The Periodicity of Daily Activity and Its Seasonal Changes in Free-Ranging and Captive Kangaroo Rats

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Summary. Populations of *Dipodomys microps* and *D. merriami* in eastern California (37°11′N. Lat.) are active on the surface throughout the night and during the whole year. These two species, and the males and females within each species, show no significant differences in times of beginning or end of activity. Beginning and end of nightly activity generally fall within the brighter part of the twilights, even though the total time spent on the surface by individuals is at times only an hour or two, or even less, per night. Near the summer solstice in southern Saskatchewan, Canada (50°45′N. Lat.), when sunset and sunrise were 7 h 43 min apart, the time from onset to end of activity in a population of *D. ordii* (the northernmost of all kangaroo rats) was only 6 h; these animals were also only on the surface at intervals during the night.

During the course of the year, the light intensity at which the first individual *D. microps* and *D. merriami* became active on the surface varied between 200 and 2,000 lux, and the light intensity at which the last individual was active in the morning varied between 50 and 20,000 lux. There was no apparent influence of the moonlight cycle upon the onset and end of activity; in fact the light levels at beginning and end of activity are about 2 to 4 orders of magnitude brighter than that at full moon. The onset of activity is fairly synchronous within the population in that most individuals surface within about a half hour of each other; furthermore, two-thirds of the individuals appearing in the first 32 min of activity had already appeared within the first 12 min. There appears to be a similar, synchronous, but less well marked end of activity in the morning.

There were systematic seasonal changes in the time relative to sunset and sunrise respectively, and in the corresponding light intensities, at which the animals began and ended activity. The phase relationship between the onset of activity and sunset (ψ_{onset}) showed two maxima and two minima per year, but the phase relationship between the end of activity and sunrise

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(ψ_{end}) showed only one maximum and one minimum per year. On the other hand, the annual range of change in the evening phase ψ_{onset} (28 min) was half the annual range of change in the morning phase ψ_{end} (57 min). Such a conspicuous difference in frequency and amplitude of ψ_{onset} and ψ_{end} has not previously been reported for any species, nor has it been predicted by models of circadian rhythms and phase relationships. The resemblance of the course of annual change in ψ_{onset} to annual change in length of twilight and the resemblance of annual change in ψ_{end} to change in length of night are discussed. These differences may underline a circadian system based on two separate, but normally coupled components, which could be separately synchronized by dusk and dawn respectively.

The daily running-wheel activity of 10 individually housed *D. merriami* under natural skylight in Los Angeles (34°05′ N.Lat.) began and ended at light intensities two to three orders of magnitude lower than corresponding values for surface activity in the field. The onset and end of activity for the captive population did not show the synchronous peaks typical of the field populations; nor did the nightly activity patterns of individuals show peaks at the beginning and end of the night. The social isolation of the captive kangaroo rats is suggested as a factor contributing to differences between activity parameters in captivity and field.

Proximate and ultimate factors shaping the periodicity of activity in kangaroo rats are discussed. It is hypothesized that social interactions involving some form of territoriality may give rise to a population peak in onset of activity in some solitary mammals such as kangaroo rats. A set of criteria is presented for comparing vertebrate species with regard to the periodicity and synchronization of both daily and seasonal functions.

Introduction

The general daily "temporal niches" occupied by animals are easily recognized and well known for many species. The principal time of activity for each species shows obvious correlations with availability of food, avoidance of predators, physiological capacities for maintaining homeostasis in the physical environment, and behavioral interactions. Much remains to be learned, however, concerning the timing mechanisms by which the many behavioral and physiological functions of an animal are synchronized with each other and with the environment, on both daily and seasonal bases. The numerous investigations of circadian rhythmicity (exemplary symposia: Cold Spring Harbor, 1960; Aschoff, 1965a; Menaker, 1971) have largely concentrated on captive organisms under a variety of experimental conditions and without regard to time of year. The empirical examination of the daily biological cycle at different times of year, particularly as it operates in the field, should provide further insight into not only the daily rhythm itself, but also the seasonal responses of organisms.

Kangaroo rats (*Dipodomys*, Heteromyidae) are common inhabitants of the deserts of western North America, where they are active on the surface at night. The timing of their activity with respect to the daily environmental cycle is of particular interest because 1) the food supply (mostly seeds or leaves)

does not vary in its availability during the course of the day, as it does for some other animals, such as insectivorous bats, and 2) kangaroo rats live solitarily in their subterranean burrows. Thus the time of beginning and end of activity on the surface is not a function of the availability of food, and furthermore the beginning of activity is not directly triggered by social interaction. This suggests that the times of onset and end of surface activity might show a relatively clear relationship to physical factors, mainly light intensity, but with possible modifying effects of temperature and weather. Because kangaroo rats move out into the open as soon as they emerge from their burrows in the evening, they are more easily observed than other, more secretive nocturnal rodents. They also readily enter live-traps. The thorough examination of beginning and end of daily activity, and its variation throughout the whole year, in both free-living and captive animals of a single species has not previously been reported. In general, such data for vertebrate classes other than the birds, and particularly for nocturnal species, have been difficult to obtain with precision, and thus are generally lacking. Some recent progress in the field study of periodicity of daily activity in nocturnal animals has been reported by Voûte et al. (1974), who measured onset and end of activity during summer in a bat colony occupying a church loft and by Laufens (1975), who studied the activity in summer and fall of two species of glirid rodents occupying artificial nest boxes located outdoors in a forest habitat. Zwahlen (1975) has reported data on beginning and end of activity in caged squirrels, *Sciurus vulgaris*, which are day-active; although he did not measure the exact time of onset and end of activity in the field, he does present a series of extensive field data on the frequency of observation of the squirrels at different times of day throughout the year. There are considerable data on beginning and end of activity in day-active birds in the field (review by Aschoff, 1969), largely because of the ready accessibility of birds to human observers. Such data have also been accumulated for some captive birds and mammals (Aschoff, 1969; Daan and Aschoff, 1975), but no single study has systematically examined the same species in this regard in both field and laboratory.

The present study was undertaken 1) to examine in detail the daily periodicity of surface activity in free-living kangaroo rats, 2) to observe seasonal changes in the daily periodicity, 3) to compare activity of animals in the field with activity of captive animals held in running-wheel cages under natural skylight and temperatures, and 4) to use the results to examine some of the theory on circadian rhythms and their seasonal synchronization as introduced in the following paragraphs. Other aspects of the general ecology and behavior of the species most intensively studied, along with the overall levels of population activity and their seasonal changes, are reported elsewhere (Kenagy, 1973a).

It is generally accepted that the endogenous component of the daily rhythm of biological activity behaves as some kind of oscillatory system (similar in many formal properties to physical oscillatory systems) coupled to the daily environmental cycle, of which the natural light-dark alteration is the prime synchronizing stimulus or "Zeitgeber". Variations in light intensity (or the amount of daily exposure to light vs. dark) are known to have a systematic effect on the various parameters of the endogenous circadian rhythmicity of animals (Aschoff, 1960; Pittendrigh, 1960). It has been shown that the phase relationship between the daily biological cycle and the daily environmental cycle is a reflection of the spontaneous endogenous rhythm of the animal and that this phase

relationship changes with variation in the light intensity or in the daily photoperiod (Aschoff and Wever, 1962a). Data on the seasonality of activity in birds were first used to test for changes in phase relationship as a function of seasonal variation in daily photoperiod (Aschoff and Wever, 1962b). In a subsequent formulation (the "Jahreszeiten-Regel" or season rule; Aschoff, 1964) it was suggested that the phase of activity (midpoint of activity in this case) should be maximally advanced relative to the phase of the daily light-dark cycle (measured from true noon or midnight) at 1) the summer solstice in day-active animals and 2) the winter solstice in night-active animals. It was further proposed (Wever, 1967) that the greatest relative delays in phase should occur at the equinoxes, and the intermediate phase-angle differences should be found at the opposite solstice of that at which the maximum advance occurs. The two seasonally changing aspects of the light-dark cycle which appear to be the prime factors promoting seasonal changes in the phase-angle difference are 1) changes in relative length of day and night and 2) changes in length of twilight (Wever, 1967).

A review and test of the theory presented above, based mostly on the available data on beginning and end of daily activity in free-living birds, shows that indeed some of the seasonal changes in the phase relationship between the biological and the environmental cycles are correlated with changes in length of day and length of twilight (Aschoff, 1969). However, a subsequent anaylsis of data from captive animals showed less fulfillment of the predictions arising from theory (Daan and Aschoff, 1975). Thus, much remains to be resolved. Relevant field and laboratory data for night-active animals in general and also for the mammals as a whole are wanting.

Several abbreviations will be used to facilitate the presentation of this paper:

ψ = phase-angle difference between Zeitgeber and biological cycle (Aschoff et al., 1965).

ψ_{onset} = phase-angle difference between onset of activity and sunset (in night-active animals) or sunrise (in day-active animals),

$\psi_{midpoint}$ = phase-angle difference between middle of activity and middle of the night or middle of the day,

ψ_{end} = phase-angle difference between end of activity and sunrise (in night-active animals) or sunset (in day-active animals).

Phase-angle difference is the difference between the phase of a biological cycle and the phase of an environmental cycle. When the biological cycle leads the environmental cycle, the phase-angle difference is defined as positive; when the biological cycle lags behind the environmental cycle, the phase-angle difference is negative.

Previous studies of seasonal change in ψ have largely focused on the significance of $\psi_{midpoint}$, both because $\psi_{midpoint}$ is the most mathematically appropriate phase point for consideration in Wever's (1965) model of circadian rhythms and because the use of $\psi_{midpoint}$ leads to less "noise" than either ψ_{onset} or ψ_{end} (Aschoff et al., 1971). A meaningful relationship for all three phase reference points has not previously been shown within a single set of data. A new, possible explanation for seasonal changes in ψ (in terms of ψ_{onset} and ψ_{end}) is presented in this paper.

Methods

Field Studies

Field studies were designed to record the time in the evening at which kangaroo rats first emerge from their burrows and become active on the surface, and the corresponding time in the morning

when kangaroo rats return to their burrows for the day. The study site was a desert scrub habitat near Big Pine, Inyo Co., California, on the east side of the Owens Valley (1,220 m) at 37°11′ N. Lat. and 118°15′ W. Long. Two species of kangaroo rats are abundant and active throughout the year at this location: *Dipodomys microps* (Great Basin Kangaroo Rat, 56 g) and *D. merriami* (Merriam's Kangaroo Rat, 35 g).

Observations were made over a two year period from December 1969 to December 1971 at each solstice and equinox, as well as most of the midpoints between them. Each observation period consisted of three consecutive evenings and three consecutive mornings. A curve of illumination at twilight was obtained with a Spectra Candela Model X-100 Photometer read every two min. Due to the arid climate of the Owens Valley, almost all of the studies were conducted under nearly cloudless sky. Air temperature was registered with a recording thermograph and with a Yellow Springs telethermometer.

In preliminary observations it was discovered that experienced rats enter live-traps (Sherman aluminum folding traps, baited with a mixed bird seed) within a few minutes of first coming to the surface. Occasional direct observations of kangaroo rats at other locations near the study site revealed that evening emergence onto and morning disappearance from the surface occurred at times and light intensities comparable to those at the trapping quadrats. Kangaroo rats are known to be readily captured in traps, and they return to traps repeatedly, which suggests minimal effects of capture and handling. *Dipodomys microps* and *D. merriami* are the predominant nocturnal rodent species and *Perognathus longimembris* is the only other species to occur in significant numbers at the particular study site (Kenagy, 1973a). However, only one *P. longimembris* was captured (one time) during all of the evening and morning trapping sessions comprising the present study. Thus there was apparently no interference by other animals during the present studies.

