SEASONAL ACTIVITY PATTERNS OF RODENTS IN A SAGEBRUSH COMMUNITY

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ABSTRACT.—Twelve species of nocturnal rodents were studied on a 2.7-hectare plot of sagebrush desert in west-central Nevada. Six species, *Dipodomys merriami*, *D. ordii*, *D. panamintinus*, *D. microps*, *Onychomys torridus*, and *Peromyscus maniculatus*, were active throughout the year. Four species, *Perognathus longimembris*, *P. formosus*, *Microdipodops megacephalus*, and *Reithrodontomys megalotis*, hibernated and were active only in spring, summer, and autumn. *Onychomys leucogaster* and *Neotoma lepida* were trapped intermittently throughout the year but were not permanent residents on the area. Differences in time of daily activity were found between potential competitors demonstrating a degree of temporal isolation. Time after sunset and amount of moonlight were the two most important factors correlated to rodent activity. Ambient temperature, wind, cloud cover, precipitation, and water vapor pressure had little effect on activity except when extreme conditions prevailed.

The desert supports a wide variety of rodents and provides a natural laboratory to study the effect of rigorous environmental conditions on small mammal species. Numerous studies have been made on rodents of the low desert of the southwestern United States, but the sagebrush community of the Great Basin has been neglected. Hall (1946) provided the most complete information on species of the Upper Sonoran Life-zone. Since then mostly fragmentary information on the biology of these rodents has become available. However, Kenagy (1973) presented excellent comparative information for several desert species.

A continuing problem in mammalian ecology concerns the methods by which sympatric species coexist. In the sagebrush desert of west-central Nevada at least 12 species of nocturnal, surface-active rodents coexist sympatrically. With such a large number of species, it was apparent that the sage desert provided a unique opportunity to study various mechanisms of coexistence.

The purpose of the present study was to examine daily and seasonal activity patterns of nocturnal rodents. The major approach was measurement of frequency of captures throughout the night. Various environmental parameters were monitored concurrently as possible correlates to activity. The focal point of the study was to describe the trends in activity of individual species and to relate the patterns exhibited by potentially competing species. Likewise, environmental factors were examined to establish a predictive base for species behavior in relation to general environmental conditions.

MATERIALS AND METHODS

The study area was located at the northern end of Warm Springs Valley, about 40 kilometers (km) north of Sparks, Highway 33, Washoe Co., Nevada (1363 meters, m, elevation). The selected site was approximately 200 m east of the highway. A 12 by 12-station grid, 2.7 hectares, was staked out at 15 m intervals. Vegetation primarily consisted of

Basin sagebrush, *Artemisia tridentata,* and hopsage, *Grayia spinosa,* grading into saltbush, *Atriplex confertifolia.* Sand dunes were present at the western part of the grid with the eastern portion situated on a steep hillside. Soil was variable with the dunes and immediate vicinity consisting of fine, wind-blown sand grading to coarse, compact, rocky soil on the hillside. A detailed description of the vegetation and physical features of the area will be presented in a later paper dealing with the disperion of sagebrush rodents.

Trapping was conducted from 18 January 1972 to 7 January 1973. One Sherman live-trap was placed at each station. Trapping was carried out for six nights each month (on three consecutive nights during the first part and again in the latter part of the month). Thus trapping occurred during various moon phases. Strict adherence to the trapping schedule was maintained even when inclement weather prevailed.

Traps were opened and baited with rolled oats at sunset and checked at 2-hour intervals throughout the night. This allowed enough time to process a large number of animals yet maintain a minimum of disturbance on the grid. Since checking traps at 2-hour intervals obviated the use of trap nights as a measure of trapping intensity, each check was considered a trap period. Therefore, each 2-hour check equaled 144 trap periods with a total of 51,822 trap periods during the study. Intensity of activity was assessed by the frequency of animals entering traps. For each animal captured, trap number, time, species, sex, relative age, reproductive condition, and weight were recorded. All animals were toe-clipped for identification.

