

CIRCADIAN RHYTHM AND LUNAR PERIODISM IN
ONYCHOMYS LEUCOGASTER BREVIAURITUS
(RODENTIA; CRICETIDAE)

By

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CHAPTER I

INTRODUCTION

Objectives of the Study

The grasshopper mouse group, including the genus Onychomys, probably diverged from the Peromyscus line in Middle Miocene and became carnivores by Upper Miocene (Ruffer, 1965a). Bailey and Sperry (1929) found that 89% of the food eaten by Onychomys was of animal origin and that 79% of this was insect material. Onychomys is unique among the North American cricetid rodents because of its primarily entomophagous diet and associated nocturnal, predatory habits.

This study was aimed at determining the ability of the northern grasshopper mouse, Onychomys leucogaster brevicaudatus, (Figure 1), to respond to changes in light intensity, which are a primary factor in the environment of a nocturnal predator such as the grasshopper mouse, in an attempt to understand the degree of rigidity and flexibility in the daily and monthly activity patterns of the species. The major objectives were to learn how light intensity influences the amount and timing of activity, and to determine if the species shows a lunar periodicity. The activity patterns of this unique rodent could then be compared with those of other mammals, especially herbivorous rodents.

Previous Studies on the Behavior of Onychomys leucogaster

The behavior of Onychomys leucogaster has been studied by a few

workers. Bailey and Sperry (1929) recorded observations on the life history and habits of the genus from notes made on a small group of individuals collected over a period of 35 years (1887 to 1922). Egoscue (1960) made an extensive laboratory and limited field study of some aspects of the behavior of Onychomys leucogaster utahensis. Clark (1962) studied aggressive behavior in O. L. utahensis and examined the effect of chlorpromazine on aggressive behavior. Svihla (1936) studied breeding of northern grasshopper mice and Egoscue (1963) described color phases and their inheritance.

Hildebrand (1961) described the voice of the grasshopper mouse using an oscilloscope. The most extensive study of this genus has been carried out by Ruffer, (1964a, 1964b, 1964c, 1965a, 1965b, 1965c, 1965d, 1966a, 1966b, 1966c, 1968), whose work consisted of a complete study of sexual behavior, agonistic behavior, and the evolution of behavior.

Early Research on Biorhythms

Wallace Craig (1918) noted that "the overt behavior of adult animals occurs largely in rather definite chains and cycles..." The discovery that day length effects changes in metabolic pathways was made for plants by Garner and Allard (1920) and for animals by Marcovitch (1924) and Rowan (1926).

Circadian Cycles

Circadian, or daily cycles, have been studied in many animal forms, both invertebrate (Karakashian and Hastings, 1963; Adkisson, 1966; Barnwell, 1966), and vertebrate (Aschoff and Wever, 1965; Wahlstrom, 1965;

Bohun and Winn, 1966; Johnson, 1966).

To date, perhaps the best work on the problem of biological rhythms in mammals is that of DeCoursey (DeCoursey, 1959, 1960a, 1960b, 1961, 1964). She found that single 10-minute light periods can cause a change in the timing of the onset of the daily locomotor activity of flying squirrels, Glaucomys volans. Under natural conditions activity coincides with the period of darkness. This relationship is maintained throughout the course of the year by the interaction of an "endogenous" activity rhythm and a related daily rhythm of responsiveness to light (DeCoursey, 1960b).

Most studies on the spontaneous locomotor activity of mammals reveal a rhythm of about 24-hours. The activity is polyphasic. Most animals have at least two periods of maximum activity every day. The timing of the activity varies from species to species (St. Girons, 1966). In some species a single peak of activity occurs every 24 hours, and other species may have three or more peaks. The majority of species, however, exhibit two main peaks of activity (Aschoff, 1966). Aschoff noted that this type of pattern has been reported for the American moose, Alces alces andersoni (Geist, 1963) and the tree shrew, Tupaia glis (Vandenbergh, 1963). Most of these species show a pattern in which the first peak is larger than the second (bigeminus). The other type of pattern in which the second peak is the larger (alternans) is less common (Aschoff, 1966).

Black rats, Rattus rattus, and brown rats, Rattus norvegicus Figala, (1965), white-footed mice, Peromyscus maniculatus (Johnson, 1926), and deer mice, Peromyscus leucopus (Belmey, 1936) show a bimodal activity pattern with the largest peak at sunset and a smaller peak just before

sunrise. European squirrels, Sciurus vulgaris (Shorten, 1954), red squirrels, Tamiasciurus hudsonicus (Hamilton, 1939), and ground squirrels, Citellus pygmaeus (Ivanov, 1957) have two activity peaks: one in the morning and one in the evening.

Lunar Periodicity

There is much evidence for a fundamental solar-lunar rhythm in marine organisms. These periodicities adjust activities to the solar day and the ocean tides. Most investigations of fresh-water and land organisms have been concerned with daily cycles. The role of a lunar periodicity in non-marine species may include regulation of activity and feeding schedules of birds and mammals in intertidal regions, the regulation of reproductive activity of animals with near-monthly or semimonthly cycles, or adjusting the amount of activity to the brightness of natural nocturnal illumination (Brown, 1967). Anderson (1966) notes that feeding behavior and other activities associated with periods of low light intensity may have evolved as a protective or avoidance mechanism to escape attack by nocturnal predators.

There has been a limited amount of work done on the problem of lunar periodicity and the related problem of response to light intensity in terrestrial species. Justice (1960) studied the activity rhythms of the Merriam kangaroo rat, Dipodomys merriami, the bannertail kangaroo rat, Dipodomys spectabilis, and the wood rat, Neotoma albigula. He noted that when kept in constant 24-hour darkness all three species had persistent daily rhythms of lunar periodicity which disappeared after the first few days in constant 24-hour darkness, and he found no evidence of lunar influence on activity. Justice did note that the wood

rat may be active within the protection of its den structure on moonlit nights, but was never seen to venture into unprotected areas of the habitat except when no moon was visible. The bannertail kangaroo rat stayed within its den when the moon was far enough above the horizon to produce distinct shadows. The Merriam kangaroo rat was found to stay out of its burrow longer after moonrise, but its activity was confined to areas of deep shadow. Cowgill et al. (1962) described an apparent lunar periodicity in the sexual cycle of the brown lemur, Lemur fulvus, the white-fronted lemur, Lemur albifrons, the Senegal bush baby, Galago senegalensis, and the potto, Perodicticus potto. Their data suggest a correlation between peaks of sexual activity and the cycle of the moon in Lemur species and possibly in the bush baby.

Brown (1965a) proposed a lunar periodicity in hamsters, Cricetus cricetus. He maintained two male hamsters in unvarying low illumination in the same enclosure: one for $9\frac{1}{2}$ months and one for $7\frac{1}{2}$ months. Both hamsters independently adopted and held for extended periods a lunar-day frequency which was reached abruptly from both significantly higher and lower frequencies. Furthermore both hamsters initiated activity at moonset.

Johnson (1939) suggested a semi-monthly variation in the progression on onsets of activity over the solar day in the deer mouse. Brown also reported substantial lunar variations in activity of male rats, Rattus norvegicus, held in continuous dim illumination (Brown, Shriner, and Ralph, 1956; Brown and Terracini, 1959; Terracini and Brown, 1962). In both studies the rats displayed much greater activity when the moon was below the horizon than when above. In the 1956 study the variation coexisted with a conspicuous 25.25 hour circadian periodism. In 1959,

the lunar periodism was large.

Prior to this study, there has been no systematic evaluation of the rhythmic behavior of the grasshopper mouse. Trapping results (Ruffer, personal communication; and personal observations) suggest that grasshopper mice are more active on moonless than on moonlit nights. The increased trapping success, under environmental conditions of low light intensity indicates that the species is probably responsive to light intensity and may show circadian and lunar periodisms in response to changing light intensity. Light may have influenced trapping results in two ways. One, the animal may have been less active during moonlit nights, alternately, the animals may have been equally active on moonlit nights and moonless nights with the difference in trapping results due to the animals confining their activity to the close proximity of the nest when light intensity was high. This study was aimed at determining how light actually does affect the behavior of grasshopper mice.

CHAPTER II

METHODS

Criteria of Activity Measurement

The activity of the grasshopper mice was determined as to time of occurrence and by the amount of activity. Time was measured on a 24 hour scale with 0000 at midnight and 1200 at noon. Time of activity was measured from the instant the animal left the nest to the time it re-entered the nest. Such a time interval was termed an activity burst. The amount of activity was measured in feet moved per activity burst and in feet moved per hour.

Description of the Apparatus Used

The method used in the present study was a modification of the technique developed by Graham and Ambrose (1967) at the University of Michigan. The technique does not require the investigator to be present continuously and permits uninterrupted monitoring of activity. As first developed by Graham, the automated recording device periodically located a radioactively tagged vole in a 30-foot-diameter enclosure every six minutes (Graham and Ambrose, 1967). The apparatus used in this study, however, recorded the location of the animal every 50 seconds.

The detection device was a gamma scintillation probe which consisted of a 1" x 1" thallium-activated sodium iodide crystal (NaI-Tl), a Dumont 6467 Photomultiplier tube, a tube socket, and an aluminum

housing. The NaI crystal was coupled to the phototube with a high viscosity optical liquid (Baird Atomic Model D-C77) covered with a rubber shielding and taped with lightproof tape. The probe was mounted on the end of a 6' 9" boom. The boom extended from a turntable which rested on a shaft connected to the motor. The shaft was supported by bearings (Figure 2).

A Baird-Atomic Model 435 Linear Log Ratemeter, located on top of the turntable, received the signal from the probe (Figure 3). The intensity of radiation from the radiation source in the mouse decreases as the square of its distance from the probe. By setting the ratemeter on log scale the signal at the recorder could be made to change linearly and proportionally with the distance. The signal from the ratemeter was fed into an analog circuit of a Rustrack miniaturized automatic chart recorder. An event channel also recorded the signal from a switch that was activated every time the boom passed north. The signal and power from the ratemeter were passed through two commutator devices located on the shaft within the housing (Figure 4).

The experimental animal was subcutaneously injected with one or more 50-100 microcurie sources of 1 cm x 18 ga. Tantalum¹⁸² wire. The emission was high-energy gamma radiation with only small amounts of beta radiation. The half-life of the sources was 119-120 days. In later experiments, more than one source was injected into the mouse to achieve the desired radiation intensity. Sources were obtained from the radiation laboratory of the University of Michigan.

The animal was anesthetized and the source or sources were injected. A calibration series was made on each animal and isotope combination by starting at the base of the boom and moving the animal, confined in

a small box, at one foot intervals. Peak radiation was recorded when the boom was directly above the animal. From the height of the peak, it was possible to determine how far from the probe the animal was when the boom was closest to it on a given revolution. The distance could be computed from the record to within one foot. If the mouse remained in the same spot, the next revolution of the boom would produce a record exactly like the previous one. If it moved the peak would increase or decrease in height depending upon whether the mouse moved away from or toward the probe. From the chart record it could also be determined (by the height of the trough between the peaks) whether the mouse was located to the inside of the circle inscribed by the rotating boom or toward the outside of this circle. The differences in trough depth were due to the differences in radiation intensity detected by the probe when it was on the opposite side of the enclosure from the mouse. A shallow trough indicated the animal was to the inside, a deep trough indicated the animal was to the outside. Peaks were also broader in profile when the animal was closer to the center (Figure 5). The direction of the animal from the center was determined by comparing the location of the peak to the north reference event on the recorder. The compass direction of the location could thus be established. By using a combination of these two knowns, the distance from the boom (and hence the distance from the center of rotation) and the compass direction the animal could be located to within one foot. Movement of the animal as the boom passed over it resulted in a skewed peak, which did not allow precise location and had to be discounted.

The output from the ratemeter was recorded as a series of peaks on the strip-chart paper and had to be read visually (Figure 5). Grass-

hopper mice spent a large amount of time in the nest when no activity was recorded.

The chart was read on a scale of 6.66 units per revolution of the boom. North was given a value of 1 on the scale, the nest was at 2. The next time the boom passed north the reading was 7.66. On the next passage the reading was 14.32 and so on. The activity was read on this continuous scale starting when the animal left the nest and ending when the animal again re-entered the nest.

The data were fed into a programmed computer in the following form: scale value and corresponding peak height, the time of the initiation of each activity bout, day number, and mouse number. The program contained the following information: 8 units= 1 minute, 6.66 units= 1 revolution, and law of cosine. From the time axis, the angle between the two radii from the center could be computed. From this angle and the length of the radii, the straight line distance from the two points was calculated by the law of cosine. The computer pooled the total calculated distance for each hour, and each activity burst and these data were used as an estimate of the true distance moved. The computation does not give exact distance because (1) the animal does not move in a straight line, (2) errors of up to one foot in measurement occurred, (3) some data were deleted due to skewed peaks, and (4) there were judgment errors in reading questionable peaks.

The boom was powered by a 2 rpm gear motor. A Hub city 2:1 gear reducer was used to reduce the speed to approximately 1 rpm. The actual rotation time of 50 seconds was caused by the low torque load on the motor.