Four trapping quadrats of 36 stations each (6 × 6, 12.5 m apart) were used one at a time. No quadrat was used more than once in the evening and once in the morning during a 3-day sequence. Animals were individually marked by toe-clipping so that they could be identified when trapped.

For evening studies, traps were set out and baited shortly before the sun disappeared below the skyline. Each of two observers walked around a separate circuit of 18 traps about every 4 min. Some records consisted of sighting animals away from the traps, but the beginning of activity was usually determined by 1) hearing a trap close and recording the exact time, or 2) coming upon a closed trap and subtracting 2 min from present time to give an estimate of the time of trapping, or 3) coming upon a trap from which bait had been robbed by a kangaroo rat and subtracting 2 min from present time to give an estimate of the beginning of activity. Only one record was allowed for contiguous traps which had been robbed. Observation was continued for at least half an hour following the first record of activity.

The sampling in the morning studies was necessarily different from the evening because animals were usually active when sampling began. Thus the appropriate time to set traps could only be determined by trial and error. Through September 1970 traps were set out the night before and opened and baited at the time of the morning study. Subsequently traps were not set out until the time of baiting in the morning. On some mornings no animals were caught, but this information showed that activity had definitely ceased by the time trapping was begun. The most meaningful records were obtained when only one or two animals were caught, since the remainder of the population was thus presumably inactive. Observations were continued for at least 15 min after the appearance of the sun above the eastern skyline. At seasons of more extended morning activity however, observation was somewhat longer, in order to verify the eventual absence of animals on the surface.

Field Study in Canada

Observations were also made in early July 1970 south of Sceptre, Saskatchewan, Canada, at 50°45′ N. Lat. and 109°15′ W. Long. This area, known as the Great Sand Hills, is the habitat of *D. ordii*, and is the northernmost locality of kangaroo rats of any species. The habitat is described by Nero and Fyfe (1956). Vegetation on these large dunes is lower in height and much sparser than in the habitat of *D. microps* and *D. merriami* in the Owens Valley. Sixty-six traps were used, but otherwise the method of observation was similar to that in California. Traps were set out on 8 July and left in position for five consecutive evenings and mornings, but data were only used for the last four evenings and mornings.

Laboratory Studies

Running-wheel activity was recorded under natural skylight in an isolated greenhouse in Los Angeles at the edge of the U.C.L.A. campus at 34°05'N.Lat. and 118°25'W.Long. from October 1970 through February 1972. *D. merriami* were used because they are maintained in captivity more easily than *D. microps*. Only males were used. Each of 10 cages, located on tables, consisted of a wooden tunnel ($6 \times 6 \times 40$ cm); a wooden antechamber ($16 \times 16 \times 8$ cm) covered with $1/4$-inch screen; and a running wheel (33 cm diameter $\times$ 10 cm width), accessible through a hole in the antechamber opposite the tunnel entrance. The tunnel and antechamber contained sand. The mouth of the tunnel was usually plugged with sand by the animal upon retiring. Sand moved from the antechamber to the running wheel by animals was lost through the hardware-cloth track of the wheel, but new sand was added during maintenance as needed. The wooden tunnel was covered on the outside by a 60 cm mound of soil, which served as a thermal buffer for the tunnel, where animals reposed during the daytime. Temperature and humidity regimes were essentially those of normal outdoors, since all window banks were open, four large oscillating fans were operated daily from 0900–1600 h to circulate fresh air across the cages, and furthermore many panes of glass were missing from the greenhouse.

Activity records were obtained with an event recorder actuated by microswitches connected to the running wheels. Maintenance was conducted during the middle of the day. Animals were fed weekly by pouring mixed bird seed into the top of the antechambers. Lettuce was provided during several hot spells. Seven animals survived throughout the study. Dead animals were replaced within a few days, but records were not included in the analysis for the first week after introduction of substitute animals. Otherwise, the data for the ten cages were analyzed simply as a population of ten animals, without regard for the fact that substitutions were made. Data analysis covers the period 1 November 1970 to 31 January 1972 and represents 13 animals.

Time Measurement

All data were recorded in Standard Time, but some are presented in Apparent Solar Time (A.S.T.). The relationship between middle of activity time and middle of night or day is more readily apparent with the use of the Apparent Solar Day, since 0000 h A.S.T. and 1200 h A.S.T. are always the middle of night and daytime respectively, being half way between sunrise and sunset by definition. This convention also includes the conversion to Local Time.

The corrections applied to Pacific Standard Time to obtain A.S.T. for Big Pine and Los Angeles both varied from -7 min in early February to $+24$ min in early November. Correction was zero in early January, late March, and late July. The annual range of corrections applied in converting to Apparent Solar Time was thus 31 min. To apply the correction, Standard Time was converted to Local Mean Time (a correction for longitudinal displacement from the standard meridian of a time zone), and then Local Mean Time was converted to Apparent Solar Time using the equation of time.

In the present study the term "observed sunset" refers to the observed disappearance of the sun below the skyline in the evening, whereas "observed sunrise" is the corresponding term for the morning. Likewise "standard" sunset and sunrise refer to the passage of the sun through the true, unobstructed horizon at 0°, as read from an almanac. The difference in time between observed and standard sunset or sunrise is thus a function of the height of mountains on the horizon and the distance of the observer from the mountains. The White and Inyo Mountains to the east and the Sierra Nevada to the west each rise to about 3,000 m above the study area at 1,220 m.

Field Studies

General

The daily time of surface activity in both *D. microps* and *D. merriami* generally follows the seasonal change in length of night, as seen for the record of first
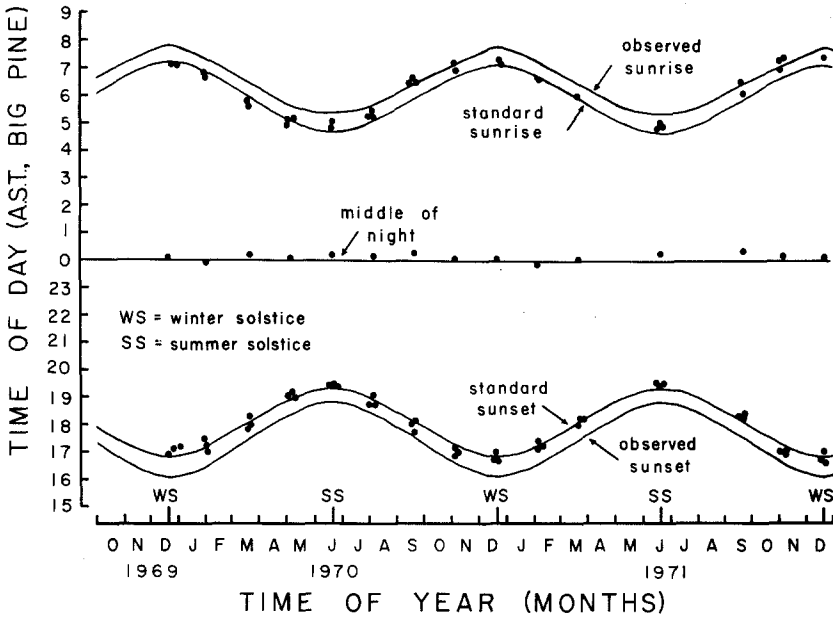
Fig. 1. Times of beginning, middle, and end of activity for *D. microps* and *D. merriami* in the field near Big Pine. Points near sunset represent the population extreme in beginning of activity on each of three consecutive evenings. Points near sunrise represent the population extreme in end of activity on 1 to 3 mornings (out of 3) for which animals were detected. The values for middle of activity are calculated as the midpoint between the mean times of beginning and end of activity over the 3 days of each sampling period. Some points are displaced slightly for graphical clarity. (Midnight A.S.T. is by definition the midpoint between standard sunset and sunrise; see "Methods" for a description of A.S.T., sunsets, and sunrises.)

animals active in the evening and last animals active in the morning (Fig. 1). However, there are seasonal changes in phase of activity on a smaller scale (Fig. 2). The time of beginning of activity is shown for the first three animals active on each of three consecutive evenings (i.e., nine points) in Figure 2. However, the end of activity is sometimes represented by fewer than nine points; in these cases the traps were set late enough on some mornings that there were only one or two animals trapped — or in a few cases none. This latter result is, however, also useful since such records confirm that activity has definitely ended by a particular time.

Due to mountains located to the east and west of the study site the observed sunset occurred 30–45 min before standard sunset, and the observed sunrise occurred 30–45 min after standard sunrise (Fig. 1). In the evening, activity always began after the observed sunset, but either before or after standard sunset. The end of activity occurred after or occasionally before standard sunrise, but generally before the observed sunrise. The only exceptions were in the fall of each year (late September and early November) when animals remained active in the morning briefly after the appearance of the sun above the horizon (Fig. 1).
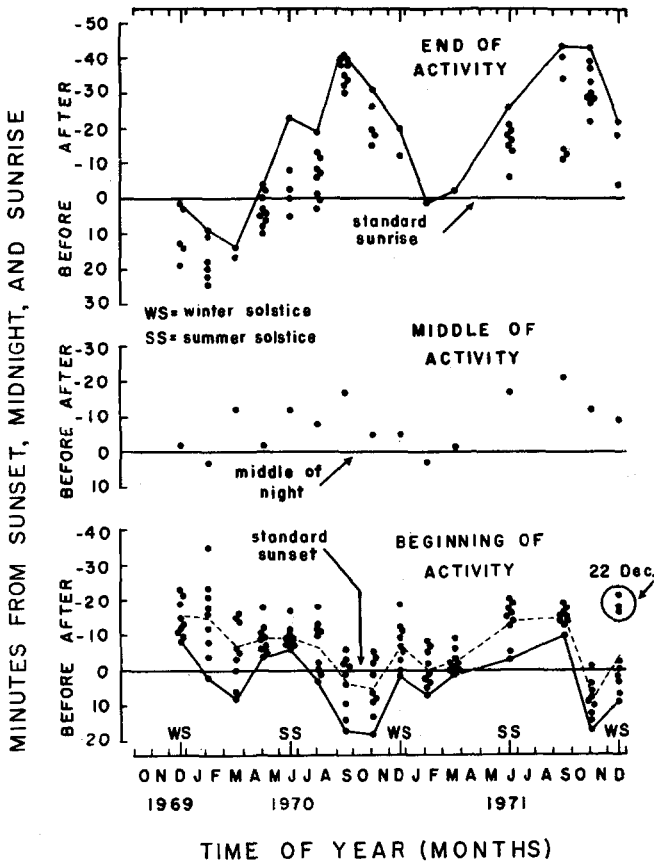
Fig. 2. Difference between beginning of activity and standard sunset (*below*), middle of activity and true midnight (*middle*), and end of activity and standard sunrise (*above*) for *D. microps* and *D. merriami* in the field near Big Pine. Points for beginning of activity represent the first three animals active on each of three consecutive nights. Points for end of activity represent up to three animals on each of three consecutive mornings, but usually represent smaller samples, as explained in the text. Values for middle of activity are the same as shown in Figure 1. Some points are displaced slightly for graphical clarity. The extreme records of each 3-day observation period are connected by a solid line, and the means of each set of 9 values for beginning of activity are connected by a dashed line

Interspecific Comparison

Of all the animals recorded in this study, 78% were *D. microps* and 22% were *D. merriami*. A similar proportion was also obtained in the data for the first or other subsequent single record in the evening or the last or other previous single record in the morning. This proportion also did not change seasonally. Since this value also corresponds to the relative numbers of the two species known to inhibit the area (Kenagy, 1973a), it can be concluded from the available data that the populations of *D. microps* and *D. merriami*

did not differ in the times at which they began and ended nightly activity on the surface. Consequently all data for both species are combined throughout the presentation.

