social dominance of *D. microps* over *D. merriami*.

Perognathus longimembris resembles *D. merriami* in diet and reproductive pattern more than it does *D. microps*. In the height of burrow hillocks and of shrubs on the hillocks *P. longimembris* and *D. merriami* do not differ significantly. However, they make different spatial and temporal use of habitat: *P. longimembris* forages over a much smaller area than does *D. merriami*; *P. longimembris* is strongly active at the beginning of the night, whereas *D. merriami* is strongly active in the last part of the night; *P. longimembris* ceases to be active on the surface in winters of food scarcity, a fact which should be particularly significant in reducing competition between *D. merriami* and *P. longimembris* during a time of such limited resources.

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