Indoor Enclosure and Experiments

Experiments 0-4 were carried out in an indoor controlled-environment room located on the campus of Oklahoma State University in Stillwater, Oklahoma (Figure 6). The room was provided with ventilation fans running through light baffles (Figure 7). Heat was provided in winter by an electric heater. A thermostat controlled temperature to $70 \pm 10^{\circ}\text{F}$. No attempt was made to control humidity. The building was completely lightproof, and a light lock was installed to allow the experimenter to enter without light. The lock and enclosure were equipped with red light. David Ruffer (1964a) reported that grasshopper mice are insensitive to red light, as are most nocturnal species. The apparatus and mouse were located in a 13'10" by 19' 2" metal mouse-proof enclosure. The northeast corner of the enclosure contained a nest box opening, which opened into a nest box containing sand to a depth of 2' for burrowing (Figure 8). A 1" deep layer of sand covered the floor.

The indoor experiments consisted of four experiments on graded light intensities (0-58.5 foot-candles) during the night period and a reversal of photoperiod experiment. These experiments were carried out to see if grasshopper mice are sensitive to light intensity in determining the amount and timing of activity.

Day-night cycles were simulated by incandescent bulbs. The lights changed intensity at 0700 and 1900 hours Central Standard Time. The change was controlled by a time switch. For the first series of experiments (Series 0) the day period (0700 to 1900 hrs) was illuminated at 78 foot-candles. There was total darkness in the night period. The second series (Series 1) was a reverse of the first with light during the night period (1900 to 0700 hrs) and darkness from 0700 to 1900 hrs.

The next three indoor experiments were in full illumination (78 foot-candles) during the day (0700 to 1900) and in reduced light during the night period. Series 2 night-period was illuminated by 58.5 foot-candles. Series 3 was 39.0 foot-candles, and Series 4 was 19.5 foot-candles during the night.

Outdoor Study Area and Experiments

The second phase of the study was carried out in an outside enclosure subject to incident weather conditions and to natural light-dark and lunar periodisms. The objectives of this phase were to determine if grasshopper mice show a lunar periodicity and how the change in light intensity associated with the lunar cycle and climatic conditions affect the behavior of grasshopper mice. The animal enclosure was of the same dimensions as the indoor enclosure, and the orientation was identical with the nest box in the northeast corner (Figure 9). The boom turntable and unit were supported on a cement base set in the earth. A weatherproof housing, containing a heating and a cooling unit equipped with a thermostat and the ratemeter, was set on top of the turntable (Figure 10). The power leads entered the enclosure from the north and passed underground to the turntable. The signal leads left via an aerial route. The sides of the animal enclosure were set 3' into the ground and extended 3' above the ground. The pen was surrounded by a large fence with a locked door. A double-strand electric fence surrounded the top of the fence to keep out predators. The entire enclosure was covered at a height of 6' by 18-gauge wire strung at 1-foot intervals as a deterrent to avian predators (Figure 11).

The light intensity recorder and activity recorder were housed in

two weatherproof units fashioned from refrigerators. Leads from the ratemeter and signal switch led to the refrigerators (Figure 12). The photocells for measuring light intensity were housed on top of one refrigerator. Besides the recorders, the refrigerators contained a heating unit, a cooling unit, extra charts, and a time switch (Figure 13). Power for the installation was obtained from two 30-amp lines. One line supplied the refrigerators and the other supplied the unit. The floor of the pen was covered with sand. A 6-ply plastic sheet was placed 3" under the sand to retard weed growth. The sheet was not placed in the northeast corner to enable the mice to burrow in this area (Figure 14).

Source of Experimental Animals

Experimental animals were obtained by live-trapping with Sherman and Havahart live traps. Best results were obtained on moonless or cloudy nights (Figure 15). All trapping was done on the Southern Plains Experimental Range which is located one mile north of Fort Supply, Harper County, Oklahoma (Figure 16).

Animals were transferred to Stillwater by car and housed individually in outdoor hardware-cloth enclosures set 1" in the ground (Figure 17). Animals were used directly from these outdoor pens. The animals were stored outdoors to insure conditions that were as close to the natural habitat as possible and to prevent entrainment to unnatural laboratory conditions.

Diet of Experimental Animals

Animals were fed a mixture of bird-seed, sunflower seed, oats,

and rabbit pellets supplemented by small mammals, insects, and meat scraps. Food and water were available ad libitum.

CHAPTER III

RESULTS

Degrees of Light Intensity in the Laboratory Situation

The results under 0 foot-candles from 1900 to 0700 are presented in Table I and in Figures 18-22. The results of the 19.5 foot-candles from 1900-0700 are presented in Table I and in Figures 23-25. Table I and Figures 26-28 present the results for 39.0 foot-candles, and the results for 58.5 foot-candles are presented in Table I and Figures 29-31. The results for the 39.0 and 58.5 foot-candles were considered together since no significant difference was found between them when compared by the least significant difference (LSD) method.

The average activity per hour over the six-day period was plotted for each mouse (Figures 19-22, 24, 25, 27, 28, 30, 31). From the Figures for the 0 foot-candle test it appears that there were three major activity peaks each day (Figures 19-22). The first peak occurred in the early evening (1900-2100); the second just after midnight; and the third in the early morning hours (0300-0600). The second peak is variable in position and may appear as two peaks when averaged over the six day period. There is some difference among mice in the timing of these peaks, but the trend can be observed in all. Brief bursts of activity occurred during all hours of the night, but they were inconsistent and small as compared to the major peaks. Such bursts averaged out over the six-day interval and are represented by the low level of

activity seen between the peaks (Figures 19-22). Activity during the daylight hours occurred occasionally, but was sporadic and of low magnitude (Figure 21).

The duration of activity was decreased and the onset of activity retarded under the higher light intensities (Figures 24, 25, 27, 28, 30, 31). Activity cessation remained the same due to the onset of 78.0 foot-candles at 0700. The onset of the higher light intensities prevented the period length from increasing.

There was a tendency for the activity to occur in the morning hours. Under the 19.5 foot-candles, the evening peak was considerably reduced or completely absent (Figures 24, 25). Under 19.5 foot-candles Mouse 4 showed some low-magnitude activity between 0700 and 0800 hours. All other mice confined all activity to the night period under 19.5 foot-candle intensity.

Under 39.0 and 58.5 foot-candles, sporadic activity occurred during the daylight hours (Figure 31).

For each mouse, the data for each test were classified by hour and day, and a factorial analysis of variance (AOV) was run on the pooled data for the males and for the females (Tables II-V). The probability that the level of day-hour interaction shown resulted from chance variation was high as indicated by the F test ($.10 < p < .25$ for both males and females under the 0 foot-candle test, $.10 < p < .25$ for males under the 19.5 foot-candle test, $.50 < p$ for females under the 19.5 foot-candle test, $.10 < p < .25$ for males under the 39.0 foot-candle test, $.50 < p$ for females under the 39.0 foot-candle test, and $.50 < p$ for both males and females under the 58.5 foot-candle test).

The variation due to differences among animals during the 0 foot-

candle test was highly significant. The probability of this value resulting from chance was less than 0.005 for all animals (Table II), indicating that there was an individual difference among the animals in the timing of the circadian rhythm, as shown in the graphs (Figures 19-22).

There was a difference between the sexes in the time of maximum activity under 0 foot-candles. In males, maximum activity occurred in the morning (Figures 21, 22). In females, the evening peak tended to be greater (Figures 19-21). The females also tended to be more active than the males but this difference in amount was not significant as determined by the AOV (Table IV).

Under 19.5 foot-candles there was a low probability that the difference among both male and female animals was due to chance (Table III). The significant differences indicated that 19.5 foot-candles, like 0 foot-candles, caused some variation among the individuals. Under the higher light intensities, individual variation was reduced, indicating that activity was highly influenced and that the amount and timing of activity were more uniform. The activity level was low for all animals, and was offset to the early morning hours. The females showed some degree of individual variation under 39.0 foot-candles but not under 58.5 foot-candles (Tables IV and V).

The results for the 0 foot-candle, 19.5 foot-candle, 39.0 foot-candle, and 58.5 foot-candle test were compared by an AOV made separately on males and females (Table VII and VIII). The results were then pooled, and the AOV was made on the pooled data (Table VI). The only significant difference found was that between treatments. The probability of this difference resulting from chance was less than .005,

indicating that grasshopper mice behaved differently under the different conditions of illumination (Table VI). The results for treatments were then compared using the least significant difference (LSD) method on the data for males and females (Table IV and X). The results under 0 foot-candles were found to differ greatly ($p < .001$ for all tests vs 0 in females, and $p < .001$ for 0 vs 39.0 and 58.5, and $p < .01$ for 19.5 vs 0 in males) from all other test results. The average for the 19.5 foot-candle test was larger in all cases from the 39.0 and 58.5 foot-candle averages. For males, activity under 58.5 foot-candles and 39.0 foot-candles was almost half or slightly more than half of the activity occurring under 19.5 foot-candles (Figure 32). This difference was not as great for the females, but all females were more active under 19.5 foot-candles than under the two higher light intensities (Figure 33). The low significance shown by the LSD test between 19.5, 39.0, and 58.5 foot candle tests ($p > .50$) was obviously due to the much greater amount of activity under the 0 foot-candles than in all other tests (Table I). The large discrepancy caused a bias in the test in the direction of large significant differences.

Since the large amount of activity under the 0 foot-candle test may have obscured differences between the 19.5, 39.0, and 58.5 foot-candles, a comparison was made using a factorial AOV for these three treatments (Table XI and XII). When an AOV was made on the pooled data, it showed that the differences due to the treatment main effects (light intensities) and the sex-treatment interaction had a low probability of being due to chance variation ($p < .005$). The significant differences indicated that light intensity affected activity and that males behaved differently from females. Males and females were analyzed separately

(Table XIII and XIV). The females showed a significant individual difference ($p < .005$) and a significant treatment difference ($p < .01$), since the F-test indicated that there was a low probability that the level of variation shown was due to chance. For the males, there was a significant treatment difference ($p < .01$). The results for these tests were then compared using the LSD method on treatments for males. Females were tested for treatment difference and individual differences. The LSD test for females showed a significant difference ($p < .05$) between tests with 19.5 and with 39.0 foot-candles. Females showed a significant difference in activity ($p < .01$) between 19.5 and 58.5 foot-candles (Table XV). For the females, there was also a significant difference ($p < .05$) between mice (Table XVI). The males showed a significant difference in activity between tests at 19.5 and at 39.0 foot-candles ($p < .01$) and between tests at 19.5 and 58.5 foot-candles ($p < .01$) (Table XVIII). No individual differences, however, were found between males ($p > .10$).

Reversal of Photoperiod

So that the records would show the response to reversal of photoperiod no time was allowed for acclimation as in the other experiments, and recording was started immediately after introducing the animal into the experimental area.

All grasshopper mice placed under reversed photoperiod adjusted their activity cycles to the new light-dark regimen (light 1900-0700 and dark 0700-1900). Figures 34-35 show the shifts occurring in individual animals. Figure 34 presents the first half of the day and Figure 35 presents the second half. In order that the uniformity of the

shift could be more readily apparent the data was arranged by consecutive days. The data for the first to sixth day of all mice are presented together (Figures 36-37). The red line indicates the time before which no activity occurred (Figure 36). Figure 36 shows that activity onset occurred progressively later each day and by the sixth day no activity occurred before 0700. In some of the mice (Mice 1 and 5) considerable activity occurred during the dark period of the first day (Figure 37).

Natural Conditions

The progressive change of light intensity due to the lunar cycle affected the activity of grasshopper mice in two ways: in the (1) time of activity and (2) amount of activity. The time of activity during the night was graphed against the lunar cycle (Figures 38-43). From these graphs it is seen that grasshopper mice tended to be more active during the time when the moon was below the horizon than when the moon was visible in the sky. This trend is most noticeable during the time of last-quarter and first-quarter moon.

During the time of new moon, the amount of time spent out of the nest was greater than any other portion of the month. When the moon was full the animals were active out of the nest much less than during the new moon. It can be seen from Figures 39-41 that after the new moon the onset of activity tended to be correlated with moonset. This trend continued until the time of moonset drifted to relatively late in the night (gibbous moon), when the onset of activity shifted back to the early evening hours. During the full moon the animals remained active but activity periods were shorter than during non-moonlit parts

of the cycle (Figure 41). Also, activity tended to occur in short bursts when the moon was full.

The amount of activity was charted against the days of the month for each mouse. The mice exhibited considerable variation in distance moved from night to night. Such variation might be readily expected in the total activity level of an animal. However, a lunar periodicity in activity as measured by total distance travelled became evident in all animals tested.

The recordings on Mouse 51 (adult female) were carried out during the early spring, which is the wet season in Oklahoma. Activity during rainy days is not included in the graphs. A dotted line is used to connect the graph over rainy days. These days were not included in the analysis for lunar periodism since they differed greatly from non-rainy days. This will be discussed in detail later.

There was an indication of lunar periodism in Mouse 51 (Figure 44). The loss of precision may have been due to the estrous cycle in this female as the recordings were made during the period of the year when grasshopper mice are in estrus (Egoscue 1960). The record for Mouse 51 shows the greatest random fluctuation of all animals and perhaps is an indication of the amount of interference in this record from rain and inclement weather. Table XIX shows that on 11 days of the 30-day period rain was recorded during the night. The high incidence of bad weather during April and May probably affected the activity of this mouse and the poor record may be due to carry-over effects from these rainy days.