Sexual and Social Comparisons

Of all the animals trapped in this study, 49% were females and 51% were males. Nearly equal numbers of males and females also comprise the sample when one considers only the first or other subsequent single record in the evening or the last or other previous single record in the morning. This indicates that neither sex tended to be more extreme than the other in time of beginning and end of daily activity.

The animals which were among the first three active at night and the last three active in the morning were adults of at least normal body weight. During the reproductive seasons, males with scrotal testes were common, as were pregnant or lactating females. Juveniles were not captured during these sampling periods at the beginning and end of the night. However, juveniles and adults of subnormal weight were captured in all-night trapping in the area (Kenagy, 1973a).

No single individual was consistently the first active in the evening or the last active in the morning. Out of 15 3-day periods during the two years of study no animal was among the first three active in the evening or last three active in the morning on more than three occasions. Only three individuals were recorded three times each, and five individuals were recorded twice each among the first three animals active in the evening or the last three animals active in the morning.

Distribution of Activity Onsets and Cessations in the Population

The onset of activity is relatively synchronous within the population. This is particularly noteworthy because individual kangaroo rats live solitarily, and the beginning of activity can thus not generally be directly stimulated socially. Two-thirds of all individuals to become active within the first 32 min were on the surface within 12 min of the first onset of activity in the population, and there were only slight shifts in this distribution during the year (Fig. 3). The number of animals recorded within the first 32 min of activity is about the same as the total number of adults known to inhabit areas the size of the trapping grids (Kenagy, 1973a); animals trapped later in the night are often individuals which have come from farther away.

The data of Figure 3 suggest than an analysis of onset of activity in terms of population extremes, which are easily and consistently measured regardless of population size, is justified. The use of any other function — such as a mean of n records — would be arbitrary and might vary during the year with changes in population size. Indeed the extreme values of onset of activity are in this case closely paralleled by the mean values of the first three animals active on each of three evenings (Fig. 2, dashed line).
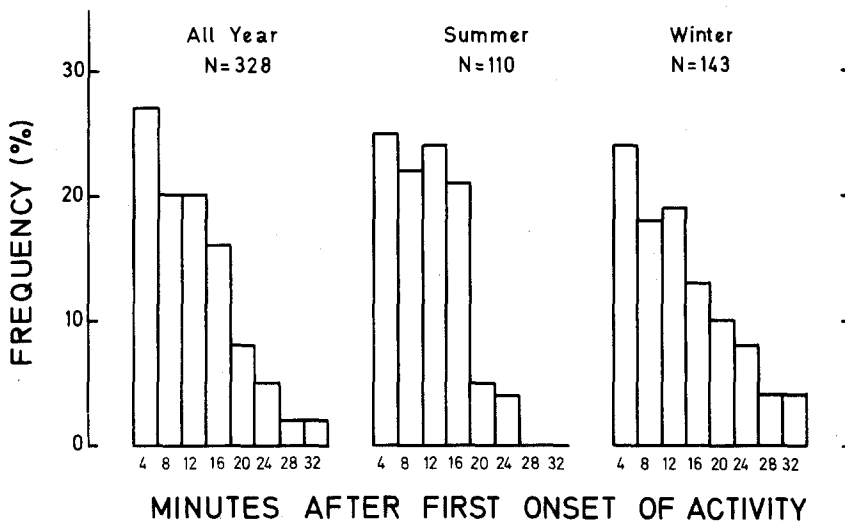
Fig. 3. Frequency histograms of observed onsets on activity during the first half hour of activity in the field population of *D. microps* and *D. merriami* at Big Pine. Data are from 45 evenings over a 2 year period. Number of animals recorded in the first half hour of activity was 4 to 10 ($\bar{x} = 7$). Each bar represents 4 successive min, beginning with 1 as the first min of activity observed in the population for each evening. Data for summer (12 evenings) and winter (21 evenings) represent only those observations within 7 weeks before and after the respective solstices

The distribution of cessations of activity could not be measured in the same way as the distribution of onsets (Fig. 3) due to the previously mentioned difference in sampling procedure (see "Methods"). However, the distribution of cessations appears to be generally similar to distribution of onsets, i.e., there are many animals active within the last 10–15 min of activity for the population in the morning. This was apparent from the nature of the trial-and-error procedure used to capture the desired sample size of two to three animals in the morning; setting the traps only 5–10 min earlier than the appropriate time resulted on several occasions in the capture of as many as eight animals.

Activity Phase in Relation to Season

Middle of activity occurred after midnight in nearly all cases for kangaroo rats in the field, i.e., there was usually a negative phase-angle difference (Fig. 2). The only positive values occurred in mid-winter, and maximally negative values occurred at the autumnal equinoxes. The annual range of change in $\psi_{midpoint}$ was 24 min.

In general the beginning of activity was advanced relative to sunset near the equinoxes and delayed near the solstices (Fig. 2). This was readily apparent from December 1969 to December 1970, but less so in 1971. Although onset of activity showed a great advance in early November 1971 equal to the great

advance at the same time in 1970, I have no adequate explanation for the great delay in onset of activity at the autumnal equinox in 1971, which does not correspond to the pattern in 1970. The annual range of change in ψ_{onset} was 28 min, based on seasonal changes in the population extreme for each 3-day period of measurement (Fig. 2).

One of the most striking observations in the field was that in autumn the kangaroo rats were active on the surface for a short while in the morning following the observed sunrise (Fig. 1). This was the only time of year in either evening or morning that normal activity was observed when the sun was above the skyline. In general the end of activity was maximally delayed relative to sunrise near the autumnal equinoxes and maximally advanced near the spring equinoxes. At both the winter and summer solstices values of ψ_{end} were intermediate to those at the equinoxes. The annual range of change in ψ_{end} was 57 min, based on seasonal changes in the population extreme for each 3-day period of measurement (Fig. 2).

Light Intensity at Beginning and End of Activity

The range of light intensities over the 2-year period was approximately 200–2,000 lux for beginning of activity and 50–20,000 lux for end of activity, based on seasonal changes in the population extreme for each 3-day period of measurement (Fig. 4). Most of the time the animals began activity at a lower light intensity than that at which they ended. The annual changes in the light intensity at which activity began and ended closely followed the changes in time of onset and cessation of activity (cf. Fig. 2). Thus they corresponded in frequency and amplitude to the seasonal changes mentioned in the previous section.

Field observations were generally conducted under clear skies. A notable exception was the evening of 22 December 1971, when the sky was heavily overcast and air temperature was 7° C at sunset. Observations had been made on the two previous nights under clear sky with air temperature at sunset about 2° C. The first three animals emerged at light intensities much lower than usual (Fig. 4, 22 December 1971). The time of emergence was not earlier than usual, as one might expect a priori for a darker sky; rather the first emergence was 26 min later relative to sunset than the first emergence on the two previous nights. It is probably more reasonable to correlate this delay with the altered light intensity than with temperature or humidity, since variation in the latter two factors was much greater on many previous 3-day periods during which little variation was shown in beginning of activity.

Activity Phase in Relation to Lunar Cycle

There was no apparent relationship between the presence or absence of the moon above the horizon at dusk and dawn and the time of onset and end of activity (Fig. 5). In fact, the kangaroo rats began and ended activity at light intensities much brighter than 0.5 lux (Fig. 4), which is the approximate
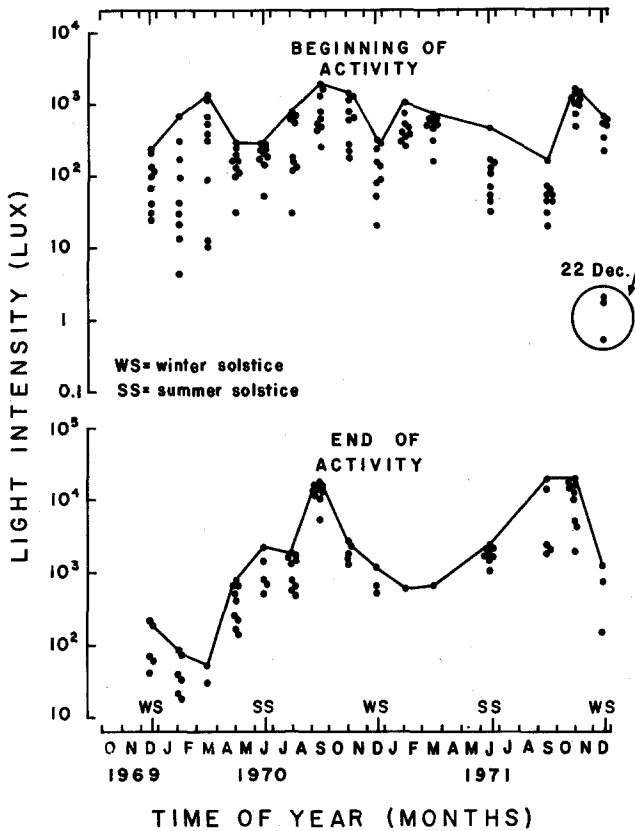
Fig. 4. Light intensity at beginning and end of activity for *D. microps* and *D. merriami* in the field near Big Pine. Points represent the same animals as those in Figure 2. The extreme records of each 3-day observation period are connected by a solid line

light intensity of full moon on a clear night. The data points for specific calendar months are closer to each other than to points for other calendar months occurring at the same part of the lunar month (Fig. 5), indicating that seasonal changes in the response of the animals to light intensities at twilight are greater than any possible lunar responses. Additionally, the variation in beginning or end of activity for some days of the lunar month was as great as for the lunar month as a whole (Fig. 5)

Various effects of moonlight on the overall nightly activity patterns of nocturnal rodents have been suggested by many casual remarks in the literature, but little attention has been given to thorough documentation of possible effects of moonlight. Pearson's (1960) measurements of activity in free-living *Reithrodontomys megalotis* variously showed a positive effect, a negative effect, or no effect at all of moonlight on activity, depending on the way the data were analyzed. It has recently been shown, however, by elaborate field recordings that *Dipodomys spectabilis* avoids visiting exposed feeding stations during moonlit portions of the night, particularly at seasons where the night is long enough to allow for this habit (Lockard and Owings, 1974a, b).
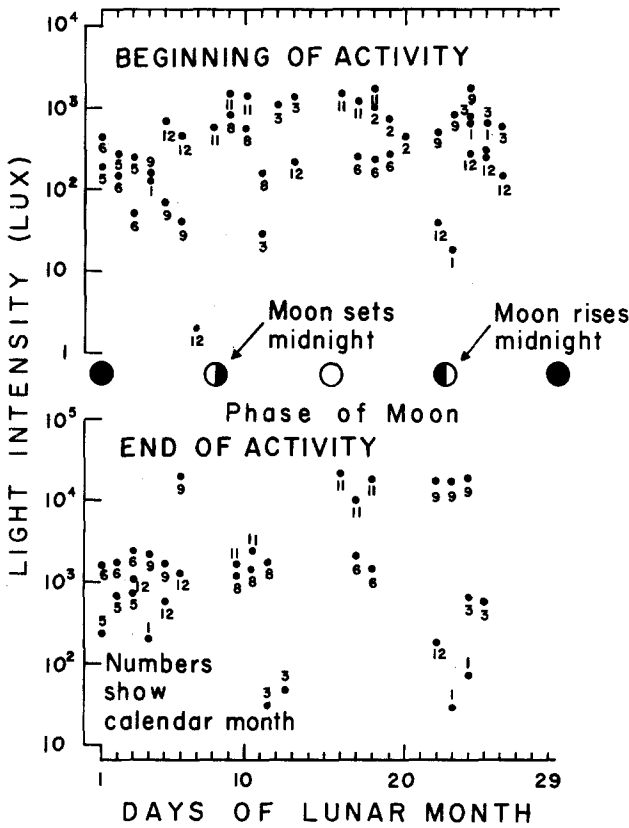
Fig. 5. Light intensity at beginning and end of activity for *D. microps* and *D. merriami* in the field near Big Pine, as a function of the lunar cycle. The data points consist only of the single daily extremes of evening and morning from the data of Figure 4, but are arranged according to the day of the lunar month on which the original field observations were made