Rodents captured on the grid belonged to two families (Heteromyidae and Cricetidae). Heteromyid species were as follows: Perognathinae—*Perognathus longimembris, P. formosus,* and *Microdipodops megacephalus;* Dipodomyinae—*Dipodomys merriami, D. ordii, D. panamintinus,* and *D. microps.* Cricetid species were *Peromyscus maniculatus, Reithrodontomys megalotis, Onychomys torridus, O. leucogaster,* and *Neotoma lepida.*

A ground level weather station was located approximately 0.5 km from the grid. Daily temperature and relative humidity were recorded using a Weather Measure 7 day recording hygrothermograph. A Weather Measure rain gauge was used to determine weekly precipitation. Ambient temperature (°C), relative humidity and precipitation are summarized in Table 1.

Additional environmental parameters were measured throughout the night. Ambient temperature (°C) and water vapor pressure (mm Hg) were measured about 6 centimeters (cm) above the ground with a YSI Dew Point Hygrometer. Wind was measured with a Dwyer wind meter and converted to the Beaufort scale (Beaufort 1 = 1 to 3 mph; 2 = 4 to 7 mph; 3 = 8 to 12 mph). Sky conditions (clear, partly cloudy, overcast, fog, drizzle, shower, and snow) and moon phase also were recorded.

Results

Seasonal Activity

The number of species actively present on the grid ranged from six in winter to 10 in autumn. Rodents were either active all year (*Dipodomys, O. torridus,* and *P. maniculatus*), seasonally active (*Perognathus, M. megacephalus,* and *R. megalotis*), or sporadic in occurrence (*O. leucogaster* and *N. lepida*).

The six species that were active all year demonstrated fluctuating abundance and activity (Table 2). This partially reflected the poor reproductive success for these species in 1972. Of the two sporadic species, *O. leucogaster* apparently was represented only by nomadic individuals, whereas *N. lepida* seemed to be represented by individuals exploiting an added food source at the edge of their foraging range.

TABLE 1.—*Maximum, minimum, and mean monthly values for ambient temperature and relative humidity on the study area. Total monthly precipitation is given in inches.*

	January[1]	February[2]	March[2]	April	May	June	July	August	September	October	November	December
						Ambient Temperature						
High												
Maximum	14	9.3	14.9	30	38	39	43	43	34	31	18	16
Minimum	—5	1.2	0.2	12	8	17	30	24	14	6	4	—13
Mean	4.3	4.9	9.3	19.9	28.2	30.8	35.4	34.7	25.8	18.4	10.3	2.9
Low												
Maximum	0	1.9	7.2	6	10	22	23	14	14	8	11	4
Minimum	—18	—7.1	—10.3	—8	—2	4	4	5	—4	—3	—10	—19
Mean	—7.6	—2.2	0.5	—2.5	4.1	12.0	13.7	9.2	3.9	2.5	—2.5	—7.2
						Relative Humidity						
High												
Maximum	80	—	—	100	100	100	100	100	95	98	86	78
Minimum	59	—	—	98	77	80	76	73	80	45	48	61
Mean	72.4	—	—	99.7	93.6	92.1	86.3	86.4	88.6	67.3	69.3	68.2
Low												
Maximum	79	—	—	79	70	76	77	59	70	72	80	73
Minimum	55	—	—	38	36	35	29	26	33	18	30	22
Mean	69.7	—	—	57.9	48.3	51.9	42.7	41.9	47.7	47.2	58.6	64.2
						Precipitation						
Total	0.66	—	—	0.20	1.00	0.62	0.09	0.34	1.02	1.41	1.04	0.54

[1] Ambient temperature and relative humidity values obtained for the first 13 days of January 1973.
[2] Ambient temperature values obtained from sunset to sunrise on trapping nights only.

Occurrence and intensity of activity in the seasonal species were variable (Table 2). *Microdipodops* was first captured on 11 March; numbers and intensity of activity increased progressively through the first half of April. Activity then declined to 5 May, with only seven subsequent recaptures until 8 August. Coincidental with the decrease in activity of *M. megacephalus* was the emergence of *P. longimembris* on 21 April. By May, *P. longimembris* was the most abundant species on the grid and remained so until August. Through August, however, *P. longimembris* declined in numbers and activity with a concomitant increase in *M. megacephalus*. Activity ceased by mid-September for *P. longimembris* but not until the end of October for *M. megacephalus*. One *P. longimembris* resumed activity on 28 October and remained active until 18 November.