The record for Mouse 52 (adult female) shows a good lunar periodicity with a great increase in activity near the time of new moon

(Figure 45). The dip in activity noted on May 26 followed two days of rain, and may have reflected a carry-over effect from the rain day. However, this value is still considerably larger than for full moon. Some of the random fluctuation may be attributed to the fact that the animal was in estrus.

Mouse 53 (adult male) showed a good lunar periodicity with maximum activity just after new moon and minimum at full moon (Figure 46). There were no major dips in the record. The small fluctuations noted are to be expected when absolute control of all other possible variables is not achieved.

Mouse 54 (adult male) had an obvious lunar periodicity, but the record showed considerable random fluctuation (Figure 47). The cause of this fluctuation is not known. The lunar periodicity was nonetheless evident.

Mouse 55 (adult female) showed a good lunar periodism with maximum activity at new moon (Figure 48). The low level of activity during the last quarter was unexpected and the reason for it is not obvious. The animal was not in estrus, and it is doubtful that sexual effects were involved.

Mouse 56 (adult male) showed a good lunar periodism with maximum activity just before the new moon and minimum at full moon (Figure 49). The record for this animal showed very little random fluctuation.

As shown by the graphs (Figures 44-49) there was a noticeable correlation between the lunar cycle and amount of activity, with maximum activity near new moon and minimum near full moon. The difference between the amount of activity occurring under the various phases of the moon was tested using the AOV method and the LSD test. For the

statistical analysis the month was divided into units termed lunar phase units. These units consisted of the non-rainy days occurring within the 5-day interval centered on the four lunar phases. The results of this analysis are presented in Tables XIX-XXV.

The analysis indicated a significant difference in activity between new moon and full moon for all mice. The quarter moons did not differ significantly from either new or full moons, and the activity level under the quarter moon lay between the low level at full and the high level at new moon.

The females showed a significant difference among mice as well. When tested by the LSD method it was found that Mice 52 and 55 differed significantly from each other ($p < .05$), and that the difference between the activity of Mice 51 and 52 was large. Female 52 was behaving differently from the other two females. This may have been the result of estrous effects since this mouse was in estrus during the study. There was no significant difference between males, similarly to the indoor experiments.

Activity on nights during which heavy cloud conditions or rain occurred was not included in the analysis for lunar periodism. However, when these charts were read an interesting correlation was noted between activity and raininess.

Rainy nights could be divided into two contrasting conditions according to type of rainfall. Condition 1 consisted of nights of light misty rain, or rain of intermittent duration throughout the night, with periods of heavy overcast and high humidity between showers. Condition 2 consisted of nights of severe rainstorms, usually thunderstorms, during which the rainfall was extremely heavy and prolonged.

These were subjective categories and reflected the type of precipitation during the period 1900-0700, and are not reflected in the total daily precipitation data given in the tables.

During Condition 1 the activity of grasshopper mice reached a level equal to or greater than the activity at new moon. Under severe rain conditions activity was reduced. The results for each mouse in these two categories were averaged and compared with the value for new and full moon (Tables XXVII-XXVIII). An AOV was run on these results and they were then compared by the LSD method (Tables XXIX-XXXII). There was a significant difference between new and full moon, between new and Condition 2, between full and Condition 2, and between Condition 1 and Condition 2. New moon and Condition 1 had similar effects, and full moon and Condition 2 had similar effects on activity level.

When the nightly activity totals were plotted against the phases of the moon, a strong correlation became evident. When the same totals were plotted for the month against maximum and minimum temperature, high and low humidity, and wind in miles per day, no clear cut correlation could be determined between any of these factors and the sum of activity (Tables XVIII, XXXII-XXXVI). Records of maximum and minimum temperature were collected in the field, and records of other environmental factors for Stillwater were secured from the United States Weather Station, 1 mile southwest of the experimental area.

CHAPTER IV

DISCUSSION

Degrees of Light Intensity in the Laboratory Situation

Rawson (1956) noted that constant light on nocturnal rodents causes a delay in the onset of activity. The results for the experimental conditions in which particular light intensities were used during the night period agree with this observation. The grasshopper mice showed a delay in activity onset under the conditions of 19.5, 39.0, and 58.5 foot-candle tests as compared with the onset of activity in the 0 foot-candle test. The delay of activity onset by nocturnal animals under increased light intensity underlies Aschoff's rule that dark-active animals show a longer circadian period in constant 24 hour light than in constant 24 hour dark (Hoffman, 1965).

That the time between one activity onset and the next did not increase in this experiment, due to the counterbalancing effect of the onset of the day period at 0700 agrees with Brown's (1965b) model of two opposing legs of the autophasing device. One operates to set the rhythm ahead and the other to set it back. Autophasing is a concept which holds that circadian periods are directly timed by the environment, and that they differ from exactly 24 hours due to activity onset and cessation being systematically retarded or advanced, by a constant amount of time, each day, by various environmental influences. Thus, a systematic increase or decrease in period length (time between one

activity peak and the next corresponding peak) results (Brown, 1965b).

Aschoff's rule also states that light would increase the period length in dark-active animals. The results under the four different intensities agree with the expectation that the greater the light intensity, the later at night the activity onset will occur. In total darkness, onset occurred in the early evening hours, under 19.5 foot-candles, the evening peak was reduced, and, under 39.0 and 58.5 foot-candles, it was either reduced or entirely absent.

The results also agree with the Circadian Rule which states that the total amount of activity per cycle in dark-active animals should decrease with increasing illumination (Table I). The grasshopper mice showed such an effect. Greater activity occurred during lower light intensities.

A definite circadian or daily cycle was evident. There were three major activity peaks per day, one in the early evening (1900-2100), a second just after midnight, and a third in the early morning hours (0300-0600). Brief bursts of activity occurred virtually every hour of the night, but were inconsistent and small as compared to the major peaks. There was a small amount of individual difference in the timing of these peaks, but individual difference was to be expected from sampling of a wild population, where the genotype itself is variable. DeCoursey (1961) found a similar situation in flying squirrels in which strong runners were distinguished from weak runners in the activity wheels. The relative uniformity of the rhythm between mice indicates that the response pattern is highly adaptive. The high probability that the day-hour interaction resulted from chance indicated that the individual animals behaved similarly during the six-day period and that

the circadian rhythm was stable.

Aschoff (1966) described activity patterns according to whether the first peak (bigeminus pattern) was higher than the second, or the second peak (alternans pattern) was higher. From the data for the total darkness experiments it appears that the female grasshopper mice show the bigeminus pattern and males the alternans type. These distinctions held for all the male and female grasshopper mice in the indoor part of the study. It must be noted however, that the sample size was small and this only indicates that there may be a difference. Aschoff (1966) noted that in the case of a bigeminus pattern the second peak was often very small, variable in position and limited to approximately one-half an hour. The second peak was variable in position in the grasshopper mice but was not small. This variability in position gave the appearance of a tetra- or quadri-modal pattern when the activity was averaged and graphed over the six-day period (Figure 21). If the data are viewed on a daily basis it becomes evident that there are three main peaks with the second having a variable position. Similar activity patterns have been reported for the chipmunk, Tamias striatus (Graefe, 1961).

The significance of the difference in pattern between males and females in the indoor phase is uncertain but may reflect the greater activity level shown by females. St. Giron (1966) reported that certain factors (sex, age, sexual condition, social rank) modify the activity rhythms and that the most regular pattern is always seen in young adult males of high social rank. Male grasshopper mice tended to show the most regular pattern.

Many female mammals have increased activity associated with the

phase of the estrous cycle, including the white rat, Rattus norvegicus, (Long and Evans, 1922) and red-backed voles, Clethrionomys (Asdell, 1949). For this reason many workers have confined their investigation of periodism to males (Terracini and Brown, 1962; Brown, 1965a). Male and female grasshopper mice were alike, however, in their response to total darkness. In spite of the high degree of individual variation among females, all mice showed the same trend toward more activity under the 19.5 foot-candles than under 39.0 and 58.5 foot-candles.

The large degree of difference in amount of activity between the total darkness and the three degrees of light intensity, and the small amount of difference among the degrees of light intensity data indicates that even small amounts of light have a great suppressing effect on the activity of grasshopper mice. Radvanyi (1959) noted that the activity of northern flying squirrels, Glaucomys sabrinus, under total darkness was much greater than under any of the light intensities used in his investigation.

Reversal of Photoperiod

The shifting mechanism seems to be the same mechanism which was responsible for the retardation of activity onset under the high illumination in the night-period experiments. This mechanism may have two resetting arms as proposed by Pittendrigh (1961): one operating at dawn and the other at dusk. In the case of the reversal of light intensity, the dawn and dusk signals were reversed in time. Reversal caused the rhythm to systematically drift each day, until the dawn and dusk effects again became equal, and the equilibrium was re-established. Brown's (1965b) concept of autophasing incorporates the same idea with

a basic disagreement with Pittendrigh as to the nature of the mechanism involved.

Numerous experiments with many organisms have been carried out in which the phase of the rhythm was shifted by changing the time at which light and dark periods occurred. In such experiments, the phase may be shifted so that it will bear any desired relationship to the solar day (Pittendrigh and Minis, 1964).

The grasshopper mice showed the expected shift in rhythm to the new phase of the light-dark cycle. Half of the mice were completely entrained to the new cycle by Day 4 of testing and all were entrained by Day 6. Halberg et al. (1958) found that white mice, Mus mus showed a shift in the circadian rhythm after a reversal in light intensity. Hayden (1965) reported pocket mice, Perognathus longimembris, took 4-7 days to shift their activity pattern into phase with a reversed photoperiod. These results concur strongly with the observations on grasshopper mice. A similar shift has been observed in other species of mammals including flying squirrels, Glaucomys, jumping mice, Zapus, and golden hamsters Mesocricetus (DeCoursey, 1961), and kangaroo rats, Dipodomys (Justice, 1960).

Lunar Cycle

The intensity of moonlight depends on the time of year, the time of night, the location of the observer, the height of the moon above the horizon, the phase of the moon, clouds or other interference, latitude and altitude. The values given in Tables XVIII and XXXI-XXXVI are average values for clear nights at midnight in Stillwater, Oklahoma. Dice (1945) found that light from the zenithal full moon on a clear

night in Michigan during November was about 0.02 foot-candles, which agrees with the average value found in this study.

It is also known that sunlight, moonlight and tungsten light have different wave lengths and polarization. Also moonlight has greater polarization at the first and last quarters (Radvanyi, 1959). No attempt was made to reproduce or measure the correct wave length or polarization of moonlight in this study.

A synodical month (29.53 days) is the time required for the moon to travel around the earth and realign with the sun. This period, also called a lunation or lunar month, begins and ends with the new moon.

A biological rhythm may be defined as having lunar periodicity if the maxima and minima of the rhythmical process appear once or twice in every lunar month in phase with the lunar cycle. In other words, events have a lunar periodicity if they follow each other periodically at intervals of about 30 (precisely 29.53) or 15 (precisely 14.77) days (Hauenschild, 1960).

There occurs in grasshopper mice a lunar periodism which closely parallels the 29.53 day cycle of the moon. A similar periodicity has been found in some other mammals. Brown et al. (1956) found an obvious lunar periodism in the time of running of the white rat. Running was about three times greater at lower than at upper lunar transit. Brown and Terracini (1959) found in another rat a lunar-day cycle with running at the time of lower transit six times greater than that occurring over the upper transit. Pearson (1960) compared the number of passages made by harvest mice, Reithrodontomys megalotis, on the three nights of fullest moon each month with the number of passages on the five nights of least moon each month. He made no allowance for cloudless nights.

The mean number of passages was 2.05 during the full moon and 3.17 on moonless nights. He concluded that there seemed to be an increase in the total amount of activity on moonless nights, but the difference was not demonstrably significant. Brown (1965a) reported a lunar periodicity in the activity of hamsters.

Radvanyi (1959) found that in northern flying squirrels there was an inverse relation between the level of activity and the intensity of the nocturnal illumination. He found activity was at a high level between the last and first quarter phases of the moon and declined markedly at full moon, or directly thereafter. He noted that the relationship appeared to be unaltered by temperature, season, or sex of animals. These results agree closely with the data for grasshopper mice. Grasshopper mice showed a similar trend, confining activity to those portions of the circadian and lunar cycles which had the lowest light intensity.

The circadian cycles of grasshopper mice shifted progressively each month in response to the change in the time of moonset over the month (Figures 38-43). The effect was especially apparent between waning gibbous and waxing gibbous moons. These were the nights when the moonless time was sufficient to allow the mice to obtain food while the moon was below the horizon. When the night was totally moonlit, or at least the greater part of the night was moonlit, the animals were active. However, the amount of activity was considerably less than that occurring under non-moonlit periods and was confined almost exclusively to the shadowed areas of the enclosure.

Brown (1965a) noted a similar tendency in rats. In his studies on rats, the animals displayed a much greater amount of activity when the

moon was below the horizon than when it was above.

Sanderson and Sanderson (1964) noted that jungle rats (Rattus mulleri, R. sabanus, and R. jalorensis) were "extremely reluctant" to expose themselves to observation. On bright moonlit nights, the rats moved mostly under heavy cover. Radvanyi (1959) noted, however, that the decline in total activity in northern flying squirrels was not associated with a decrease in the number of hours during which the activity occurred during the month, but rather by a general decrease in activity during each of the hours when activity normally occurs. It is perhaps significant that the flying squirrel is a woodland species which is habitually active in areas of heavy shade and concealing shadow. Flying squirrels may not find it as necessary to limit activity to the moonless portion of the night as a desert and grassland rodent such as the grasshopper mouse.