Effects of Latitudinal and Seasonal Extreme on Daily Periodicity

Kangaroo rats (*Dipodomys*) occur between 18° and 51° N. Lat. (Hall and Kelson, 1959). The *D. ordii* observed in southern Saskatchewan in early July 1970 are the northernmost population of kangaroo rats of any species. At the season of the field studies in Saskatchewan these animals were undergoing the shortest nights experienced by any natural population of kangaroo rats at any season or locality. Although these *D. ordii* differ in habitat, behavior, and population density from other species of *Dipodomys*, the observations made at this unique latitudinal and seasonal extreme do provide a useful estimate of the activity of kangaroo rats in general under the constraints of short nights.

Average length of nighttime (sunset to sunrise) was 7 h 43 min. Average activity time (average daily extreme onset to average daily extreme end) was only 6 h (Table 1). Therefore the ratio of activity period on the surface at night to period of occupying the burrow in the day was 6:18. It is now obvious

Table 1. Beginning and end of activity for individual *D. ordii* in Saskatchewan (50°45′ N. Lat.) on four consecutive evenings and mornings, 9–13 July 1970. Record is not shown for more than the first three animals active on any one night. Lack of concurrence between some successive evening records of light intensity was due to the presence of large cloud masses near the western horizon.

Night of observation	Minutes past standard sunset	Light intensity (lux)	Minutes before standard sunrise	Light intensity (lux)
1	54	1	—[a]	—
2	38	2	62	0.1
	60	0.1		
3	43	1	53	0.5
	73	0.1		
	73	0.1		
4	37	2	64	0.1
	55	0.1		
	65	0.1		
Average 43[b]			Average 60	

[a] No record after trapping began at 43 min before sunrise
[b] For the four absolute daily extremes only

that the requirements of *D. ordii* for being on the surface can be met within a relatively short time at night.

The 6-h time over which the population of *D. ordii* was active was not only shorter in absolute length than that of kangaroo rats at lower latitudes (cf. Fig. 1), but also occurred later relative to sunset and earlier relative to sunrise (Table 1) than the activity in California at any time of year (cf. Fig. 2). Light intensities at onset and cessation of activity for *D. ordii* in Saskatchewan (Table 1) were lower than those of *D. microps* and *D. merriami* in California for any time of year (cf. Fig. 4).

Light intensities at beginning of activity were greater than at end of activity (Table 1), which is the reverse of the situation at Big Pine at the summer solstice (cf. Fig. 4). The middle of activity (calculated from average daily extreme beginning and end of activity) was 8 min before midnight, i.e., a positive phase-angle difference of 8 min. This differs from the negative phase-angle differences of 12 and 17 min for animals at the summer solstices of 1970 and 1971 at Big Pine.

Observations of Free-Ranging Behavior

Field observations on the emergence and beginning of surface activity in individual kangaroo rats were made in the nearby vicinity in order to supplement the data from the regular trapping experiments. By sitting quietly at burrows known to be occupied, we were able to watch the behavior of animals as they emerged. We sometimes simultaneously saw as many as four animals from a single vantage point, at light levels comparable to those shown for first emergences in Figure 4.

Dipodomys microps and *D. merriami* were solitary within their burrows; thus the initial nightly emergence of individuals was not directly triggered socially. Animals often urinated or defecated near the burrow entrance within a few seconds of their first emergence; sand-bathing was also common. The most commonly sighted direct behavioral interaction (both intra- and inter-specific) was the threat or short chase by a resident of an intruding passer-by. I observed intraspecific locked fighting on three occasions during this study. The sighting of overt interactions was not commonplace. On some occasions, particularly at non-reproductive seasons, animals passed within several meters of each other without incident. On one occasion (described in detail elsewhere: Kenagy, 1976) a male *D. microps* copulated with a female outside her burrow entrance during the twilight at a light intensity of 5 lux.

Within about a minute of emergence, some individuals moved out into the open and began to forage. *D. merriami* moved around the edges of hillocks and shrubs in search of seeds in the sand, but *D. microps* climbed into shrubs after leaves. Although the foraging behavior of *D. microps* differs from the typical pattern for the genus (Kenagy, 1973b), *D. microps* does begin foraging in the tops of shrubs at the same light intensities at which *D. merriami* begins foraging in the soil.

The burrow sites of some individuals were observed during the night for as long as 3 h at a time. During these observations *D. microps* and *D. merriami* spent most of the time in their burrows and were rarely on the surface for more than 5–10 min at a time. At this rate, total time spent on the surface per night was generally only 1 to 2 h, and at times less. The observations of Tappe (1941) suggest that *D. heermanni* is at times only active on the surface for a total of about 1 h at night.

A series of observations on one *D. microps* suggests that 1) individuals may be remarkably precise in the time of onset of activity from one day to the next, and that 2) the emergence from the burrow need not be a direct, daily response to ambient light intensity. On the evening of 20 March 1971 two observers were stationed at the burrow of a *D. microps* which had plugged the main entrance to its burrow with sand upon retiring early that morning. All other possible entrances were visible to both of us. At 1805 h P.S.T. (33 min past observed sunset, light intensity 400 lux) the animal emerged abruptly, pulling the sand inward with its forelimbs. Its eyes were squinted, it blinked them several times, and finally moved off for foraging. By next morning the animal had again plugged the entrance. That evening the animal emerged at 1806 h (33 min past observed sunset, light intensity 380 lux), again squinting and blinking a few times before moving out to forage. Although this timing may have been coincidental, it is suggestive that individuals may show considerable day-to-day precision in the onset of activity, and that the endogenous state of an already synchronized animal may provide a sufficient cue for the onset of activity, without direct, de novo, daily response to a particular light intensity. It should also be pointed out that daily temperature cycles in the soil are also available as a gross cue to the progression of the day. It has been shown that *D. microps, D. merriami,* and *Perognathus longimembris* respond to changes in the profile of soil temperatures in the soil by locating themselves

at depths where the ambient temperature is the most economical metabolically; this response was observed not only on a seasonal, but also on a daily basis (Kenagy, 1973a).

Studies on Captive *Dipodomys merriami*

General

The beginning and end of running-wheel activity in captive male kangaroo rats generally followed the seasonal change in day length (Fig. 6). The beginning of activity occurred after standard sunset almost without exception. The end of activity was generally prior to standard sunrise, but occasional exceptions are apparent (Fig. 6). Because of the flatness of the terrain in Los Angeles, the times of observed sunset and sunrise did not differ greatly from official local sunset and sunrise.
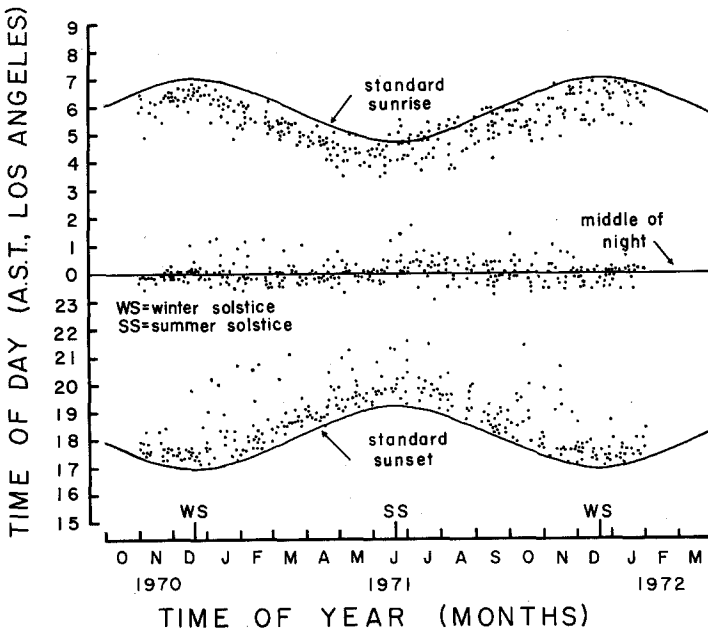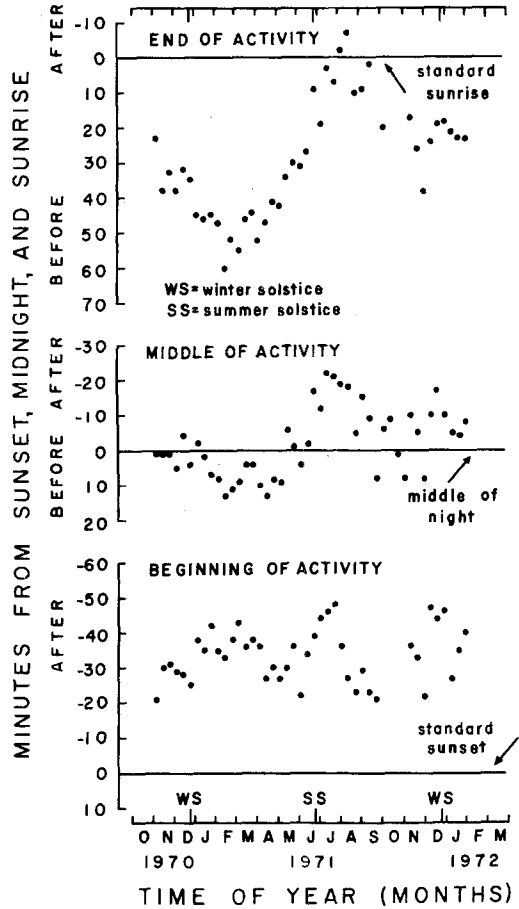

Fig. 6. Beginning and end of running-wheel activity depicted by individual, semimonthly extreme values for each individual in a group of 10 male *D. merriami* In Los Angeles. Points near sunset represent the semimonthly extremes in beginning of activity for each animal. Points near sunrise represent the semimonthly extremes in end of activity for each animal. Semimonthly values for middle of activity are calculated for each individual as the midpoint between the extreme beginning and end of activity (relative to sunset and sunrise respectively) and plotted on the middle date between those extremes. (Midnight A.S.T. is by definition on the midpoint between standard sunset and sunrise, see "Methods")