The other two seasonally active species, *P. formosus* and *R. megalotis*, did not exhibit clear-cut patterns (Table 2). Only two individual *P. formosus* were captured and these occurred only at the easternmost edge of the grid. *Reithrodontomys megalotis* began with a pattern similar to that of *M. megacephalus* and then disappeared at the height of the breeding season.

Daily Activity

Seasonal activity of *M. megacephalus* and *P. longimembris* in relation to time from sunset is shown in Fig. 1. In all cases there is an initial burst of activity up to 2 hours after sunset. The distinct bimodal, crepuscular activity of *M. megacephalus* males during the summer is the notable exception to similarities between these species. *Perognathus formosus* demonstrated a similar pattern of activity with highest activity at 2 hours after sunset, declining rapidly beyond this time with a total cessation at 6 hours after sunset.

The four species of *Dipodomys* exhibited two major trends of activity. Seasonal changes in daily activity of *D. merriami* and *D. microps* in relation to time from sunset are similar (Fig. 2). Although sexual differences are present in certain seasons, the primary variation is one of intensity with males exhibiting higher abundance and intensity of activity. The distinct trimodal winter activity and a tendency for relatively high stable activity through the remainder of the night during other seasons marks the similarities between these species.

Similarities in activity for *Dipodomys ordii* and *D. panamintinus* are illustrated in Fig. 3. Marked sexual differences are present for most seasons. The major tendency throughout the year for both species is a bimodal pattern with activity low or absent towards sunrise. Abundance and intensity of activity between sexes was similar to that found in *D. merriami* and *D. microps* (a higher ratio of males).

Patterns of daily activity for *O. torridus* and *P. maniculatus* are given in Fig. 4. Sexual differences in activity are more a function of time than magnitude in *O. torridus*, but in *P. maniculatus* the converse is true. The tendency for middle and late night activity with a lack of crepuscular peaks character-

TABLE 2.—*Comparison of population changes by month and sex for all rodents studied on the grid. Values indicate the number of different individuals for each month.*

Species	January		February		March		April		May		June		July		August		September		October		November		December	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Microdipodops megacephalus	–	–	–	–	4	3	4	3	2	1	1	1	1	1	3	2	6	3	3	1	–	–	–	–
Perognathus longimembris	–	–	–	–	–	–	4	2	18	14	20	24	22	30	12	8	3	1	1	–	1	–	–	–
Perognathus formosus	–	–	–	–	–	–	–	–	–	2	–	2	–	1	–	1	–	–	–	–	–	–	–	–
Dipodomys merriami	5	3	7	4	10	3	8	2	9	3	7	3	5	2	4	2	4	4	4	1	5	1	2	1
Dipodomys ordii	2	1	2	1	4	1	3	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1
Dipodomys panamintinus	3	1	3	1	3	1	1	1	1	1	2	–	2	–	–	–	–	–	1	–	–	–	–	–
Dipodomys microps	4	1	3	–	4	–	3	–	4	1	4	1	4	1	1	–	3	1	3	3	3	2	3	2
Onychomys torridus	1	2	2	2	1	2	–	2	–	2	–	–	–	1	–	–	–	–	–	1	–	1	–	–
Onychomys leucogaster	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
Reithrodontomys megalotis	–	–	–	–	2	1	3	1	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–
Peromyscus maniculatus	7	5	9	3	5	3	3	8	5	3	2	–	2	1	1	2	4	3	6	1	9	6	7	3
Neotoma lepida	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	1	1	1	–	1	–	–