The density of the vegetation in the natural environment affects the amount of light reaching the earth's surface. The light under dense clumps of shrubs may be one two-hundredth of the value in the open (Radvanyi, 1959). A decrease in activity corresponding to an increase in illumination has been reported for beach mice, Peromyscus polionotus, by Blair (1951). He found that the illumination effect was more pronounced on open beaches than in dense vegetation. Justice (1960) noted that the moon has a well-marked suppressing effect on the activity of the Merriam kangaroo rat, the bannertail kangaroo rat, and the wood rat. The bannertail kangaroo rat stays within its den when the moon is far enough above the horizon to produce distinct shadows. The Merriam kangaroo rat stays out longer after moon rise, but its activity at such time is confined to deep shadow, as was the case for grasshopper mice

in the present study. The wood rat may be active within the protection of its den structure on moonlit nights. It is never seen in unprotected areas of the habitat except when no moon is visible. The addition to the tendency to confine activity to shadowed areas, grasshopper mice also evidenced a general decrease in amount of activity as the light intensity rose due to the lunar cycle.

Neal (1958) found that during periods of bright moonlight badgers, Meles meles, came out much later than usual. In grasshopper mice there was a slight tendency for the activity to occur later on moonlit nights (Figure 41), but it was at no time as pronounced as in badgers.

There appeared to be a difference in the records between males and females, both in the timing of the rhythm and in amount of activity. The record for females was not as distinct as that for males and showed many more small-term fluctuations. These small fluctuations may be in part due to the estrous cycles of the females. Long and Evans (1922) have shown that the amount of activity of the female white rat reached sharp peaks regularly about every fourth night. These peaks coincided with the increase in the cornified cells of the vaginal epithelium.

Colton (1933) found that the Mexican wood rat, Neotoma mexicana, did not show a cycle difference in males and females. However he noted that wood rats probably had only one period of estrus in the spring because they have only a single litter each year. Radvanyi (1959) found similar results in northern flying squirrels which breed once a year, and hence would not be expected to have a 4-day estrous cycle. He did note an increase in female activity in March which coincided with the breeding season. Egoscue (1960) reported that grasshopper mice are seasonally polyestrous. The period extended from January through July.

The small term fluctuation of 4-5 days noted in Females 51 and 52 are probably due in part to an estrous effect similar to that of the white rat.

Pearson (1960) found that on nights when the moon was half full harvest mice, Reithrodontomys megalotis, had a tendency to be more active during the moonlit half of the night rather than the moonless half. He concluded that moonlight of half-maximum intensity not only failed to suppress activity of the harvest mice but probably encouraged it. Such an observation is in direct contrast to the results for grasshopper mice. Perhaps this difference is due to a difference of exposure in the grass runways in which harvest mice are active and the more exposed sand-sage grassland and desert inhabited by grasshopper mice.

Under outside conditions grasshopper mice showed the same trimodal circadian pattern as they did in the laboratory. The pattern was much more obvious at the time of new and quarter moon (Figure 50). At full moon activity was often limited to one or two major peaks of moderate size (Figure 50). In both males and females, the relative size of the peaks was related directly to light intensity. The major peak each night tended to occur when the moon was below the horizon and the light intensity less. This meant that at last quarter the major peak was in the morning hours while at first quarter, the major peak was in the evening hours (Figure 50). At both new and full moon, the first peak tended to be larger; however, at full moon total activity was reduced and often occurred later in the night than at new moon (Figure 50).

Rain and Inclement Weather

The increase in activity due to light rain was also apparent from

trapping when the animals were being caught in the wild. The most productive trapping was under conditions of intermittent rain and mist (July 18 to July 19, 1967) during which 11 grasshopper mice were captured. Five other trips yielded between one and three mice per night.

Pearson (1960) reported that the mean number of passages made by harvest mice during 109 rainy nights was slightly greater than the corresponding number of passages on 128 rainless nights within two days of the rainy period (2.46 vs 2.37 per recorder night). Pearson subtracted the number of passages per night during each rainy period from the number of passages per night during the adjacent rainless nights, and compared them using the Wilcoxon signed rank test. This test showed the small average difference to be statistically insignificant. He considered days in which more than trace precipitation occurred to be rainy. However, St. Giron (1966) notes that rain and wind are often factors limiting activity.

Radvanyi (1959) observed that clouds reduce the skylight reaching the earth's surface to between one-tenth and one-thirty-second of the cloudless values. The amount of reduction depended upon the nature of the cloud cover. The increase noted under dense cloud cover and misty or intermittent rainfall may have been a direct result of the reduction in light intensity. If the rainfall became too severe then an inhibiting effect as noted by St. Giron may have come into play and activity was reduced.

The increase of activity could also be due, in part, to an increase in the abundance and availability of food when the humidity was high and the rain not severe enough to inhibit activity. Ruffer (1964a) noted that grasshopper mice prefer invertebrates and other animal matter

to other foodstuffs. Such forms as earthworms, various insects, snakes, toads, and kangaroo rats become more active under these conditions (Anderson, 1966; Bragg et al., 1950). St. Giron (1960) noted that the amount of available food and the composition of it act on the circadian rhythm, as well as on the symptoms of the secondary short-duration rhythms. Bolles and Ogilvie (1966) found that feeding is a strong source of periodic stimulation, and this stimulation appears to have an inherent periodicity of approximately 24 hours. The increased humidity at such times would also aid in the detection of prey by olfaction giving added value to hunting under conditions of light or intermittent rainfall.

CHAPTER V

CONCLUSIONS

An inverse relationship between the amount of activity and light intensity exists in the northern grasshopper mouse. Light was, also, found to be the prime factor influencing the timing of the circadian rhythm.

A definite lunar periodicity is shown by grasshopper mice under natural environmental conditions, with minimum activity during the period of the full moon and maximum activity during the period of the new moon.

The rhythm of grasshopper mice seems to limit their activity to the most favorable hunting times. Anderson (1966) noted that feeding behavior and other activity patterns associated with periods of low light intensity may have evolved as a protective or avoidance mechanism to escape attack by predators that usually seek their prey at night. In grasshopper mice a dual mechanism may be operating. Through limitations upon movements which are affected by light the species may avoid predation by owls, coyotes, etc. Further there may be a second factor of increased food availability. Grasshopper mice are also predators, and the species (insects, annelids) upon which they feed may be more active under lower light intensities (Anderson, 1966).

Radvanyi (1959) concluded that food taken in a pre-dawn meal presumably allows the animal to remain inactive throughout the day with-

out exposing themselves to predation while searching for food. By dusk the stomach is empty again and the intense period of activity during the first hours of the night probably represents the effort to obtain the next meal.

The trimodal pattern observed in grasshopper mice may be the result of three major periods of feeding activity. The first and third peaks may represent the initial meal in the evening and the last meal before retiring for the day.

Under natural environmental conditions the mechanism which underlies the shift noted in the reversal experiment enables the grasshopper mice to shift their activity patterns to conform with the monthly shift in time of minimum light (moonset effect), and to conform with the seasonal change in time of sunrise and sunset. Without such an adaptive ability the animals would soon lose synchronism with the environment and their rhythm would lose its adaptive importance.

The way in which these daily and lunar periodisms come into being may be similar to the mechanism involved in imprinting. Early workers have given the impression that imprinting is unique to the development of the "following response" in the young (Lorenz, 1935). Recent workers (Hinde, 1955; Bateson, 1964) now believe that there is no reason to view imprinting as fundamentally different from other forms of learning. They contend that the end of the sensitive period during which imprinting occurs is brought about by other types of behavior which had not previously appeared, for example by fear responses in particular (Guiton, 1959; Hinde, Thorpe and Vince, 1956). It seems probable that the sensitive period is one in which the animal learns the details of its environment in which it is reared.

In this connection Thorpe (1963) has emphasized that attachment to an environment may be akin to imprinting. This concept of the formation of an imprint or concept of the familiar environment may logically be extended to the area of periodicity. Richter (1927) found that white rats had a 2-4 hr cycle of general activity and quiescence when food was available. When these animals were deprived of food, the periodicity of the rhythm was reduced to 1 to 2 hrs. Richter (1927) concluded that the period of activity in rats was associated with the periods of gastric movement and hunger. Munn (1950) stated that it could not be assumed that stomach contractions could cause hunger cycles, although they were related. Calhoun (1945) considered these short-term rhythms to be more basic because they have been found in the young of several species. As the young animals are repeatedly exposed to light and darkness, the circadian cycle develops and becomes superimposed on these short-term rhythms.

The results of this study point out that the rhythmicity of grasshopper mice is not a fixed phenomenon but a response to the environment. Perhaps these rhythms are set up early in development by a method similar to if not identical to the mechanism by which the animal forms a perception of the environment.

That the animal is directly responsive to changes in light intensity is indicated by the increase in activity under cloudy or rain conditions, and by the inhibiting effects of high light intensity on activity as noted in the laboratory. The fact that the grasshopper mice showed both a daily circadian and a lunar monthly rhythm is not surprising in view of the selective pressure on the species to be active during the time of the day and month during which its particular

adaptations are most effective. Selective pressure by the environmental complex requires that an animal species be highly adapted if it is to maintain itself and if the species is to survive. The rhythmic flux in light intensity is one of the most important factors to which an animal must adapt.

Foremost among the advantages of the nocturnal habit is the avoidance of diurnal enemies. There is also reduction in competition for food and shelter sites. Animals engaged in feeding are especially vulnerable to their natural enemies. For many predatory animals the preferred food may be more easily acquired at night. Night helps to conceal the hunter as well as the prey, and there is greater ease of detecting food by smell. Odors remain in the air longer at night due to greater humidity and the decrease in upward air currents. Thus some predators may be able to find food more easily at night owing to better conditions for olfaction.

Southern (1955) has suggested that nocturnal animals possess a kinesthetic sense which guides them in moving about familiar territory. Such animals have become thoroughly familiar with every aspect of their territory, and are able to move about without hesitation even in the dark. Radvanyi (1959) suggested that activity under very low light intensities may not involve the eyes at all but other sensory organs such as vibrissae and olfactory organs, which permit activity in complete darkness. Movement of the grasshopper mice was noticeably uninhibited by the total darkness of the laboratory; therefore, such methods of orientation may have been employed by the species.

Grasshopper mice are well adapted for hunting at night with large eyes, long vibrissae, and quick reflexes. Ruffer (1964a) noted that

the grasshopper mouse relies on its quick reflexes for capturing prey in close quarters. When the humidity is high prey more abundant, and light intensity low grasshopper mice are most active. These conditions occur during periods of light or intermittent rain, or when the moon is below the horizon.

In conclusion, there exists in the northern grasshopper mouse daily and lunar periodisms brought about by the daily and monthly flux in light intensity which are obviously very adaptive for an animal with its ecological requirements.

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APPENDIX A

TABLES

TABLE I

AVERAGE DISTANCE (FEET) MOVED PER DAY BY EACH MOUSE UNDER 0 FOOT-CANDLES,
19.5 FOOT-CANDLES, 39.0 FOOT-CANDLES AND 58.5 FOOT-CANDLES DURING
THE NIGHT PERIOD

	0fc	19.5fc	39.0fc	58.5fc	Total
♀ Mouse 1	1858.55141	123.24789	60.96958	87.98549	2130.66437
♀ Mouse 2	3788.36186	227.54491	172.44799	146.88298	4336.23777
♀ Mouse 3	1489.51166	375.28491	243.58548	318.56035	2426.94242
Totals	7136.42494	726.07721	477.00107	553.42883	8893.84456
♂ Mouse 4	780.44913	598.89003	217.89541	224.29941	1821.53399
♂ Mouse 5	1553.75885	443.12831	91.27900	189.47033	2277.63651
♂ Mouse 6	2279.99238	416.80835	158.48354	277.96194	3133.24623
Totals	4614.20037	1458.82670	467.65797	691.73169	7232.24623
TOTALS	11750.62531	2184.90390	944.66104	1245.16352	16126.26129

TABLE II

POOLED ANALYSIS OF VARIANCE FOR DISTANCE (FEET) MOVED PER HOUR DATA
UNDER 0 FOOT-CANDLES FOR MALE AND FOR FEMALE ONYCHOMYS

MALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	1632690.51	816345.25	40.215	P < .005
hour	11	210030.71	19911.88	.982	.50 < P
day	5	229691.48	45938.29	2.263	.05 < P < .10
hour x animal	22	787050.99	35775.02	1.76	.025 < P < .05
day x animal	10	794672.00	79467.19	3.914	P < .005
hour x day	55	1162666.73	21139.39	1.04	.10 < P < .25
H x D x A	110	2233197.00	20301.78		
Total	215	7049996.00			

FEMALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	493922.40	246961.19	16.18	P < .005
hour	11	262793.55	23890.32	1.56	.10 < P < .25
day	5	93393.86	18678.77	1.22	.25 < P < .50
hour x animal	22	555982.58	25271.93	1.65	.05 < P < .10
day x animal	10	229096.13	22909.61	1.50	.10 < P < .25
hour x day	55	985148.48	17911.78	1.17	.10 < P < .25
H x D x A	110	1678693.00	15260.84		
Total	215	4299029.00			

Probability refers to the probability that the amount of variation shown was due to chance variation.