Fig. 7. Difference between beginning of activity and standard sunset (*below*), middle of activity and true midnight (*middle*) and end of activity and standard sunrise (*above*) for the group of 10 male *D. merriami* in running-wheel cages in Los Angeles. The daily extreme in the beginning and end of the activity for the whole groups was expressed in min relative to standard sunset and sunrise respectively, averaged over 10-day periods, and plotted at the corresponding time of day in the middle of each 10-day period; the midpoint of these 2 values is plotted as the midpoint of activity for the same 10-day period. (The four data points for both beginning and end of activity at the time of the previously mentioned anomalies occurring in late September and October 1971 are omitted from this plot)

The beginning of running-wheel activity in captive animals occurred later relative to sunset than activity in the field, and the end occurred earlier relative to sunrise than in the field (Fig. 7, cf. Fig. 2). Readings taken at intervals with the same photometer used in the field showed that running-wheel activity usually did not occur at light intensities greater than 1 lux, although some of the occasional extreme records (mainly for end of activity) were at brighter intensities. In contrast, surface activity in the field generally occurred at light intensities as great as 1,000 lux, or even greater (cf. Fig. 4). The beginning of running-wheel activity in captive animals generally occurred at lower light intensities than the end, which is the same relationship observed in the field. In general, the beginning and end of running-wheel activity in Los Angeles occurred within the period when the brightest stars and planets should normally be visible, whereas surface activity near Big Pine usually began and ended under skies in which stars and planets were not apparent.
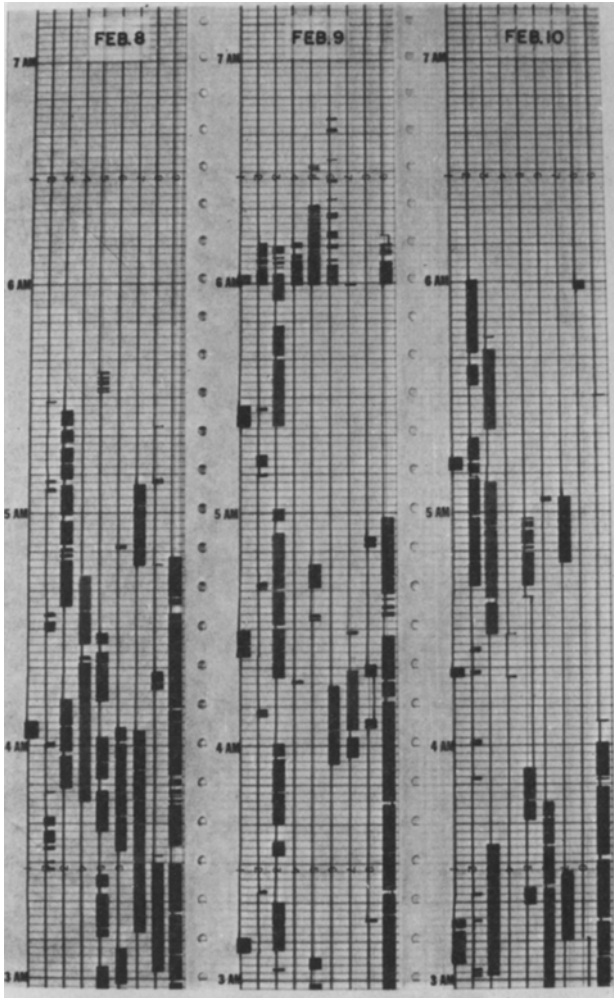
Fig. 8. Photograph of activity records of 9 male *D. merriami* in Los Angeles for mornings of 8, 9, and 10 February 1971. Responses to an earthquake are seen at 0600 h on 9 February. Animal 3 was still active at the time of the quake; channel 7 was activated once, probably by the earthquake itself; there were only 9 animals at this time because cage 10 (not represented in photograph) was unoccupied for several days.

An anomaly appeared in the behavior of the animals in late September and October 1971; this consisted of a marked delay in the onset of activity (occurring about 1 h after standard sunset) and an advance in the end of activity (occurring about 1 h before sunrise), resulting in a shortening of activity time (see Fig. 11) during a time of year when the available time for activity was increasing. These points were not plotted in Figure 7 to avoid obscuring the regular seasonal patterns. Although it is without explanation in terms of any natural factors, including weather, this systematic disruption of the normal

course of events is interesting because of its symmetry on both ends of the night.

The only significant departure of the activity time of the animals outside the normal time occurred on 9 February 1971, when an earthquake struck Los Angeles at 0600 h (Fig. 8). Magnitude on the Richter Scale was 6 and peak ground acceleration measured at U.C.L.A. was 0.1 times gravity. Six of nine animals emerged and began running precisely at 0600 h (Fig. 8). After 0644 h (1 min before sunrise), at which time animal 6 stopped running, there was no further activity during the daytime. Onset of activity that evening was normal, and the end of activity the following morning was also essentially normal (Fig. 8). The abrupt cessation of activity by animals 2 and 8, and the single revolution by animal 9 at exactly 0600 h (Fig. 8) may have been only coincidence. Seven of the nine animals increased their total activity (number of 10-min periods active) on the first night following the earthquake over the level of the night prior to the earthquake. This result was statistically significant (one-sided Wilcoxon signed-ranks text, $P = 0.037$) and suggests long-duration response to the earthquake. The data on cessation of activity on 9 and 10 February were omitted from all other analyses presented in this paper.

Individual and Group Variation

Each individual was occasionally the first of the group active in evening or the last active in the morning (Table 2 A and B). Thus no one or several animals predominated exclusively as the extreme individuals of evening or morning. However, the observed frequencies at which each animal was the first active in the evening or the last active in the morning do differ significantly (χ^2 test, $P < 0.001$) from frequencies expected for a uniform distribution within the sample of ten animals.

There was no strong tendency for the first individual active on a given evening to be the last individual active on the following morning (Table 2 C). Furthermore, individuals were not generally extreme at either evening or morn-

Table 2. Number of times on which each of 10 male *D. merriami* in running-wheel cages was A) the first individual active in evening, B) the last individual active in morning, or C) both the first and the last on the same night. Data cover a period of 457 days, of which a total of 445 evenings and 446 mornings were used in the analysis.

	Cage number									
	1	2	3	4	5	6	7	8	9[a]	10[a]
A) First in evening	12	29	25	70	61	17	7	46	91	87
B) Last in morning	54	54	23	42	25	29	50	58	77	34
C) First and last on same night	2	7	1	7	9	2	1	14	21	14

[a] Many of these records were immediately prior to death of animals

Table 3. Frequencies for each number of consecutive days at which each of 10 male *D. merriami* in running-wheel cages was A) the first individual active in evening or B) the last individual active in morning. Values based on the same data used for Table 2.

	Cage number									
	1	2	3	4	5	6	7	8	9[a]	10[a]
A) Consecutive days first in evening										
2	0	4	3	9	9	3	0	3	13	8
3	0	0	0	4	2	0	0	2	3	4
4	0	1	0	1	0	0	0	1	2	1
5	0	0	1	0	1	0	0	0	1	2
6	0	0	0	1	1	0	0	0	2[b]	1
B) Consecutive days last in morning										
2	9	7	2	4	3	6	6	6	6	4
3	1	0	0	2	0	1	3	4	2	2
4	2	0	0	0	0	0	1	0	3	1
5	0	1	0	0	0	0	0	0	1	0
6	0	0	0	0	0	0	0	0	2[c]	0

[a] Many of these records were immediately prior to death of animals
[b] Also first active for 8 consecutive days one time
[c] Also last active for 11 consecutive days one time

ing for much more than 1 or 2 days in a row (Table 3). About 6 consecutive days was generally the maximum period over which animals were extreme in either evening or morning. On no occasion was any animal the first active in evening and the last active in morning for 2 or more consecutive days.

There was generally more variation within the group in onset of activity than in end of activity (Fig. 6). This is substantiated by calculations of the standard deviation (S.D.) of the ten individual extreme onsets and ends for each of the 30 half-months from November 1970 through January 1972. [The reciprocal of S.D. of activity parameters has recently been used as a measure of precision by Aschoff et al. (1972).] The mean S.D. of onsets was 32.29 min and ends was 24.99 min (significantly different at $P < 0.01$). However, this trend is not significant in all cases when broken down by season. The only three-month seasons (bases were Nov.-Dec.-Jan., Feb.-Mar.-Apr., etc.) at which S.D. of onset of activity was significantly ($P < 0.05$) more than S.D. of end were Feb.-Mar.-Apr. and May-June-July; the greater relative scatter of onsets with respect to ends is particularly apparent during these six months of 1971 (Fig. 6).

Nightly Distribution of Running-Wheel Activity

Running-wheel activity was most intense during the middle part of the night (Fig. 9). In fact, the "center of gravity" of activity for the population generally
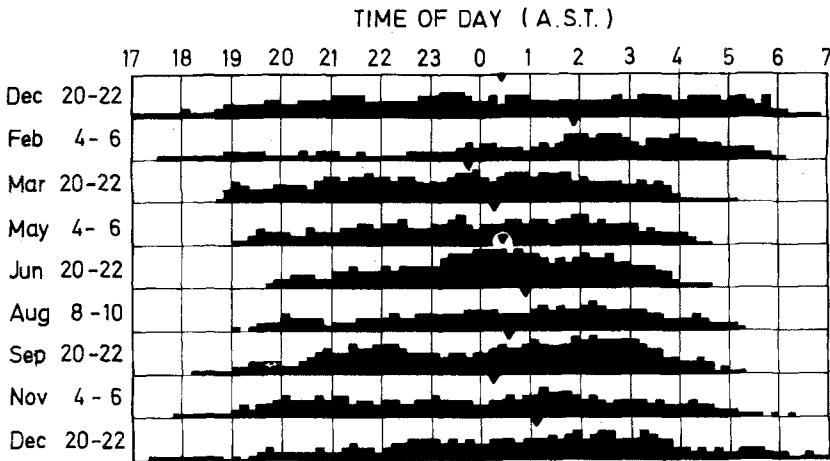
Fig. 9. Mean distribution of running-wheel activity throughout the night for each of 9 3-day periods between December 1970 and December 1971 in the 10 male *D. merriami* in Los Angeles. Each hour was divided into 6 10-min periods, and each of these 10-min periods was scored 0–10 (vertical scale) according to the number of animals which showed any activity at all during that period. The data for each of the 9 times of year represent the average number of animals active per 10-min period for a 3-day duration. The triangles indicate the 10-min period of each night during which the middle score ("center of gravity") of all such scored activity fell; because the activity is shown in A.S.T., 0000 h equals true middle of the night

occurred after midnight (Fig. 9; only exception 20–22 March). Only a few individuals were active in running wheels at the beginning and end of the night. This differs markedly from the onset of activity in the field, where many animals become active on the surface within a few minutes of each other during early twilight (Fig. 3).

Phase and Length of Activity (Mean Values)

Mean activity parameters (Figs. 10 and 11) were calculated for the captive animals for comparison with the analysis by population extremes in free-living (Fig. 2) and captive (Fig. 7) animals. Mean beginning of activity was generally $1\,^1/_2$ to 3 h after sunset (i.e., mostly following twilight), and mean end of activity was generally 1 to 2 h before sunrise (i.e., mostly before morning twilight) (Fig. 10).