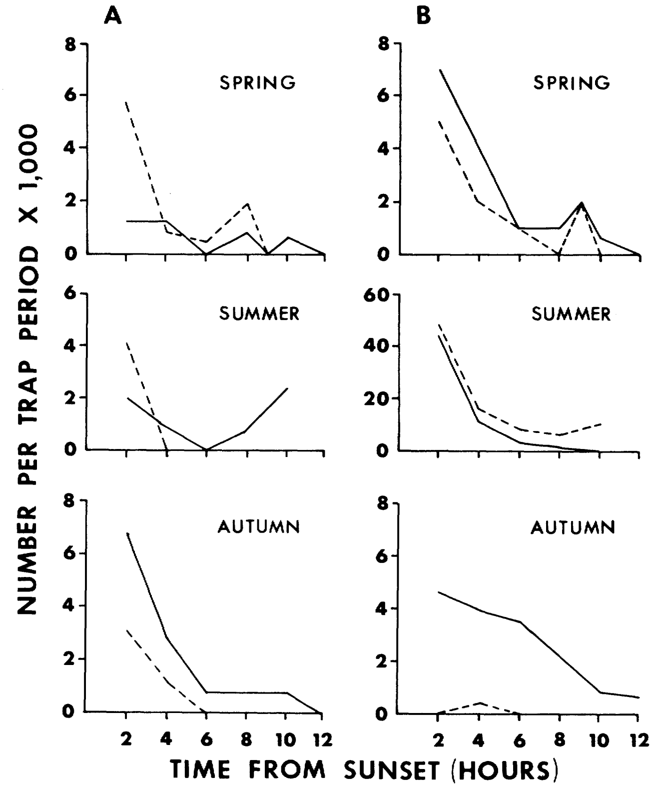

FIG. 1.—Activity of *Microdipodops megacephalus* (A) and *Perognathus longimembris* (B) in relation to time from sunset in 2-hour intervals. Males, solid lines; females, dashed lines.

izes *O. torridus*. Relatively high activity through most of the night with several distinct peaks distinguishes *P. maniculatus*. The activity of *R. megalotis* was virtually identical with that of *O. torridus* in spring. Limited data for *O. leucogaster* coincided with that of *O. torridus*. The information for *N. lepida* showed a low, relatively constant activity through most of the night.

Activity and Environmental Conditions

Although an attempt was made to trap under as many different conditions as possible, a much larger percentage of the trapping effort occurred during a limited range of environmental conditions. With respect to ambient temperature certain patterns were apparent. Fifty per cent or more of the trapping effect occurred between −4 to 5°C in winter, 1 to 10°C in spring, 11 to 20°C in summer, and 1 to 10°C in autumn. For the year-round residents, the percentage of captures by season was highly correlated with per cent of trapping effort at different ambient temperature ranges ($r > 0.90$) except for *D. microps*

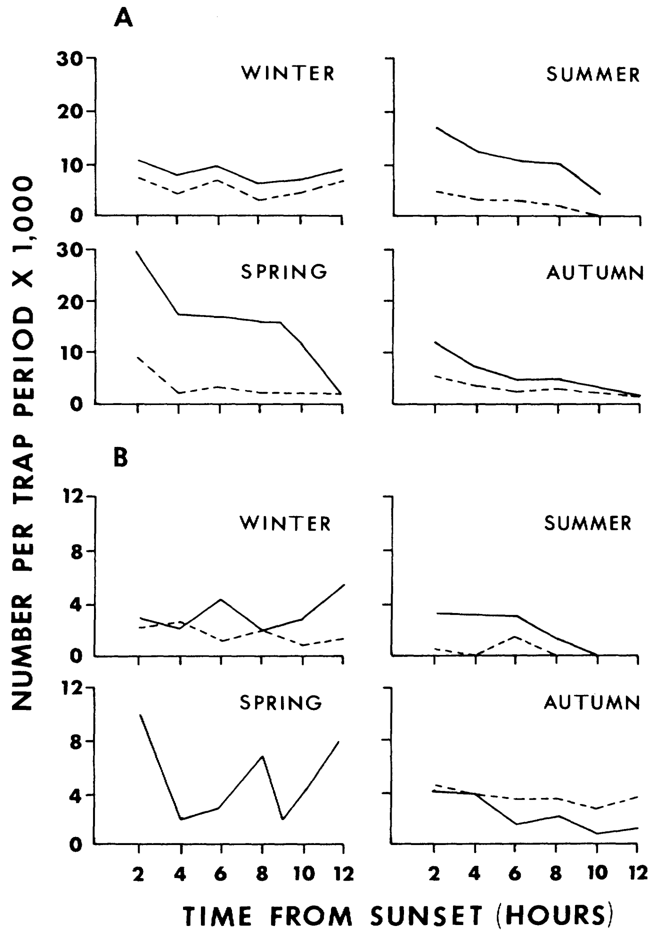

FIG. 2.—Activity of *Dipodomys merriami* (A) and *Dipodomys microps* (B) in relation to time from sunset in 2-hour intervals. Males, solid lines; females, dashed lines.

in summer. In this species, more than 50 per cent of all captures occurred in the range of 6 to 10°C.