TABLE III

POOLED ANALYSIS OF VARIANCE FOR DISTANCE (FEET) MOVED PER HOUR DATA
UNDER 19.5 FOOT-CANDLES FOR MALE AND FOR FEMALE ONYCHOMYS

MALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	66862.60	33431.30	8.994	$P < .005$
hour	11	30385.34	2762.30	.743	$.05 < P$
day	5	47935.74	9587.15	2.579	$.025 < P < .05$
hour x animal	22	51654.86	2347.95	.632	$.50 < P$
day x animal	10	36504.93	3650.49	.982	$.25 < P < .50$
hour x day	55	142359.94	2588.36	.952	$.50 < P$
H x D x A	110	408895.50	3717.23		
Total	215	784598.69			

FEMALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	26106.09	13053.04	5.2974	$.005 < P < .01$
hour	11	41528.99	3775.36	1.532	$.10 < P < .25$
day	5	31085.20	6217.03	2.523	$.05 < P < .10$
hour x animal	22	117507.67	5341.26	2.167	$.005 < P < .01$
day x animal	10	62211.13	6221.11	2.525	$.005 < P < .01$
hour x day	55	109786.05	1996.11	.810	$.50 < P$
H x D x A	110	271080.87	2464.37		
Total	215	659305.87			

Probability refers to the probability that the amount of variation shown was due to chance variation.

TABLE IV

POOLED ANALYSIS OF VARIANCE FOR DISTANCE (FEET) MOVED PER HOUR DATA
UNDER 39.0 FOOT-CANDLES FOR MALE AND FOR FEMALE ONYCHOMYS

MALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	1817.68	908.84	.595	.50 < P
hour	11	34210.17	3110.02	2.041	.025 < P < .05
day	5	6549.72	1309.94	.859	.50 < P
hour x animal	22	63180.09	2871.82	1.884	.025 < P < .05
day x animal	10	23781.12	2378.11	1.560	.10 < P < .25
hour x day	55	104080.21	1892.38	1.241	.10 < P < .25
H x D x A	110	167634.69	1523.95		
Total	215	401253.56			

FEMALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	8275.25	4137.62	3.454	.025 < P < .05
hour	11	22160.68	2014.61	1.682	.05 < P < .10
day	5	3215.23	643.05	.536	.50 < P
hour x animal	22	24502.77	1113.76	.929	.50 < P
day x animal	10	18003.89	1800.39	1.503	.10 < P < .25
hour x day	55	56888.72	1034.34	.863	.50 < P
H x D x A	110	131762.25	1197.83		
Total	215	264808.75			

Probability refers to the probability that the amount of variation shown was due to chance.

TABLE V

POOLED ANALYSIS OF VARIANCE FOR DISTANCE (FEET) MOVED PER HOUR DATA
UNDER 58.5 FOOT-CANDLES FOR MALE AND FEMALE ONYCHOMYS

MALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	9470.55	4735.27	2.394	.05 < P < .10
hour	11	24165.74	2196.88	1.111	.25 < P < .50
day	5	3839.16	767.83	.383	.50 < P
hour x animal	22	50313.39	2286.97	1.157	.25 < P < .50
day x animal	10	7695.42	769.54	.389	.50 < P
hour x day	55	90202.46	1640.04	.829	.50 < P
H x D x A	110	217500.25	1977.27		
Total	215	403186.87			

FEMALES					
Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
animal	2	3963.45	1981.72	.916	.25 < P < .50
hour	11	53713.73	4883.07	2.257	.01 < P < .025
day	5	5184.89	1036.97	.479	.50 < P
hour x animal	22	51480.77	2340.03	1.081	.25 < P < .50
day x animal	10	36044.83	3604.48	1.666	.05 < P < .10
hour x day	55	82922.86	1507.69	.691	.50 < P
H x D x A	110	238006.62	2163.70		
Total	215	471317.06			

Probability refers to the probability that the amount of variation shown was due to chance.

TABLE VI

POOLED ANALYSIS OF VARIANCE ON DATA FROM TABLE I FOR DEGREES OF LIGHT
INTENSITY DURING THE NIGHT PERIOD FOR ALL MICE

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Sex	23	115014.27	115014.27	.490	$.25 < P < .50$
Mouse in Sex	4	938202.49	234550.62		
Treatment	3	13379956.85	4459985.61	16.005	$P < .005$
Sex x Treatment	3	1037944.81	345981.60	1.241	$.25 < P < .50$
T. x M. in Sex	12	3343931.21	278660.93		
Total	23	18815049.63			

TABLE VII

ANALYSIS OF VARIANCE ON DATA FROM TABLE I FOR DEGREES OF LIGHT
INTENSITY DURING THE NIGHT PERIOD FOR FEMALE ONYCHOMYS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Mouse	2	716478.62	358239.21	.892	$.24 < P < .50$
Treatment	3	10738148.89	3579382.96	8.913	$.01 < P < .025$
Mouse x Treat.	6	2409602.26	401600.37		
Total	11	13864229.77			

TABLE VIII

ANALYSIS OF VARIANCE ON DATA FROM TABLE I FOR DEGREES OF LIGHT
INTENSITY DURING THE NIGHT PERIOD FOR MALE ONYCHOMYS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Mouse	2	221723.88	110861.93	.725	.50 < P
Treatment	3	3696419.43	1232139.81	8.056	.01 < P < .025
Mouse x Treat.	6	917662.28	152943.71		
Total	11	4835805.59			

Probability refers to the probability that the amount of variation shown was due to chance.

TABLE IX

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN AMOUNT OF ACTIVITY
UNDER DEGREES OF LIGHT INTENSITY DURING THE NIGHT PERIOD
FOR MALE ONYCHOMYS

	0 fc	19.5 fc	39.0 fc	58.5 fc
0 fc		1051.79 ft	1382.18 ft	1307.49 ft
19.5 fc	1051.79 ft		330.38 ft	255.69 ft
39.0 fc	1382.18 ft	330.39 ft		74.69 ft
58.5 fc	1307.49 ft	255.69 ft	74.69 ft	

Probability = .02 for a LSD of 1003.43 ft.

TABLE X

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN AMOUNT OF ACTIVITY
 UNDER DEGREES OF LIGHT INTENSITY DURING THE NIGHT PERIOD
 FOR FEMALE ONYCHOMYS

	0 fc	19.5 fc	39.0 fc	58.5 fc
0 fc		2136.78 ft	2219.81 ft	2194.33 ft
19.5 fc	2136.78 ft		83.03 ft	57.55 ft
39.0 fc	2219.81 ft	83.03 ft		25.48 ft
58.0 fc	2194.33 ft	57.54 ft	25.48 ft	

Probability = .01 for a LSD of 1918.11 ft.

TABLE XI

AVERAGE DISTANCE (FEET) MOVED PER DAY BY EACH MOUSE UNDER 19.5,
39.0 AND 58.5 FOOT-CANDLES DURING THE NIGHT PERIOD

	19.5	39.0	58.5	Totals
Mouse 1	123.24789	60.96058	87.98549	272.20297
♀ Mouse 2	227.54491	172.44799	146.88298	546.87590
Mouse 3	375.28491	243.58548	318.56035	937.43075
Total	726.07721	477.00307	553.42883	1756.50910
Mouse 4	598.89003	217.89541	224.29941	1041.08485
♂ Mouse 5	443.12831	91.27900	189.14703	723.87766
Mouse 6	416.80835	158.48354	277.96194	853.25385
Total	1458.82670	467.65797	691.73169	2618.21636
TOTALS	2184.90390	944.66104	1245.16352	4374.72546

TABLE XII

POOLED ANALYSIS OF VARIANCE ON DATA FROM TABLE XI FOR
19.5, 39.0 AND 58.5 FOOT-CANDLES DURING THE NIGHT
PERIOD FOR ALL MICE

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Sex	1	41252.19	41252.18	1.35	.25 < P < .50
Mice in Sex	3	91460.80	30486.93		
Treatment	2	139535.68	69767.84	35.61	P < .005
Sex x Treat.	2	51436.04	25718.02	13.13	P < .005
T. x M. in Sex	9	17632.98	1959.22		
Total	17	340917.69			

TABLE XIII

ANALYSIS OF VARIANCE ON DATA FROM TABLE XI FOR 19.5, 39.0 AND 58.5
FOOT-CANDLES DURING THE NIGHT PERIOD FOR FEMALE ONYCHOMYS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Treatment	2	10854.03	5427.05	6.93	.05 < P < .01
Mouse	2	74500.90	37250.45	46.23	P < .005
M x T	4	3223.01	805.75		
Total	8	88577.94			

TABLE XIV

ANALYSIS OF VARIANCE ON DATA FROM TABLE XI FOR 19.5, 39.0 AND 58.5
FOOT-CANDLES DURING THE NIGHT PERIOD FOR MALE ONYCHOMYS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Treatment	2	180117.69	90058.85	24.99	.005 < P < .01
Mouse	2	16959.89	8470.95	2.35	.10 < P < .25
M x T	4	14409.97	3602.49		
Total	8	211487.56			

TABLE XV

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN ACTIVITY UNDER 19.5, 39.0
AND 58.5 FOOT-CANDLES DURING THE NIGHT PERIOD FOR FEMALES

	19.5 fc.	39.0 fc.	58.5 fc.
19.5 fc.		83.02 ft.	57.55 ft.
39.0 fc.	83.02 ft.		25.47 ft.
58.5 fc.	57.55 ft.	25.47 ft.	
Probability = .10 for a	LSD of 49.33 ft.		
Probability = .05 for a	LSD of 64.34 ft.		

TABLE XVI

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN ACTIVITY BY INDIVIDUAL FEMALE
ONYCHOMYS UNDER 19.5, 39.0 AND 58.5 FOOT-CANDLES DURING THE NIGHT

	Mouse 1	Mouse 2	Mouse 3
Mouse 1		91.56 ft.	221.74 ft.
Mouse 2	91.56 ft.		130.18 ft.
Mouse 3	221.74 ft.	130.18 ft.	

Probability = .01 for a LSD of 106.71 ft.

TABLE XVII

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN ACTIVITY UNDER 19.5, 39.0,
 AND 58.5 FOOT-CANDLES DURING THE NIGHT PERIOD FOR MALES

	19.5 fc.	39.0 fc.	58.5 fc.
19.5 fc.		330.39 ft.	255.69 ft.
39.0 fc.	330.39 ft.		74.69 ft.
58.5 fc.	255.69 ft.	74.69 ft.	

Probability = .01 for a LSD of 225.23 ft.

TABLE XVIII

CLIMATOLOGICAL DATA AND DISTANCE (FEET) MOVED DURING THE MONTH FOR MOUSE 51 (FEMALE)

Date	Day of Mouse	Light intensity in foot candles	Wind mpd.	Temperature max. min.		Humidity % h. l.		Rainfall in.	Feet moved per day
April 12									
April 14	1	.02000 ft c.		83	41	90	16	0	929
April 15	2	.01700 ft c.		75	37	58	10	0	1769
April 16	3	.01420 ft c.		80	59	94	46	2.38	1925
April 17	4	.01190 ft c.		80	59	94	34	0	1425
April 18	5	.00880 ft c.		80	47	94	82	.29	2010
April 19	6	.00560 ft c.		72	56	94	44	.53	45
April 20	7	.00380 ft c.		76	53	91	16	.13	1374
April 21	8	.00200 ft c.		74	52	92	60	.22	3102
April 22	9	.00180 ft c.		74	54	70	51	.74	83
April 23	10	.00140 ft c.		62	44	82	20	0	2785
April 24	11	.00120 ft c.		75	35	92	10	0	1926
April 25	12	.00090 ft c.		75	47	66	16	.07	3003
April 26	13	.00040 ft c.		73	41	91	34	0	2253
April 27	14	.00009 ft c.		74	50	84	26	0	933
April 28	15	.00008 ft c.		72	48	91	34	0	2990
April 29	16	.00009 ft c.		75	49	84	16	0	960
April 30	17	.00009 ft c.		83	46	78	14	0	1201
May 1	18	.00040 ft c.	78	88	56	58	14	0	1284
May 2	19	.00090 ft c.	64	89	55	82	33	0	618
May 3	20	.00020 ft c.	111	88	59	94	30	0	1073
May 4	21	.00140 ft c.	46	78	42	91	11	0	2238
May 5	22	.00180 ft c.	102	79	49	88	20	0	1515
May 6	23	.00200 ft c.	174	77	59	94	34	.71	0
May 7	24	.00380 ft c.	193	76	57	92	20	0	772
May 8	25	.00560 ft c.	173	80	44	94	40	0	460
May 9	26	.00880 ft c.	51	80	55	94	44	.66	775
May 10	27	.01190 ft c.	77	69	57	92	60	.42	2821
May 11	28	.01420 ft c.	74	67	52	92	70	0	550
May 12	29	.01700 ft c.	38	67	45	94	54	0	723
May 13	30	.02000 ft c.	47	70	58	94	80	.33	

TABLE XIX

AVERAGE DISTANCE (FEET) MOVED PER DAY UNDER THE FOUR
PHASES OF THE MOON BY FEMALE ONYCHOMYS

	Full Moon	First Q.	New Moon	Last Q.	Total
51	826	1399	1568	1425	5218
52	1160	1858	4231	2585	9734
53	441	1095	1832	305	3673
Σ	2427	4352	7631	4215	18625
\bar{x}	809	1450	2544	1405	

TABLE XX

AVERAGE DISTANCE (FEET) MOVED PER DAY UNDER THE FOUR
PHASES OF THE MOON BY MALE ONYCHOMYS

	Full Moon	First Q.	New Moon	Last Q.	Total
53	840	2595	3601	1098	8134
54	602	1313	2021	1483	5419
56	622	776	2088	1588	5074
Σ	2064	4684	7710	4169	18627
\bar{x}	688	1561	2570	1389	

TABLE XXI

ANALYSIS OF VARIANCE ON DATA FROM TABLE XIX FOR THE FOUR
PHASES OF THE MOON BY FEMALE ONYCHOMYS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Mice	2	4959750	2479875	6.53	$.025 < P < .05$
Lunar	3	4701987	1568329	4.73	$.05 < P < .10$
M x L.	6	2276542	379423		
Total	11	11938279			

Probability refers to the probability that the amount of variation shown was due to chance.