During November and December 1970 (the first 2 months following capture of the animals) the mean beginning of activity (Fig. 10, lower) and mean length of activity (Fig. 11, upper) show a trend not apparent in the other analyses. Apparently some sort of "adaptation" to conditions of captivity in running-wheel cages was occurring, in that these data from late 1970 deviate from the subsequently established pattern, including values shown one year later. Further-more, the data on captive animals are more similar to the field data (Fig. 1) during the first two months of captivity than at any other time.
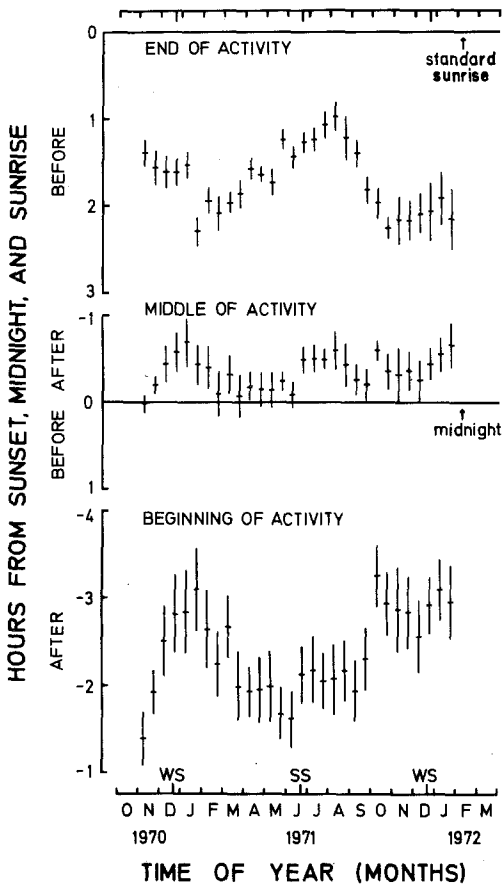
Fig. 10. Difference between beginning of activity and standard sunset (*below*), middle of activity and true midnight (*middle*), and end of activity and standard sunrise (*above*) for the 10 male *D. merriami* in running-wheel cages in Los Angeles. These values are population means of the average daily beginning, middle, and end of activity of each animal for each day, calculated as follows: beginning, middle, and end of activity were determined for each day of the 15-month period for each animal; these daily values were averaged during each of the 30 half-months for each animal; the 10 individual means for each half-month were averaged to produce the population means shown in this figure. Vertical lines show 1 standard error (S.E.) on each side of the mean. (In contrast, the values shown in Figure 7 are 10-day means of the single daily extreme in beginning and end of activity for the whole group of 10 animals)

Mean length of activity varied systematically with season, but was always much shorter than length of night (Fig. 11). The difference between length of activity and length of night varied from three to five hours during the year (Fig. 11, lower). Length of activity did not differ significantly between times of year at which photoperiod was equal (e.g., spring and fall equinoxes, etc.; Fig. 11, upper).

The previously mentioned symmetrical anomaly in onset and end of activity during September and October 1971 is also apparent in Figures 10 (beginning and middle of activity) and 11 (length of activity).

Activity Phase in Relation to Season

Laboratory Results and Their Relation to Field Data. Phase-angle differences for beginning, middle, and end of activity in the captive animals were analyzed in terms of 1) "population extremes" (Fig. 7) and 2) "population means"
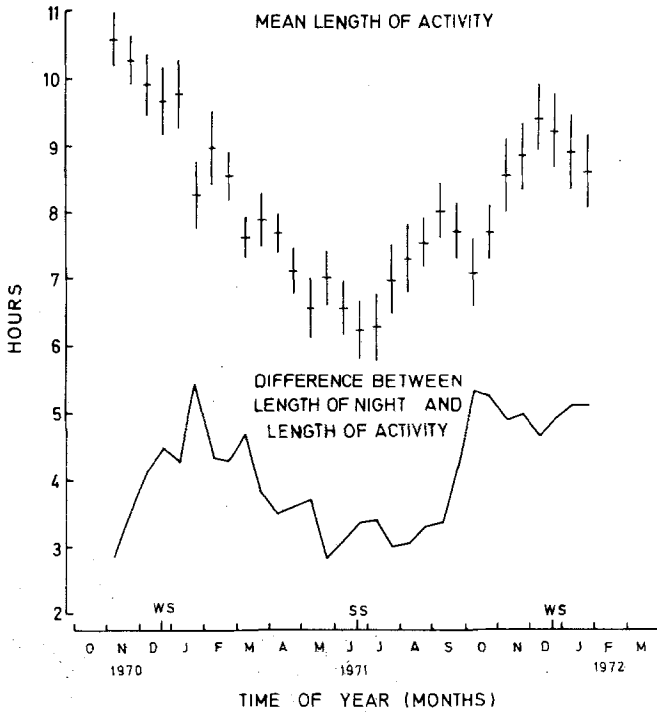
Fig. 11. *Upper:* Semimonthly mean length of nightly running-wheel activity for the 10 male *D. merriami* in Los Angeles, calculated from daily beginning and end of activity in each animal for each day, as in Figure 10. Vertical lines show 1 S.E. on each side of the mean. *Lower:* Difference between the semimonthly mean length of night (standard sunset to sunrise) and the semimonthly mean length of activity (as shown in the upper part of the figure).

(Fig. 10). Phase-angle differences are markedly dissimilar when determined by these two different analyses. Of the two analyses, the "extremes" analysis bears more resemblance to the situation in the field. A great difference between extremes and means would not be expected in the field (if it were possible to measure mean daily onset and end of activity for all members of a population) because we already know that most of the animals to become active did so within the first half hour of the first animal, and furthermore that most of these became active within the first 12 min (Fig. 3). Thus in the field the mean and extreme are close. The generality and utility of extreme onsets and ends of activity in the field is further indicated by the fact that neither the same individuals nor members of one sex predominated as the constituents of the "extreme" samples (see "Sexual and Social Comparisons"). The similarity in the field of extremes and means is of course important from the practical standpoint that extremes can be easily and discretely measured. In the laboratory only about 10 to 20% of the population of 10 animals was often active during the first hour or more of activity for the population as a whole (Fig. 9). The imprecision of onset and end of activity in the captive animals is also apparent in Figure 6. Thus in the laboratory the means and extremes are relatively far

Table 4. Amplitude, given as total range in min, of the seasonal changes in phase-angle difference for beginning (ψ_{onset}), middle ($\psi_{midpoint}$), and end (ψ_{end}) of activity for: 1) free-living population at Big Pine, where data are presented in terms of the population extremes in beginning and end of activity (Fig. 2); 2) 10 captive animals in running-wheel cages in Los Angeles, where data are also presented in terms of population extremes in beginning and end of activity (Fig. 7); and 3) the same captive animals, but with data presented in terms of mean daily onset and end of activity for all members of the group (Fig. 10). Roman numerals in parentheses show the number of maxima or minima during a year, i.e., the number of times the function cycled in a year, or the "annual frequency of ψ". The annual frequency of $\psi_{midpoint}$ could not be clearly determined; the low resolution of the $\psi_{midpoint}$-data are due in part to the fact that $\psi_{midpoint}$ is a direct function of two other functions (ψ_{onset} and ψ_{end}) which differ in frequency and amplitude.

	ψ_{onset}	$\psi_{midpoint}$	ψ_{end}
1) Natural population (extremes)	28(II)	24	57(I)
2) Captive animals (extremes)	33(II)	35	73(I)
3) Cative animals (means)	113(I)	42	80(I)

apart, which accounts for the dissimilarities of the phase-angle differences in the analyses by extremes and by means.

The following two sub-sections describe the differences in the magnitude of ψ and in annual changes in the frequency, amplitude, and phase of ψ as analyzed by the two methods. The seasonal changes in ψ for both laboratory and field are summarized in Table 4; the more detailed comparison of field and laboratory data on seasonal change in ψ (in the General Discussion) uses only the "extremes" analysis of the data on captive animals.

Analysis by Population Extremes (Fig. 7). The 10-day mean beginning of activity for the first animal active in the population each night showed two general advances relative to standard sunset (each about 2 months before the respective solstices) and two relative delays (each about a month after the respective solstices) during the first 12 months of the record (Fig. 7). The change in ψ_{onset} showed a range during the year of 33 min.

The 10-day mean end of activity for the last animal active in the population each morning followed a well defined course over the year (Fig. 7). There was a conspicuous advance in the end of activity relative to standard sunrise about 2 months after the winter solstice and a similar relative delay about 2 months after the summer solstice. Intermediates occurred about a month before the solstices. The change in ψ_{end} showed a range during the year of 73 min.

The midpoint of activity (determined from the above extreme onsets and ends) showed its greatest advance relative to midnight about a month before and after the vernal equinox, and its greatest delay about a month after the summer solstice (Fig. 7). Midpoint of activity occurred within at least 22 min of midnight throughout the year, and the annual range of change in $\psi_{midpoint}$ was 35 min (Fig. 7).

Analysis by Population Means (Fig. 10). The semimonthly mean beginning of activity for all individuals in the population showed a maximum advance relative

to standard sunset just before summer solstice and a maximum delay just after the winter solstices of both years (Fig. 10), allowing for the deletion of several records associated with the previously mentioned anomaly in September-October 1971 and the "adaptation" to captivity during November-December 1970. The change in ψ_{onset} showed a range during the year of 113 min (Fig. 10).

The semimonthly mean end of activity for all individuals in the population showed a maximum advance relative to standard sunrise after the winter solstice the first year and before the winter solstice the second year, and a maximum delay after the summer solstice (Fig. 10). The change in ψ_{end} had a range of 80 min during the year (Fig. 10).

The midpoint of activity (determined from the above mean onsets and ends) was maximally advanced relative to midnight at the equinoxes and some of the adjacent months, and was maximally delayed near the solstices. Midpoint of activity generally occurred after midnight throughout the year (Fig. 10) and the annual range of change in $\psi_{midpoint}$ was 42 min (Fig. 10).

General Discussion

General Nature and Distribution of Daily Activity in Kangaroo Rats

Populations of *Dipodomys microps* and *D. merriami* show above-ground activity throughout the night and during the whole year (Kenagy, 1973a; present study). Time from onset to end of activity near Big Pine, California, fluctuates between about $9^{3}/_{4}$ h in summer and $14^{1}/_{2}$ h in winter (Fig. 1). However, individuals of these and other kangaroo rat species do not remain on the surface throughout the whole night; in fact they may at times spend only an hour or two, or even less total time on the surface per night. The requirement for surface activity is also sufficiently met within the short 6-h activity time of *D. ordii* at the summer solstice in Saskatchewan, Canada; and even these animals are only on the surface at intervals during the night. The strict nocturnality of *D. ordii* at the latitudinal and seasonal extreme for the genus *Dipodomys* is evidence of a major difference in the activity pattern of kangaroo rats from that of several other types of rodents, most notably some microtines, which, particularly at higher latitudes, change the phase of their activity between night and day as the seasons progress (review by Erkinaro, 1969, pp. 21–24). The external, fur-lined cheek pouches of heteromyid rodents may be a preadaptation which has contributed to the evolution of the relatively shortened requirement for surface activity in the genus *Dipodomys*. By the use of these commodious cheek pouches, a kangaroo rat can gather large amounts of food on the surface without the necessity of hulling or otherwise processing, or of eating the food until the animals reaches the safety of its burrow.