Per cent captures of hibernators in spring also was correlated with trapping effort, but showed no correlation during summer and autumn ($r < 0.30$). More than 50 per cent of summer captures of these species occurred at temperatures above 21°C and more than 70 per cent of autumn captures occurred at temperatures above 11°C. Differences were observed between the species in relation to minimum ambient temperature at which captures occurred (Table 3).

In most instances, the per cent captured at various wind speeds showed the same high correlation with per cent of trapping effort. Deviations from this pattern were observed only at high wind speeds when sand began blowing.

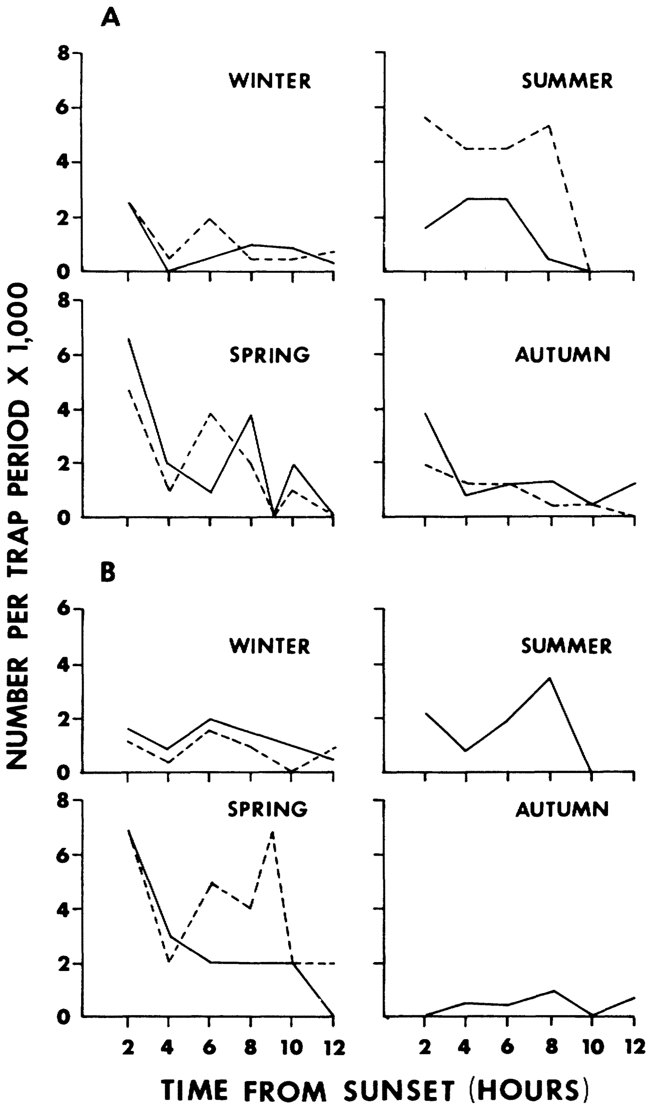

FIG. 3.—Activity of *Dipodomys ordii* (A) and *Dipodomys panamintinus* (B) in relation to time from sunset in 2-hour intervals. Males, solid lines; females, dashed lines.