TABLE XXII

ANALYSIS OF VARIANCE ON DATA FROM TABLE XX FOR THE FOUR
PHASES OF THE MOON BY MALE ONYCHOMYS

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Mice	2	1404488	702244	1.99	.10 $<P< .25$
Lunar	3	5427777	1809259	5.15	.025 $<P< .05$
M x L.	6	2107056	351176		
Total	11	8939321			

Probability refers to the probability that the amount of variation shown was due to chance.

TABLE XXIII

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN AMOUNT OF ACTIVITY DURING
THE FOUR PHASES OF THE MOON FOR MALE ONYCHOMYS

	Full moon	Last quarter	New moon	First quarter
Full moon		701 ft.	1882 ft.	873 ft.
Last quarter	701 ft.		1181 ft.	172 ft.
New moon	1882 ft.	1181 ft.		1009 ft.
First quarter	873 ft.	172 ft.	1009 ft.	

Probability = .05 for a LSD of 1345.00 ft.

TABLE XXIV

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN AMOUNT OF ACTIVITY DURING
THE FOUR PHASES OF THE MOON FOR FEMALE ONYCHOMYS

	Full moon	Last quarter	New moon	First quarter
Full moon		596 ft.	1735 ft.	641 ft.
Last quarter	596 ft.		1139 ft.	45 ft.
New moon	1735 ft.	1139 ft.		1094 ft.
First quarter	641 ft.	45 ft.	1094 ft.	

Probability = .05 for a LSD of 1398.25 ft.

TABLE XXV

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN ACTIVITY BY INDIVIDUAL
FEMALE ONYCHOMYS DURING THE FOUR PHASES OF THE MOON

	Mouse 51	Mouse 52	Mouse 55
Mouse 51		1129 ft.	386 ft.
Mouse 52	1129 ft.		1515 ft.
Mouse 55	386 ft.	1515 ft.	

Probability = .05 for a LSD of 1398.25 ft.

TABLE XXVI

AVERAGE DISTANCE (FEET) MOVED BY FEMALES UNDER NEW AND
FULL MOON AND LIGHT AND HEAVY RAINFALL

Mouse	Full moon	New moon	Heavy rain	Light rain	Total
51	826	1568	54	2353	4801
52	1160	4231	867	3663	9921
55	441	1832	299	2351	4912
Total	2427	7631	1220	8367	19634
\bar{x}	809	2544	407	2789	

TABLE XXVII

AVERAGE DISTANCE (FEET) MOVED BY MALES UNDER NEW AND
FULL MOON AND LIGHT AND HEAVY RAINFALL

Mouse	Full moon	New moon	Heavy rain	Light rain	Total
53	840	3601	1072	3811	9324
54	602	2021	611	2328	5562
56	622	2088	513	1521	4744
Total	2064	7710	2196	7760	19630
\bar{x}	688	2570	732	2553	

TABLE XXVIII

ANALYSIS OF VARIANCE ON DATA FROM TABLE XXVI FOR ACTIVITY UNDER NEW
AND FULL MOON AND LIGHT AND HEAVY RAINFALL BY FEMALES

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Mice	2	4276400	2138200	7.20	P < .005
Treatment	3	13081363	4360454	14.68	
M x T	6	1781692	296948		
Total	11	19139455			

TABLE XXIX

ANALYSIS OF VARIANCE ON DATA FROM TABLE XXVII FOR ACTIVITY UNDER NEW
AND FULL MOON AND LIGHT AND HEAVY RAIN BY MALES

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F Test	Probability
Mice	2	2983181	1491590	5.86	P < .005
Treatment	3	10289329	3429776	13.49	
M x T	6	1524776	254129		
Total	11	14797286			

TABLE XXX

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN ACTIVITY UNDER
NEW AND FULL MOON AND LIGHT AND HEAVY RAIN BY FEMALES

	Heavy rain	Full moon	Light rain	New moon
Heavy rain		402 ft.	2382 ft.	2137 ft.
Full moon	402 ft.		1980 ft.	1735 ft.
Light rain	2382 ft.	1980 ft.		245 ft.
New moon	2137 ft.	1735 ft.	245 ft.	

Probability = .05 for a LSD of 1236.79 ft.

TABLE XXXI

LEAST SIGNIFICANT DIFFERENCE TEST ON MEAN ACTIVITY UNDER
NEW AND FULL MOON AND LIGHT AND HEAVY RAIN BY MALES

	Heavy rain	Full moon	Light rain	New moon
Heavy rain		44 ft.	1821 ft.	1838 ft.
Full moon	44 ft.		1865 ft.	1882 ft.
Light rain	1821 ft.	1865 ft.		17 ft.
New moon	1838 ft.	1882 ft.	17 ft.	
Probability = .05 for a LSD of 1144.24 ft.				

TABLE XXXII

CLIMATOLOGICAL DATA AND DISTANCE (FEET) MOVED DURING THE MONTH FOR MOUSE 52 (FEMALE)

Date	Day of Mouse	Light intensity in foot candles	Wind mpd.	Temperature max. min.	Humidity % h. l.	Rainfall in.	Feet moved per day
May 13	1	.02000 ft c.	47	70 58	94 80	0	996
May 14	2	.01700 ft c.	91	89 62	94 50	0	1160
May 15	3	.01420 ft c.	155	86 72	80 64	t	3915
May 16	4	.01190 ft c.	54	80 50	- -	0	642
May 17	5	.00880 ft c.	133	71 54	- -	0	2131
May 18	6	.00560 ft c.	100	72 54	- -	0	2010
May 19	7	.00380 ft c.	85	68 47	- -	0	3314
May 20	8	.00200 ft c.	43	68 42	90 30	.86	212
May 21	9	.00180 ft c.	49	56 49	90 88	t	3412
May 22	10	.00140 ft c.	155	85 52	94 50	0	4630
May 23	11	.00120 ft c.	170	84 66	80 50	0	4201
May 24	12	.00090 ft c.	64	71 57	92 68	.09	329
May 25	13	.00040 ft c.	72	76 61	90 40	2.55	1046
May 26	14	.00009 ft c.	78	74 50	88 40	0	2067
May 27	15	.00008 ft c.	47	78 50	- -	0	4310
May 28	16	.00008 ft c.	62	81 49	- -	0	4447
May 29	17	.00009 ft c.	11	88 54	- -	.64	829
May 30	18	.00040 ft c.	96	86 61	- -	0	3935
May 31	19	.00090 ft c.	75	84 52	- -	t	4131
June 1	20	.00120 ft c.	22	73 64	- -	.14	3605
June 2	21	.00140 ft c.	20	81 55	- -	0	2239
June 3	22	.00180 ft c.	18	82 60	- -	0	2068
June 4	23	.00200 ft c.	39	86 68	- -	0	1266
June 5	24	.00380 ft c.	55	85 66	- -	t	1942
June 6	25	.00560 ft c.	102	85 64	- -	0	1222
June 7	26	.00880 ft c.	137	85 71	- -	0	1472
June 8	27	.01190 ft c.	122	84 66	94 50	0	1427
June 9	28	.01420 ft c.	141	90 67	90 52	0	1220
June 10	29	.01700 ft c.	122	89 71	91 48	0	1103

TABLE XXXIII

CLIMATOLOGICAL DATA AND DISTANCE (FEET) MOVED DURING THE MONTH FOR MOUSE 53 (MALE)

Date	Day of Mouse	Light intensity in foot candles	Wind mpd.	Temperature		Humidity %		Rainfall in.	Feet Moved per day
				max.	min.	h.	l.		
June 11	1	.02000 ft c.	38	94	63	90	30	0	464
June 12	2	.01700 ft c.	25	94	60	94	18	0	1217
June 13	3	.01420 ft c.	91	95	65	88	28	0	1027
June 14	4	.01190 ft c.	176	94	74	89	31	0	976
June 15	5	.00880 ft c.	83	91	65	94	54	1.71	3100
June 16	6	.00560 ft c.	24	82	63	94	42	0	817
June 17	7	.00380 ft c.	38	82	64	88	30	0	1101
June 18	8	.00200 ft c.	50	87	60	92	32	0	1096
June 19	9	.00180 ft c.	55	89	66	94	32	0	424
June 20	10	.00140 ft c.	58	91	67	92	30	0	1854
June 21	11	.00120 ft c.	57	90	64	91	33	0	1684
June 22	12	.00090 ft c.	21	90	69	91	33	0	2396
June 23	13	.00040 ft c.	133	89	67	94	40	0	2231
June 24	14	.00009 ft c.	123	87	71	80	30	1.28	1972
June 25	15	.00008 ft c.	45	82	66	74	32	0	2215
June 26	16	.00008 ft c.	155	82	55	78	32	0	4972
June 27	17	.00009 ft c.	61	88	50	64	30	0	4529
June 28	18	.00040 ft c.	159	92	67	88	30	0	3701
June 29	19	.00090 ft c.	231	91	75	90	52	0	3100
June 30	20	.00120 ft c.	255	94	78	82	40	t	4522
July 1	21	.00140 ft c.	67	90	71	90	50	t	4100
July 2	22	.00180 ft c.	95	84	62	94	28	0	3612
July 3	23	.00200 ft c.	61	83	56	91	30	0	2841
July 4	24	.00380 ft c.	50	86	56	94	30	0	1497
July 5	25	.00560 ft c.	21	84	54	90	30	0	2432
July 6	26	.00880 ft c.	36	86	60	94	28	0	923
July 7	27	.01190 ft c.	53	88	66	78	30	t	1025
July 8	28	.01420 ft c.	92	92	64	92	30	0	819
July 9	29	.01700 ft c.	8	91	66	92	20	0	1200

TABLE XXXIV

CLIMATOLOGICAL DATA AND DISTANCE (FEET) MOVED DURING THE MONTH FOR MOUSE 54 (MALE)

Date	Day of Mouse	Light intensity in foot candles	Wind mpd.	Temperature		Humidity %		Rainfall in.	Feet Moved per day
				max.	min.	h.	l.		
July 10	1	.02000 ft c.	2	95	65	90	22	0	301
July 11	2	.01700 ft c.	46	94	64	88	30	0	189
July 12	3	.01420 ft c.	45	96	67	90	40	0	1341
July 13	4	.01190 ft c.	110	92	70	91	50	0	1640
July 14	5	.00880 ft c.	135	90	69	91	50	.89	3104
July 15	6	.00560 ft c.	130	87	71	-	-	0	2054
July 16	7	.00380 ft c.	205	91	76	92	76	.27	2716
July 17	8	.00200 ft c.	188	96	76	-	-	0	1144
July 18	9	.00180 ft c.	70	95	68	-	-	.81	888.9
July 19	10	.00140 ft c.	29	93	66	-	-	0	1251.8
July 20	11	.00120 ft c.	46	92	67	94	32	0	1915
July 21	12	.00090 ft c.	55	92	69	92	30	.80	333.9
July 22	13	.00040 ft c.	74	96	72	90	40	0	2506
July 23	14	.00009 ft c.	57	97	72	-	-	0	2719
July 24	15	.00008 ft c.	93	97	73	-	-	0	2512
July 25	16	.00008 ft c.	85	96	74	-	-	0	1389
July 26	17	.00009 ft c.	98	96	73	-	-	0	1463
July 27	18	.00040 ft c.	87	98	76	-	-	t	1014
July 28	19	.00090 ft c.	93	96	73	-	-	t	1502
July 29	20	.00120 ft c.	56	90	70	80	40	0	1149
July 30	21	.00140 ft c.	154	99	73	90	28	0	1743
July 31	22	.00180 ft c.	158	97	77	64	40	0	166
Aug. 1	23	.00200 ft c.	-	95	68	-	-	0	1165
Aug. 2	24	.00380 ft c.	97	100	69	-	-	0	1298
Aug. 3	25	.00560 ft c.	116	99	69	-	-	0	2044
Aug. 4	26	.00880 ft c.	104	98	72	-	-	0	1976
Aug. 5	27	.01190 ft c.	112	97	73	-	-	0	488
Aug. 6	28	.01420 ft c.	108	98	74	-	-	0	1095
Aug. 7	29	.01700 ft c.	91	101	73	-	-	0	901
Aug. 8	30	.02000 ft c.	109	103	75	-	-	0	526