Even though they apparently do not require all the time between the two twilights for surface activity, kangaroo rats are active in relatively bright twilight (Fig. 4). That *D. microps* and *D. merriami* continue to show activity in the morning twilight throughout the winter is especially noteworthy, since nights were long (Fig. 12) and temperatures in the last hours of the night were the
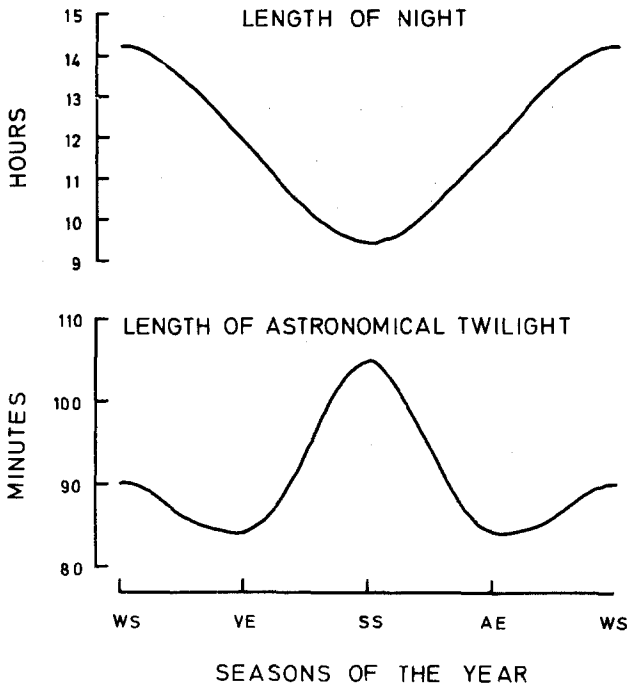
Fig. 12. Seasonal changes in length of night and length of astronomical twilight (time from standard sunset until sun is 18° below horizon) at 35° N. Lat. These values are nearly the same as for Los Angeles (approximately 34° N.Lat.) and Big Pine (approximately 37° N.Lat.). *WS* winter solstice, *VE* vernal equinox, *SS* summer solstice, *AE* autumnal equinox

coldest (measured as low as −19°C) to be encountered by the animals a. any time of year. The twilight activity of *D. microps* and *D. merriami* is of further interest in light of the findings of Lockard and Owings (1974a, b) that *D. spectabilis* discriminates between lighter and darker portions of the night by avoiding foraging in the open when the sky is moonlit; the light intensities at which *D. microps* and *D. merriami* were active in the twilights were as much as four orders of magnitude brighter than those of the sky at full moon.

Activity on the surface during the twilights also exposes kangaroo rats to added predatory pressure from day-active raptors. I have observed red-tailed hawks and rough-legged hawks at the study area during the normal activity times of *D. microps* and *D. merriami*. It is known that kangaroo rats may account for a small percentage of the normal diet of some day-active raptors (Fitch, 1948; Stendell and Myers, 1973). Kangaroo rats may also be taken under unusual circumstances by day-active raptors (Childs, 1952).

The preceding paragraphs point out four aspects of the paradoxical nature of the activity of kangaroo rats during the brighter portions of the twilights. Such extreme activity appears unnecessary because 1) the animals apparently do not require all the time in between the twilights for surface activity, and

2) the availability of food is no greater during the twilight than during the darker portions of the night. It would seem that such activity should be selected against because 3) the animals are exposed to additional predator species during brighter twilights, and 4) the animals are exposed to the coldest temperatures both daily and seasonally (applies only to the morning twilight).

What, then, is the survival value for kangaroo rats of being active in the brighter portions of the twilights? Maintaining temporal homeostasis of daily functions has obvious selective value, but it is not clear, in terms of our present understanding of circadian rhythms and their evolution, how selective pressures for more reliable synchronization of the circadian rhythm by a species' beginning and ending activity in bright twilight could have been so strong as to favor such activity. A further understanding of the mechanisms of synchronization of circadian rhythms (as discussed below) is necessary before the ecological importance of synchronization can be tested and evaluated in evolutionary terms. One of the possible ecological explanations of the activity of kangaroo rats in the bright twilights relates to social interaction and utilization of space. This possibility can be subjected to testing, and its basis is discussed in the following two paragraphs.

I should like to suggest that there might be a requirement for establishing or maintaining exclusive, or nearly exclusive, utilization of space ("territoriality") in the vicinity of the home burrow, which could be responsible for the emergence of many *D. microps* and *D. merriami* from their isolated individual burrows within minutes of each other in the early twilight. Several kinds of direct and indirect interactive behavior (both inter- and intra-specific) are performed at this time (see "Observations of Free-Ranging Behavior"), and these may function to establish spatial exclusivity, of which access to food is one important consequence. Direct interactions include short chases and locked fighting. Indirect interactions include such potential marking behavior as sand-bathing, urination, and defecation. Mating behavior, and its attendant preliminary interactions — important in only part of the year — are also known to occur in relatively early evening twilight (Kenagy, 1976). In the performance of these several kinds of social behavior, greater benefit might be expected to accrue to individuals performing them as early as possible, up to a limit. Selection by predation would occur against individuals becoming active too early, and selection by failure to maintain efficiently spatial exclusivity or by failure of individuals to encounter eligible mates would occur against individuals becoming active too late. Thus the onset of activity may be one of the most important times on the daily social calendar of solitary-living animals such as kangaroo rats. (Members of colonial species, on the other hand, maintain contact with conspecifics throughout the day and night.) It is not yet clear if there could be advantages to performing some of the interactions during the last minutes of nightly activity as well. In general, it seems that just as it is important for a territorial animal to extend its territory spatially to the maximum defensible limits, it may also be advantageous to extend the territory temporally to the maximum prudent limits.

The endogenous circadian rhythms of many animals show two programmed peaks of activity, associated with dawn and dusk (Aschoff, 1966). That social

interactions can be important at beginning and end of activity is supported by the observations of Ziesenis et al. (1975) that there are two daily peaks of aggressiveness in male *Mus musculus* in the laboratory, which are indeed associated with the two light-dark transitions. The group of 10 captive *D. merriami* in individual running-wheel cages did not show synchronous peaks of population activity at the beginning and end of the night (Figs. 6 and 9) as observed in the free living populations of *D. merriami* and *D. microps* (Figs. 2 and 3). A possible explanation of this is the social isolation or "deprivation" of the captive *D. merriami*. In experiments with 18 *Glaucomys volans* (night-active) and 9 *Tamias striatus* (day-active) all occupying the same large outdoor cage, Graefe (1961) found that the most intense population activity for these two squirrel species occurred in the first hour of their respective daily times of activity, i.e., not during the middle as in individually housed *D. merriami* (Fig. 9).

The time of activity on the surface is not the only daily time of general alertness in kangaroo rats. It has been shown that kangaroo rats and pocket mice move around within their burrows throughout the daytime; in warmer parts of the year, no *D. microps, D. merriami*, or *Perognathus longimembris* studied by automatic recording of radioactively tagged animals in the field remained in a single position in the burrow for more than half an hour at a time during the daytime (Kenagy, 1973a). This means that the onset of surface activity in these rodents represents a qualitative change in the nature of locomotor activity and not simply a gross change from the sleeping to the waking state.

In spite of many ecological differences in the two species, *D. microps* and *D. merriami* were equivalent in their times of onset and end of activity throughout the year. However, the relative activity of the two species during the full course of the night did differ. *D. microps* showed a gradual decrease in relative activity in the field during the four successive quarters of the night, whereas *D. merriami* showed an increase; it has been suggested that interspecific social interaction might play a role in this complementary activity pattern (Kenagy, 1973a).

Activity Phase in Relation to Season

Seasonal changes in ψ_{onset} and ψ_{end} differ from each other in two distinct ways (Table 4: field data, and laboratory data analyzed by "extremes"):
1) The annual amplitude of change in ψ_{onset} is about half that in ψ_{end}.
2) The annual frequency of change in ψ_{onset} is twice that in ψ_{end}.
No previous studies of seasonal changes in daily activity have found a pattern such as this (for reviews see Aschoff, 1969; Daan and Aschoff, 1975).

Considering these conspicuous differences between the annual courses of ψ_{onset} and ψ_{end}, it seems possible that these two functions might be influenced independently by separate environmental phenomena. Assuming still that length of twilight and length of day and night are the two most important environmental factors that somehow determine the phase of activity as a whole (Kavanau, 1962; Wever, 1967; Aschoff, 1969), I should like to suggest a possible explanation which is based on the resemblance of the annual courses of ψ_{onset} and ψ_{end} to the annual courses of length of twilight and length of night respectively (Fig. 12). Such an arrangement can be summarized as follows:

a) ψ_{onset} *and Length of Twilight.* The seasonal course of change in ψ_{onset} for *D. microps* and *D. merriami* resembles that of change in length of twilight, in that both show two cycles per year (Figs. 2 and 7, Table 4, cf. Fig. 12). The two cycles of ψ_{onset} between December 1969 and December 1970 in the field (Fig. 2) are in phase with the two cycles of length of twilight (Fig. 12); the two yearly cycles of ψ_{onset} in the laboratory (Fig. 7) are delayed by approximately one month (30°, where 1 year = 360°) with respect to ψ_{onset} in the field.

b) ψ_{end} *and Length of Night.* The seasonal course of change in ψ_{end} in these kangaroo rats resembles change in length of night, in that both show one cycle per year (Figs. 2 and 7, Table 4, Fig. 12). The annual cycle of ψ_{end} in the field (Fig. 2) is advanced by about 3 months (90°) with respect to the annual cycle of length of night (or delayed by 90° with respect to the annual cycle of length of day) (Fig. 12); the annual cycle of ψ_{end} in the laboratory (Fig. 7) is advanced by about one month (30°) with respect to ψ_{end} in the field.

It should be possible to test the responses of kangaroo rats to various experimental combinations of twilight length and photoperiod in the laboratory in order to see to what extent the responses correspond to those predicted from the present field observations.

In both a) and b) above, the modifying influences of other physical and biological factors may exert influences as well. Such influences might be responsible for minor year-to-year variation in ψ in nature, as well as differences between field and laboratory measurements. Environmental factors such as precipitation, temperature, and primary productivity, which vary from year to year, can give rise to year-to-year differences in the annual cycle of body weight and reproduction in kangaroo rats (Kenagy, 1973a).

The net result of the above mentioned differences in the annual course of change in ψ_{onset} and ψ_{end} is that $\psi_{midpoint}$ is a complex function bearing little resemblance to either ψ_{onset} or ψ_{end} alone. The model to which seasonal changes in the phasing of activity have commonly been related (Wever, 1965) supposes that changes in the length of the activity and rest components of the daily rhythm result from changes in the level of an oscillation above and below a threshold. In such a model the phase relationship of the activity cycle to the environmental cycle can only be considered from the midpoint of activity (in terms of $\psi_{midpoint}$), because the beginning and end of activity, which are merely the resulting times at which the oscillation crosses the threshold, are not fixed phase points of the oscillation. Therefore phasing of activity has generally been described in terms of $\psi_{midpoint}$ (Wever, 1967; Aschoff, 1969). The present data on kangaroo rats, however, suggest a relationship of seasonal changes in ψ_{onset} and ψ_{end} to seasonal changes in two different factors, namely twilight and photoperod respectively; for such cases it appears that the explanatory utility of $\psi_{midpoint}$ is limited.