High correlations also were found in relation to sky condition with some notable exceptions. For all winter residents, except *Peromyscus maniculatus,* weak correlations ($r^2 < 0.80$) were evident with most captures occurring during overcast and fog conditions. During inclement weather conditions in all seasons very little activity was observed. This was particularly noticeable during conditions of snow. *Peromyscus* was the onlv species that was active

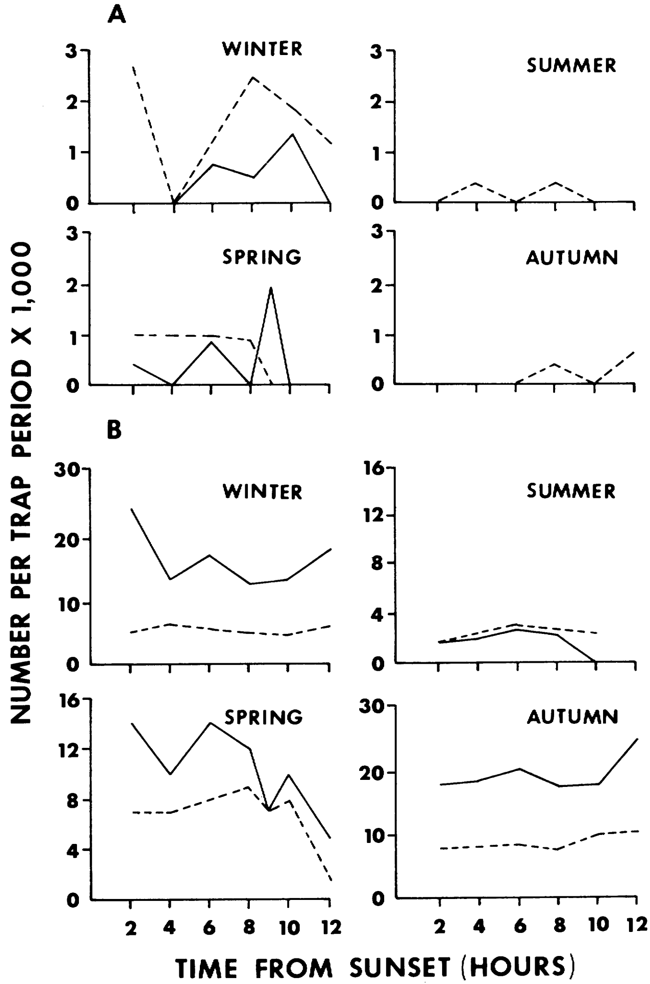

FIG. 4.—Activity of *Onychomys torridus* (A) and *Peromyscus maniculatus* (B) in relation to time from sunset in 2-hour intervals. Males, solid lines; females, dashed lines.

when snow was present on the grid. Heteromyids were not active when more than 40 per cent snow cover was present.

Per cent of captures in relation to nighttime light conditions showed the most striking correlation to per cent trapping effort. In all seasons more than 60 per cent of trapping effort occurred under conditions of no moon, which is an accurate reflection of the low percentage of nighttime hours that the moon is actually present. Although the correlations indicate no influence of moon on rodent activity, a definite negative effect was observed in the field. When the moon was present activity was low but if a cloud were to pass in front of the moon activity immediately increased. Although this was true of all rodents studied, this effort was not as pronounced among the small, cryptic species. Residuals were calculated for all regressions between per cent of

TABLE 3.—*Comparison of minimum ambient temperatures (°C) at which the common species of rodents were captured during each season.*

Species	Winter	Spring	Summer	Autumn
Microdipodops megacephalus	—	−3	13	1
Perognathus longimembris	—	−3	5	−5
Dipodomys merriami	−15	−5	1	−5
Dipodomys ordii	−11	−5	1	−3
Dipodomys panamintinus	− 3	−5	1	−1
Dipodomys microps	−15	−5	3	−5
Onychomys torridus	− 5	−3	7	3
Peromyscus maniculatus	−25	−5	1	−7

captures and trapping effort (Draper and Smith, 1966), and were consistently low at no moon. However, the residuals fluctuated wildly at the various moon phases. This wide variance about the regression line indicates that trapping effort does not explain well the frequency of captures under moonlight conditions.

Water vapor pressure proved to be a disappointment as a factor that might affect activity. No trends were noticeable in activity over the range of vapor pressures encountered. In the sage habitat studied the total yearly variation in vapor pressure was between 1 and 10 millimeters (mm) Hg. A total fluctuation of 9 mm Hg is probably too small to detect whether this is an influential parameter with respect to rodent activity.