TABLE XXXV

CLIMATOLOGICAL DATA AND DISTANCE (FEET) MOVED DURING THE MONTH FOR MOUSE 55 (FEMALE)

Date	Day of Mouse	Light intensity in foot candles	Wind mpd.	Temperature		Humidity %		Rainfall in.	Feet Moved per day
				max.	min.	h.	l.		
Sept. 6	1	.02000 ft c.	18	88	51	94	16	0	252
Sept. 7	2	.01700 ft c.	149	86	55	94	16	0	107
Sept. 8	3	.01420 ft c.	88	88	60	80	34	0	982
Sept. 9	4	.01190 ft c.	85	86	55	80	26	0	76
Sept. 10	5	.00880 ft c.	50	80	46	92	18	0	306
Sept. 11	6	.00560 ft c.	13	84	45	92	10	0	210
Sept. 12	7	.00380 ft c.	51	86	46	91	16	0	193
Sept. 13	8	.00200 ft c.	69	86	56	82	24	0	442
Sept. 14	9	.00180 ft c.	76	84	57	86	29	0	281
Sept. 15	10	.00140 ft c.	81	80	58	91	59	.01	2301
Sept. 16	11	.00120 ft c.	113	86	67	92	36	t	382
Sept. 17	12	.00090 ft c.	123	77	54	87	14	0	365
Sept. 18	13	.00040 ft c.	93	90	43	82	10	0	347
Sept. 19	14	.00009 ft c.	99	95	60	50	19	0	636
Sept. 20	15	.00008 ft c.	136	93	66	70	34	0	1832
Sept. 21	16	.00008 ft c.	187	90	67	99	38	.78	217
Sept. 22	17	.00009 ft c.	191	89	71	90	30	0	2209
Sept. 23	18	.00040 ft c.	112	90	69	-	-	.15	2401
Sept. 24	19	.00090 ft c.	65	76	67	-	-	.63	106
Sept. 25	20	.00120 ft c.	27	80	51	-	-	0	1130
Sept. 26	21	.00140 ft c.	26	85	50	-	-	0	1031
Sept. 27	22	.00180 ft c.	35	88	51	-	-	0	1514
Sept. 28	23	.00200 ft c.	63	87	58	-	-	0	1086
Sept. 29	24	.00380 ft c.	26	83	54	-	-	0	712
Sept. 30	25	.00560 ft c.	4	83	51	60	30	0	984
Oct. 1	26	.00880 ft c.	184	87	61	69	24	0	346
Oct. 2	27	.01190 ft c.	138	90	64	70	20	0	825
Oct. 3	28	.01420 ft c.	159	84	49	62	20	0	513
Oct. 4	29	.01700 ft c.	44	70	38	92	10	0	349
Oct. 5	30	.02000 ft c.	148	67	49	94	30	1.08	264

TABLE XXXVI

CLIMATOLOGICAL DATA AND DISTANCE (FEET) MOVED DURING THE MONTH FOR MOUSE 56 (MALE)

Date	Day of Mouse	Light intensity in foot-candles	Wind mpd.	Temperature		Humidity %		Rainfall in.	Feet Moved
				max.	min.	h.	l.		
Oct. 6	1	.02000 ft c.	42	74	49	92	20	t	1521
Oct. 7	2	.01700 ft c.	69	76	51	72	40	0	464
Oct. 8	3	.01420 ft c.	169	73	58	90	72	.85	385
Oct. 9	4	.01190 ft c.	187	72	54	92	28	0	780
Oct. 10	5	.00880 ft c.	50	63	39	94	22	0	1168
Oct. 11	6	.00560 ft c.	77	73	49	94	60	0	1001
Oct. 12	7	.00380 ft c.	149	77	64	90	60	0	928
Oct. 13	8	.00200 ft c.	216	86	70	90	41	0	1600
Oct. 14	9	.00180 ft c.	98	87	68	72	40	0	2237
Oct. 15	10	.00140 ft c.	167	85	70	92	41	.80	
Oct. 16	11	.00120 ft c.	212	80	62	94	44	0	1998
Oct. 17	12	.00090 ft c.	183	73	46	94	26	0	2309
Oct. 18	13	.00040 ft c.	81	67	36	9	12	0	2489
Oct. 19	14	.00009 ft c.	52	78	42	80	19	0	3444
Oct. 20	15	.00008 ft c.	26	77	44	94	32	0	1553
Oct. 21	16	.00008 ft c.	67	80	49	90	46	0	1267
Oct. 22	17	.0009 ft c.	85	77	43	92	32	0	641
Oct. 23	18	.00040 ft c.	43	67	41	92		0	1205
Oct. 24	19	.00090 ft c.	71	59	40	92		0	1326
Oct. 25	20	.00120 ft c.	44	74	34	92		0	1352
Oct. 26	21	.00140 ft c.	51	81	36	94		0	1331
Oct. 27	22	.00180 ft c.	139	80	47	60		0	856
Oct. 28	23	.00200 ft c.	25	63	32	90	12	0	526
Oct. 29	24	.00380 ft c.	33	84	34	90	9	0	571
Oct. 30	25	.00560 ft c.	57	90	44	92	10	0	596
Oct. 31	26	.00880 ft c.	81	82	65	81	40	0	688
Nov. 1	27	.01190 ft c.	83	75	59	94	60	0	625
Nov. 2	28	.01420 ft c.	157	64	58	96	96	1.31	
Nov. 3	29	.01700 ft c.	183	58	46	96	30	.38	
Nov. 4	30	.02000 ft c.	58	62	31	86	50	0	

APPENDIX B

FIGURES



Figure 1. Onychomys leucogaster brevicauritus.



Figure 2. Baird-Atomic model SP-145 Miniature scintillation probe mounted on boom in field situation.

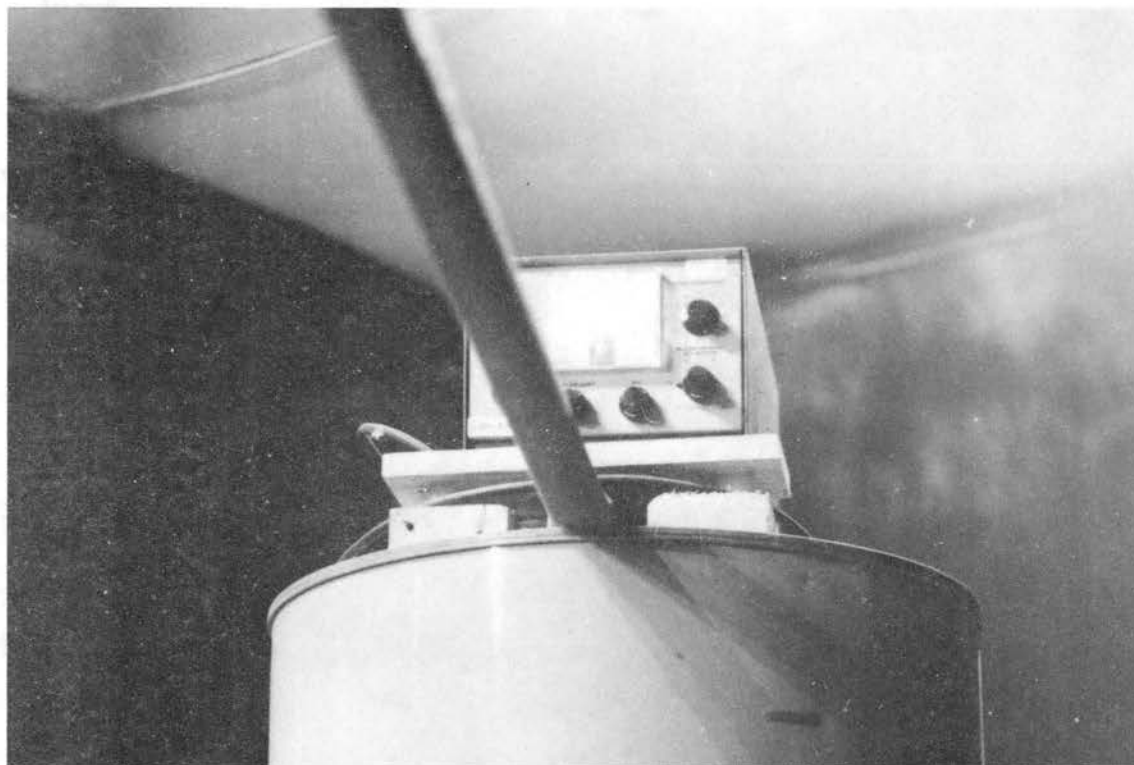


Figure 3. Ratemeter on top of turntable.

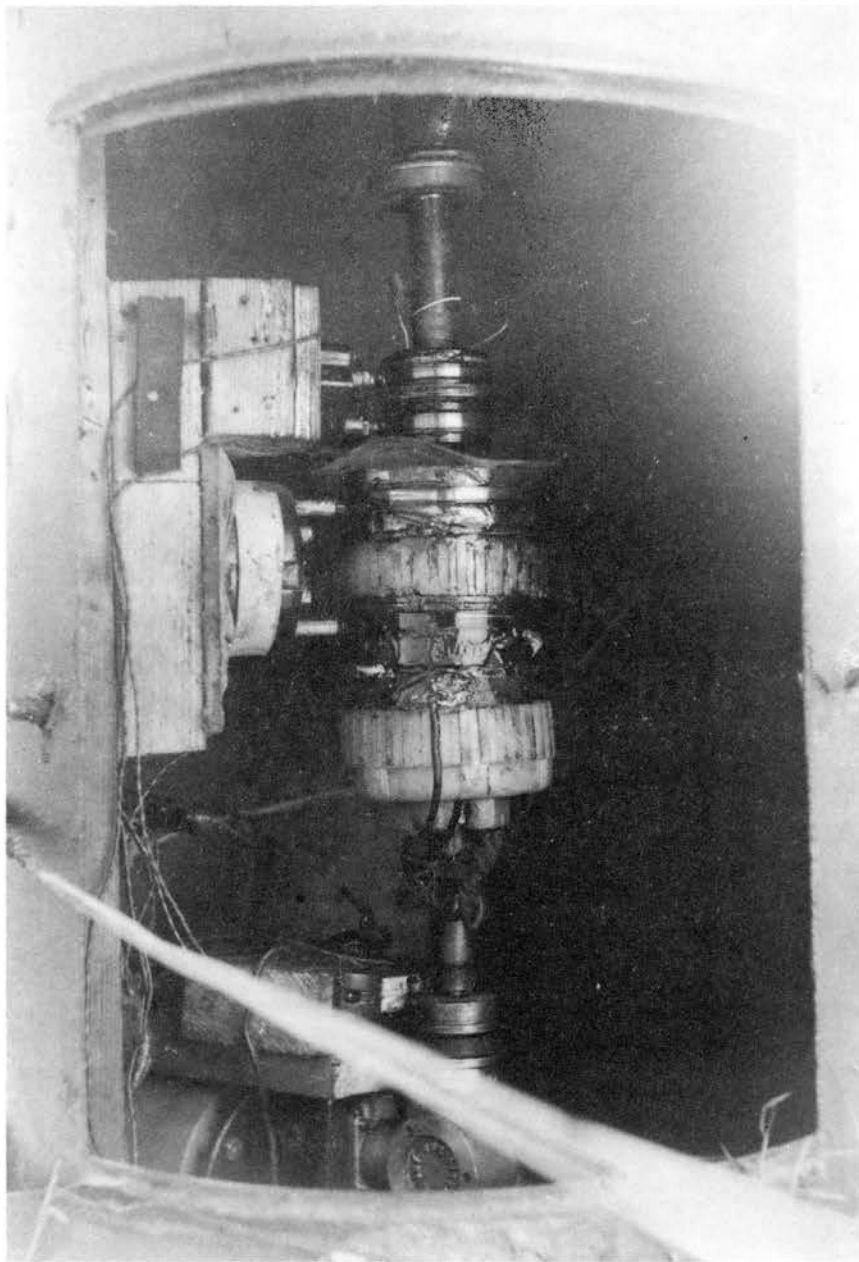
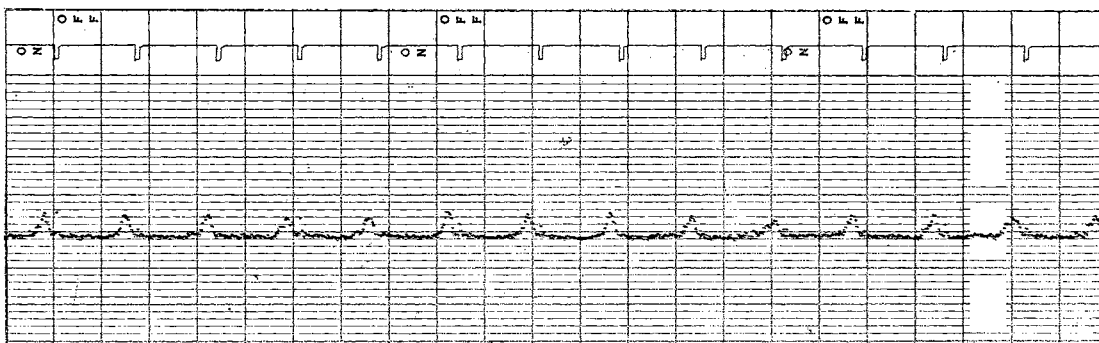
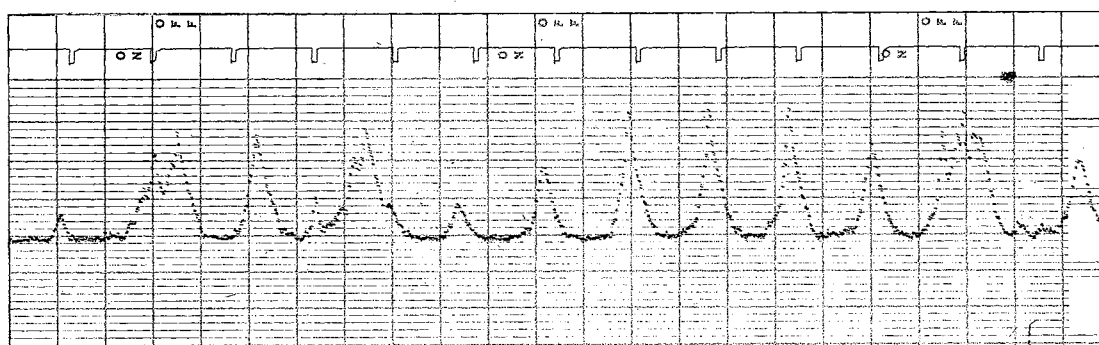