In one regard there is agreement between the kangaroo rat data (Fig. 2, middle of activity) and the theory of seasonal phasing of circadian rhythms (Aschoff and Wever, 1962a; Aschoff, 1964; Wever, 1967; Aschoff, 1969): the $\psi_{midpoint}$ of kangaroo rats in the field showed a maximally positive relative

value—in fact the only positive value of each year—in midwinter. Such a relationship was first suggested by the Jahreszeiten-Regel (Aschoff, 1964), which is a seasonal application of the basic circadian rule (Aschoff, 1960). In other regards the present data on kangaroo rats are not consistent with theory. For example, it has been suggested that as activity time becomes longer, an animal should show greater relative advance in phase of activity with respect to the Zeitgeber (Aschoff, 1969); although the greatest relative advance in $\psi_{midpoint}$ for the animals in the field (predicted by the Jahreszeiten-Regel, as just pointed out) does occur shortly after the winter solstice, when the activity time is at its longest for the year, the corresponding greatest relative delay in $\psi_{midpoint}$ does not occur at the season of shortest activity time (at the summer solstice), but rather in the autumn (late September-November), when the animals also show a great delay in ψ_{end} (Fig. 2).

Evidence for Different Morning and Evening Responses to the Environment

It is possible that the beginning and end of activity in kangaroo rats are associated with two separate circadian oscillators, each synchronized independently by one of the two respective daily twilight transitions and in turn synchronized internally with each other as part of the integrated circadian system. The perception of the evening twilight by kangaroo rats follows a daytime of relative inactivity by the animal in total darkness, whereas the morning twilight follows a nighttime of occasional activity on the surface where light intensities begin to increase as daybreak approaches. Thus there are differences in both the state of activity of the animals and the light intensity perceived by the animals prior to each of the two daily twilights. In a hypothetical system of evening and morning oscillators, the beginning of activity would be synchronized by evening twilight, and, as suggested in the previous sections, would show seasonal changes with respect to sunset paralleling the changes in length of twilight. Similarly, end of activity would be synchronized by morning twilight, but would show seasonal changes with respect to sunrise paralleling changes in length of night. Synchronization by the action of the twilights implies non-parametric entrainment, but it is still possible for parametric effects to act on the system (Daan and Aschoff, 1975). Experimental investigations of the interaction of evening and morning components of such a system, as they continually change in opposite directions along with the sunset and sunrise during the course of the year, should lead to further understanding of the control of seasonal physiological cycles in the vertebrates.

Evidence is available in plants and in insects demonstrating separate "light-on" and "light-off" responses, which in some cases may represent separate oscillations within the overall circadian system (Engelmann, 1966; Tyshchenko, 1966; Chandrashekaran, 1967; Saunders, 1974; Hamner and Hoshizaki, 1974a, b). Studies of free-running rhythms in mammals under conditions of constant illumination demonstrate in at least a few cases that two separate self-sustained oscillators are associated with the daily cycle; in such cases the free-running circadian activity rhythm splits into two separate components with different

periods. Pittendrigh (1960) first pointed out this phenomenon in rodents, and Hoffmann (1971) studied the "splitting" of circadian locomotor activity in detail in a tree-shrew; it has also been reported in a squirrel (Pohl, 1972), and most recently in a bird, the starling (Gwinner, 1974). Although there is presently no strong experimental evidence, it is possible that the separate components observed in splitting could be differentially associated with the sunrise and sunset signals. Based on the evidence in the studies cited above, models of circadian rhythms have recently been constructed, which emphasize the independent synchronization of two separate components of the circadian rhythm with "on" and "off", or "dawn" and "dusk" signals (Danilevsky et al., 1970; Hamner and Hoshizaki, 1974a, b; Pittendrigh, 1974).

Synchronization of Daily and Seasonal Functions in the Vertebrates

Light is the most important Zeitgeber or environmental cue used by animals to synchronize their circadian rhythms. The daily light regime is also somehow involved via the endocrine system in promoting longer-term changes of state (e.g., cycles of reproduction, molt, etc.) in many organisms. Only a few vertebrate species, which have been selected by physiologists as "models", have been throughly studied with regard to mechanisms of control of and interaction between daily and seasonal rhythms. Thus a truly comparative understanding of daily and seasonal rhythms in the vertebrates at both physiological and ecological levels has not yet been achieved. I should like to discuss four categories of criteria to be considered in comparing vertebrate species in this regard:

a) Natural Light Regimes. The nature of daily light regimes actually experienced by animals (Fig. 13) is more diverse than indicated by the usual two simple cases of day activity and night activity. Perhaps some new patterns will become apparent from applying a more diverse taxonomy of light regimes. The daily light regime of nocturnal, burrowing rodents, such as kangaroo rats, differs from those of other types of animals in that it consists of relatively high intensity light pulses at the beginning and end of activity (Fig. 13). Nocturnal, burrowing rodents are similar to day-active animals in that they experience higher light intensities during their activity period than during their rest period; in this sense, these animals might be considered "light active". In fact, the only animals which could normally be exposed to brighter light during their time of inactivity than during activity are some of the Night-active I animals. Another kind of difference is that type-II or type-III animals (for example, inhabitants of burrows, holes, or caves) must actively select their daily light regime, whereas type-I animals are passively exposed to the natural daily light-dark cycle. It may be important in some experimental situations to offer type-II animals the opportunity of selecting their natural daily light-dark cycle by providing them with a closed nest box. Indeed the captive kangaroo rats in Los Angeles normally plugged their burrow entrances with sand, so that they presumably spent the daytime in total darkness. Daan and Aschoff (1975) have recently pointed out that synchronization of activity is more precise under conditions of rapid change of light intensity. It should be possible to test
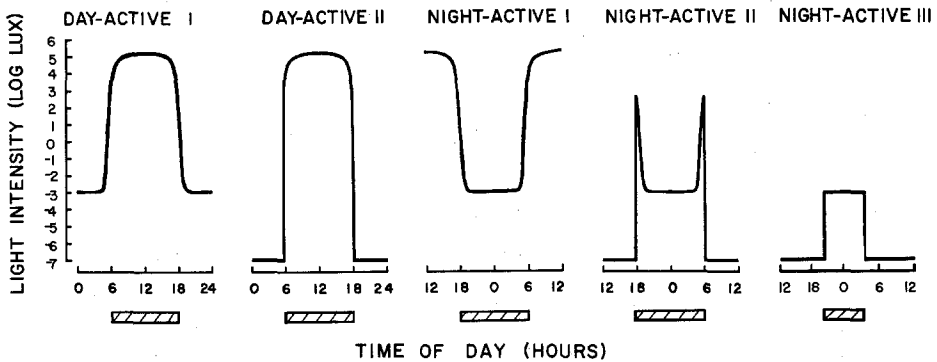
Fig. 13. Five of the simplified, general types of daily light regimes experienced by different types of animals. The hashed bars represent the activity time of the animals (10^{-7} lux = "physiological darkness"; 10^{-3} lux = sky on clear, moonless night; 5×10^{-1} lux = night sky at full moon; 10^5 lux = sky on clear day). *Day-active I.* Day-active animals which rest at night essentially under the open sky (e.g., many birds and the large mammals) experience the complete natural light-dark cycle, including the full extent of both twilights. This light regime would, however, also be experienced by non-burrowing animals which are active predominately in the twilights. *Day-active II.* Day-active animals which rest at night in a burrow or nest hole where light intensity may be that of total darkness (e.g., ground squirrels or to some extent the hole-nesting birds) emerge from darkness to join the daily light-dark cycle in the midst of morning twilight. The animals retire permanently for the night during the evening twilight. *Night-active I.* Similar to Day-active I, in that these night-active animals (e.g., some owls) experience the complete natural light-dark cycle. *Night-active II.* Night-active animals which rest by day in a burrow or cave where light intensity may be that of total darkness (e.g., kangaroo rats and other burrowers, or cavernicolous bats) emerge from total darkness to join the natural daily light-dark cycle in the midst of twilight, continue their activity at the light intensities of the night, and remain active into the midst of morning twilight. *Night-active III.* Any night-active, burrowing animal which does not begin and end its activity during the twilights would not experience the two peaks of light intensity to which Night-active II animals are exposed

this idea further by comparing the precision of synchronization among species naturally exposed to different kinds of light regimes and also among those showing different phase relationships to a given kind of light-dark cycle.

b) Photoreceptive Physiology. The reception of and response to light differs greatly among the vertebrate classes. For example, birds can synchronize their daily activity and show a photoperiodic gonadal response to light cycles even when blinded, whereas mammals require the eyes for such normal function; the role of the pineal varies among the vertebrate classes (Menaker, 1974). The nature of synchronization of the daily activity rhythm also differs between mammals and birds. For example, the daily activity time of birds shows a closer resemblance to day or night length than does the daily activity time of mammals (Aschoff, 1969); the resynchronization to an artificial shift of the Zeitgeber is generally more rapid in birds than in mammals (Hoffmann, 1969); and mammals require a larger critical amplitude of the light-dark cycle than birds in order to become entrained experimentally (Hoffmann, 1969).

c) Endogenous Rhythms of Activity and Sensitivity to Light. That many animals show two daily peaks in the endogenouus activity drive (Aschoff, 1966) suggests that the form of a circadian rhythm is adaptive to temporal ecological requirements for activity; such endogenous peaks match the times of intense activity of these species in nature. Animals also show an endogenous daily rhythm of sensitivity to light, which is measured as a "phase response curve" (Aschoff, 1965b). It is adaptive for an animal to respond to potentially synchronizing stimuli when they are likely to be offered and to ignore extraneous stimuli which might be delivered at inappropriate times, but we do not yet know in what way the exact form of phase response curves reflects adaptation to the natural light regimes (Fig. 13) to which various species are exposed. Interactions of the daily rhythm of sensitivity to light with seasonal changes in day length may also play a role in mechanisms of seasonal change in the state of animals. Comparative studies in the laboratory should reveal the extent of the diversity of adaptive matching a) between the endogenous pattern of daily activity and the ecological requirements of a species, and b) between the endogenous daily rhythm of sensitivity to light and the natural light regime experienced by a species.

d) Special Ecological or Behavioral Characteristics. The daily activity rhythm in nature also shows adaptive variation as a function of special ecological characteristics, even in animals otherwise similar with regard to a), b), and c). For example, the daily light regime of kangaroo rats resembles that of cavern-dwelling bats. However, there are differences in the behavior of bats and kangaroo rats at the onset of activity. Emergence of a population of bats from a cave is a phenomenon involving direct social stimulation, and furthermore it may occur following "light sampling behavior". Up to 15 min before the emergence of several hundred bats en masse from small entrances in a cave, there are a few individuals which occasionally fly out into the twilight and return to the cave; these test flights increase in intensity until finally large masses of bats fly out and forage (Twente, 1955). Kangaroo rats, on the other hand, are solitary within their burrows, and their first emergence from the burrow generally leads to a bout of activity on the surface. As another example, the onset of activity in one species of bat is more closely correlated with temperature than light intensity within the twilight time, in that the animals emerge later on warmer days and earlier on cooler days (Engländer and Laufens, 1968). It is possible that this situation or at least others like it could also be a reflection of day-to-day variation in the availability of insects as a function of temperature. It is apparent that a variety of ecological conditions – such as food availability and foraging requirements; predator presence; physical factors in addition to light, such as temperature and moisture; and social biology – interact to determine the exact temporal patterns of individual species on both daily and seasonal bases.

In conclusion, the four general criteria which I have mentioned should be useful in deriving a comparative approach to the temporal biology of species. Points a) and d) are environmental and ecological; points b) and c) represent adaptive physiological characteristics of the animals. It is of course likely, in

view of the diversity of biology, that animals apparently alike in all four of these points will show still further differences in the periodicity and synchronization of daily and seasonal functions. Such puzzles are the continual challenge to the comparative biologist and student of evolution.

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