DISCUSSION

Seasonal Activity

Rodents that were active throughout the year demonstrated several strategies for dealing with seasonal extremes. In winter, the four species of *Dipodomys* were active at temperatures down to −15°C. However no activity was noted at temperatures below this and when more than 40 per cent of the substrate was covered by snow. Reynolds (1958) stated that *D. merriami* was discouraged from traveling because its food supply was covered by snow. This species is known to hibernate under laboratory conditions of low temperature and starvation (Yousef and Dill, 1971). However, hibernation usually terminated in death after 7 days due to a loss of 25 per cent of body weight and body temperature dropping below 14°C. Mullen (1971) found that *D. merriami* and *D. microps* apparently went into a diurnal torpor in nature. Kenagy (1973) found *D. merriami* and *D. microps* active at temperatures down to −19°C with no cessation of movements in powdery snow. Wet snow, which I encountered, appeared to inhibit activity. If kangaroo rats cached seeds in the burrow and utilized a diurnal torpor, periods of snow and extreme temperatures could be withstood easily.

In addition to the winter pattern, *D. microps* appeared to be heat sensitive. Low activity was observed during the hottest part of the year. Number of captures differed significantly from trapping effort expended at this time, with 76 per cent of the captures occurring below 15°C.

Slight activity was observed for *P. maniculatus* during the first 2 weeks of December owing to the snow cover and low temperatures. I followed the tracks of this species through the snow and observed that individuals made long forays, moving from shrub to shrub with little random wandering. Feeding may have occurred, but such forays probably represent movement from one nest to another. If cache dens are maintained near or within nest burrows, surface foraging would not be necessary during periods of weather extremes. Stebbins (1971) documented periods of torpor in *P. maniculatus* in the Northwest Territories of Canada during periods of severe cold and snow, and mentioned slight activity occurring even during these conditions. In the sage desert, *P. maniculatus* possibly utilizes cache dens and periodic torpor during inclement weather.

Of the seasonally active species, only *Perognathus longimembris* has been documented as a hibernator (Hall, 1946; Bartholomew and Cade, 1957; Chew and Butterworth, 1964; Jorgensen and Hayward, 1965). *Microdipodops megacephalus* has been presumed to be active throughout the year. Hall (1946) reported trapping kangaroo mice on nights that were so cold that their bodies were frozen solid. *Reithrodontomys megalotis* was active on the grid through the spring and early summer, although the species has been considered active throughout the year (Hall, 1946) and was found not to hibernate in California marshes (Fisler 1965). *Reithrodontomys* is capable of torpor in the laboratory (Fisler, 1965) and hibernation in the present study would explain the winter absence and spring emergence similar to other hibernators.

Daily Activity

The daily activity patterns of *M. megacephalus* and *P. longimembris* were similar (Fig. 1) with bimodal activity in the spring and the initial high peak of activity occurring just after sunset. The initial burst of activity following sunset has been documented for *M. megacephalus* (Hall, 1946) and *P. longimembris* (Chew and Butterworth, 1964; Jorgensen and Hayward, 1965). Spring activity differed in *P. longimembris* with the major peak of activity occurring at 5 hours after sunset (Jorgensen and Hayward, 1965), with a small, secondary increase prior to sunrise (Chew and Butterworth, 1964; Jorgensen and Hayward, 1965).

The activity patterns of *D. merriami* and *D. microps* in relation to time from sunset showed similar patterns (Fig. 2). Studies of *D. merriami* in creosote desert suggested bimodal activity pattern during August (Reynolds, 1960). The peaks occurred 3 hours after sunset and 3 hours before sunrise. He further noted that individuals of this species seldom spent more than 35 per cent of any hour outside the nesting box. Chew and Butterworth (1964) found an initial peak of activity shortly after sunset with activity declining through the rest of the night, with winter data indicating an increase in activity up to sunrise. Data from Jorgensen and Hayward (1965) showed a bimodal activity pattern for *D. merriami* with peaks at 4 and 8 hours after sunset, but *D. microps* exhibited trimodal activity in winter and spring with bimodal activity occurring in the summer. Kenagy (1973) described temporal partitioning between these two species, with *D. microps* active in the early evening and *D. merriami* the early morning hours.

Differences in activity patterns between *D. ordii* in the present study and in the creosote desert also exist. During winter, activity occurred only after midnight; trimodal activity was prevalent in spring and there was a bimodal pattern with the preponderance of activity occurring after midnight in summer (Jorgensen and Hayward, 1965).

Peromyscus maniculatus demonstrated marked changes in activity patterns in relation to time from sunset (see Fig. 4). In summarizing *Peromyscus* activity, Falls (1968) reported similar seasonal changes. He noted that winter activity was longer probaby due to scarcity of food, and pointed out that bimodal crepuscular activity occurred during this time. The discrepancies between these observations and my study are probably due to geographical variation or the manner of data collection.

Activity and Environmental Conditions

With respect to various environmental parameters as potential factors affecting activity, several trends are striking. The first is that rodents appear to be little affected within the natural range of fluctuations in any factor examined. Extremes in any of these parameters, which do not occur often, appear to have the major effect on most rodents. Different tolerances of extremes are also exhibited (see Table 3). Temperature differences were most apparent between hibernators and year-round residents in summer and autumn. Significantly more hibernators were captured at temperatures above 21 and 11°C, respectively, demonstrating a physiological acclimatization for higher temperatures. Jorgensen and Hayward (1965) stated there was no correlation between ambient temperature and activity of desert rodents. Preferred temperature ranges were observed in the present study and correspond with those found in Poland (Sidorowicz, 1960) and Canada (Falls, 1968).

In the past, most workers considered weather parameters to be maximum and minimum temperatures, cloud cover, and rain. These conditions usually were measured by someone else at a weather station under conditions that did not necessarily approximate natural conditions at the study area. Moreover, many studies considered only part of a year, while others implicated weather conditions as an afterthought or by experimental manipulation in the laboratory. Contrary to the variability of these methods, similar observations have been reported. In general, clear nights inhibit small mammal activity; cloudy nights increase activity and rain usually results in peak movement of small mammals (Gentry and Odum, 1957; Sidorowicz, 1960; Getz, 1961; Mystkowska and Sidorowicz, 1961; Gentry *et al.*, 1966; Bider, 1968; Getz, 1968). Contrary to these findings, Jorgensen and Hayward (1965) reported that clouds and rain had little influence on desert rodent activity. I found that cloudy weather, particularly in the winter, resulted in increased activity. Rain had an increasingly negative effect depending on the severity of the rain. This may be due to the fact that I was following the short term hourly effects whereas most previous workers were interested in longer term day-to-day activity changes.

Chew and Butterworth (1964) and Jorgensen and Hayward (1965) found that captures of desert rodents were not inhibited by moonlight. Doucet and Bider (1969) reported that activity of *Microtus pennsylvanicus* was reduced during the full moon phase; they suggested that not only light intensity but lunar periodicity was responsible for this reduction. Owings and Lockard (1971) described different responses to moonlight by *Peromyscus californicus* and a smaller species, *P. eremicus*. The former species was negatively influenced, while the latter was more active in moonlight. They suggested that this differential might be an example of temporal competitive exclusion. Lockard and Owings (1974) found similar differences in two species of kangaroo rats. *Dipodomys spectabilis* exhibited strong avoidance of moonlight, whereas *D. nitratoides*, a much smaller species, did not show such strong inhibition.

In the present study, moon had a definitive negative effect. It need not influence the overall biology of the rodents since the percentage of time when the moon is present was actually quite small. Although all rodents behaved similarly, the small, cryptic species did not exhibit as pronounced an effect as did the larger, more conspicuous species. Because activity increased sharply whenever the moon was hidden by clouds, it is apparent that light intensity and not lunar cycling affects activity.

Jorgensen and Hayward (1965) further found that wind did not affect rodent activity in the low desert. I found this was true except at the higher wind speeds accompanied with blowing sand. Fine, wind-blown sand would be highly uncomfortable and a hindrance to vision; additionally, since many rodents locate seeds by olfaction, high wind speeds would greatly affect this ability negatively.

It appears that the primary factors correlated to desert rodent activity are time from sunset and moonlight. The other environmental parameters examined influence activity but only secondarily. Only the extremes of weather seem to have a significant effect on the activity patterns of sagebrush rodents.

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