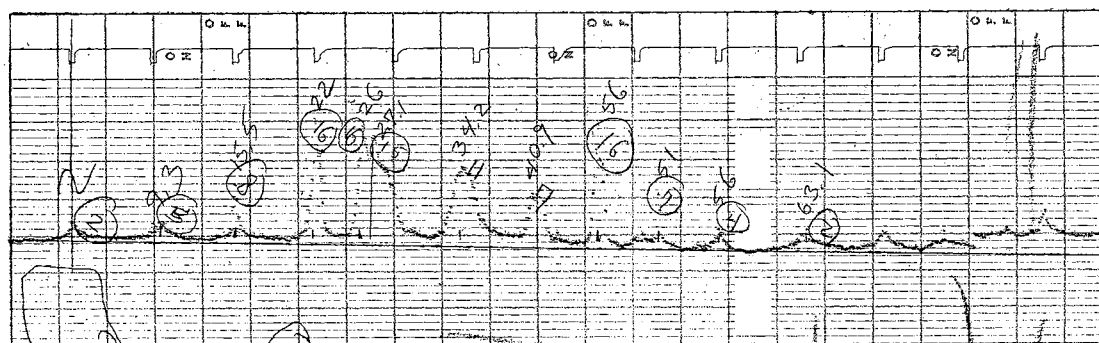
Figure 4. Inside of turntable showing commutator devices and gear unit.



RECORD OF ANIMAL AT REST



RECORD OF ACTIVE ANIMAL



PORTION OF CHART READ

Figure 5. Rustrack Recorder Chart.



Figure 6. Building used for indoor laboratory. Windows were covered to keep it light proof. Note cooling unit in window.

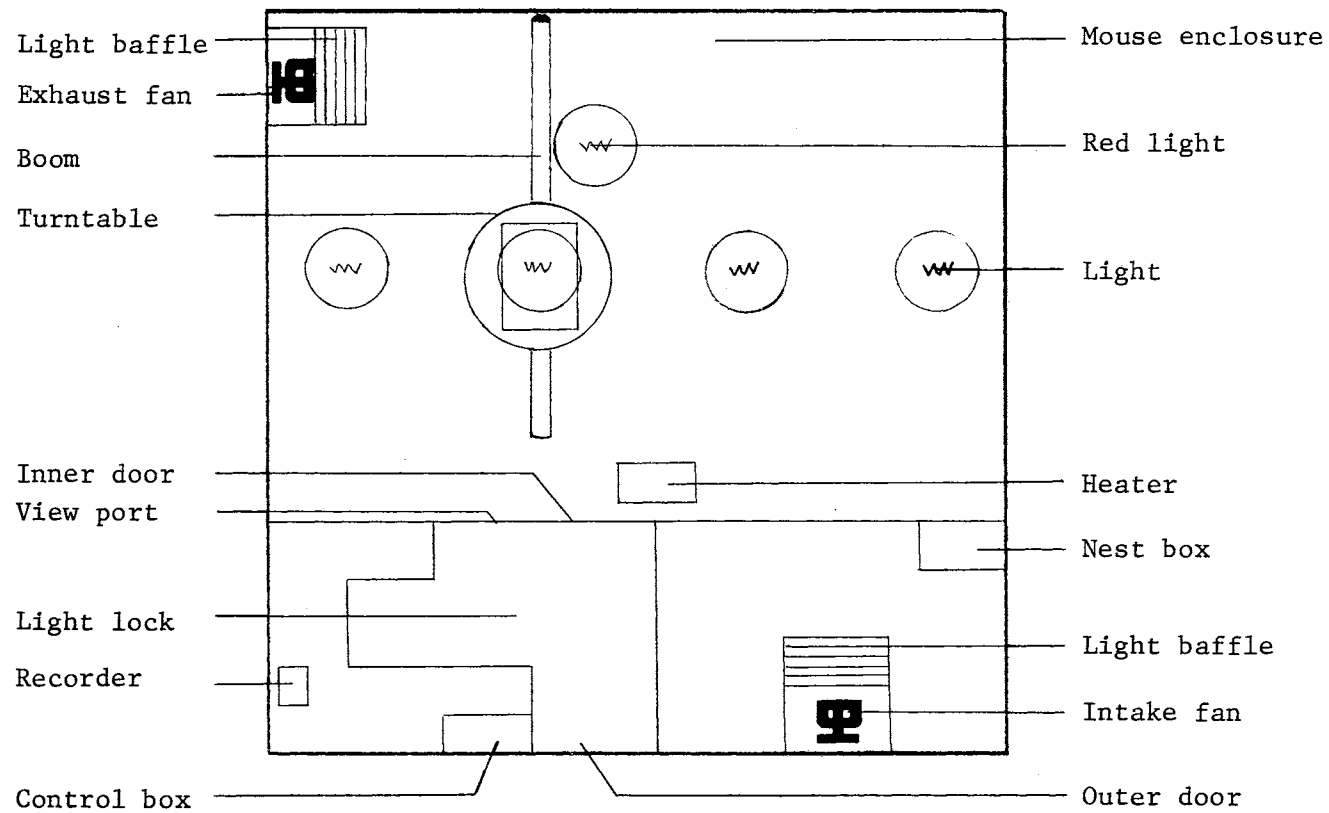


Figure 7. Schematic diagram of indoor laboratory.

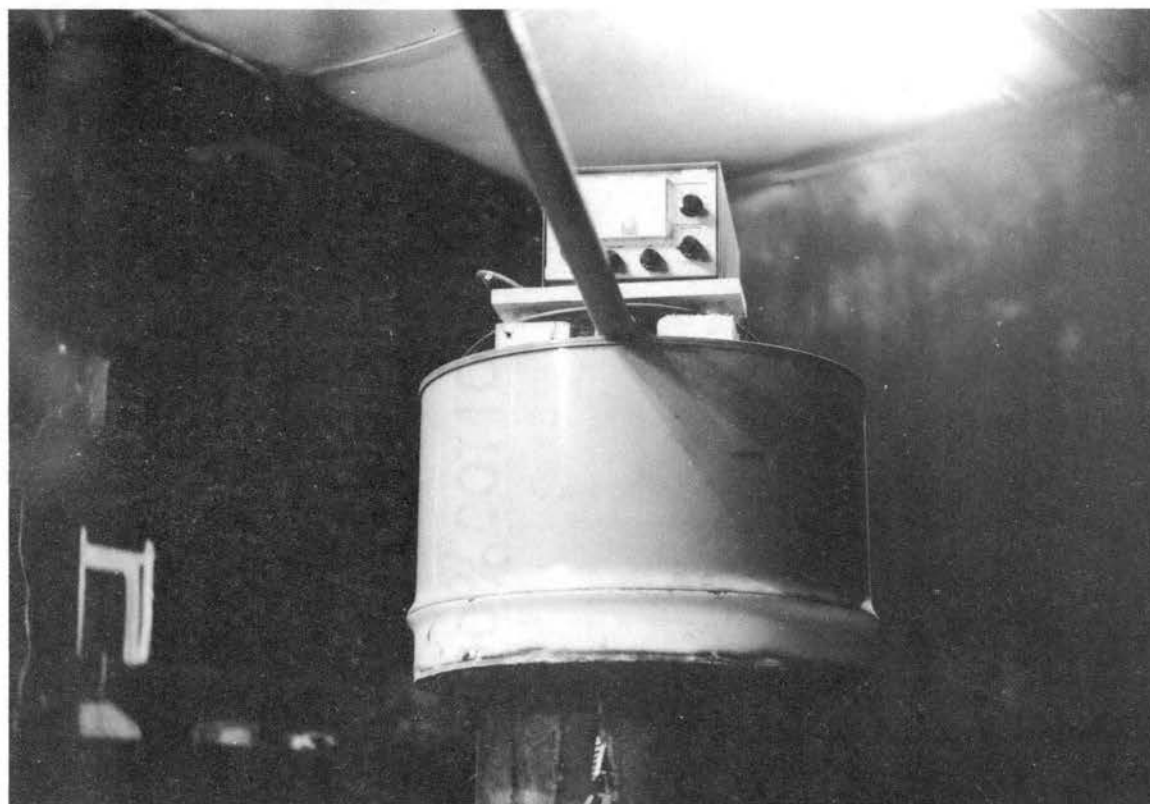


Figure 8. Apparatus setup in indoor laboratory.

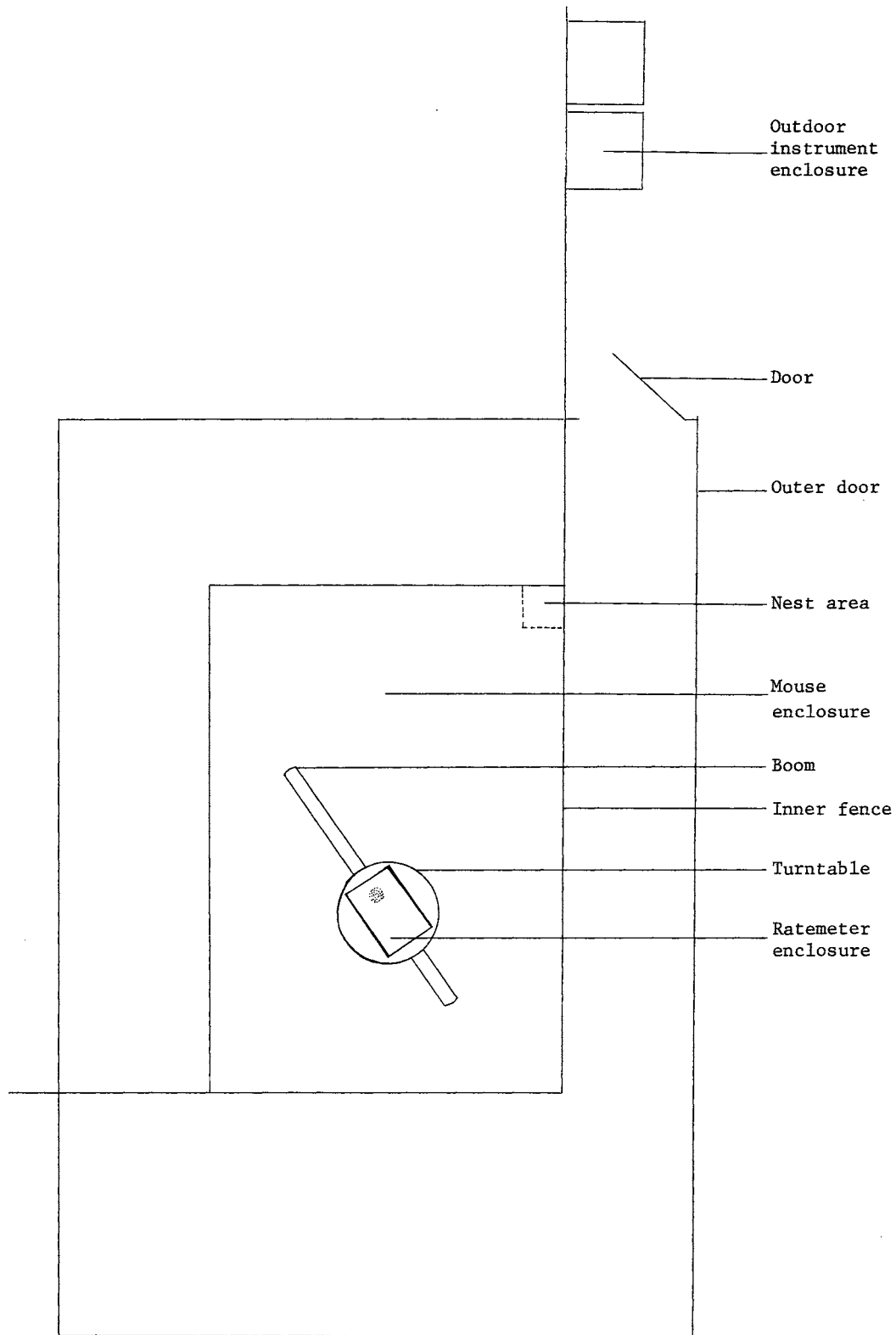


Figure 9. Schematic diagram of outdoor enclosure.

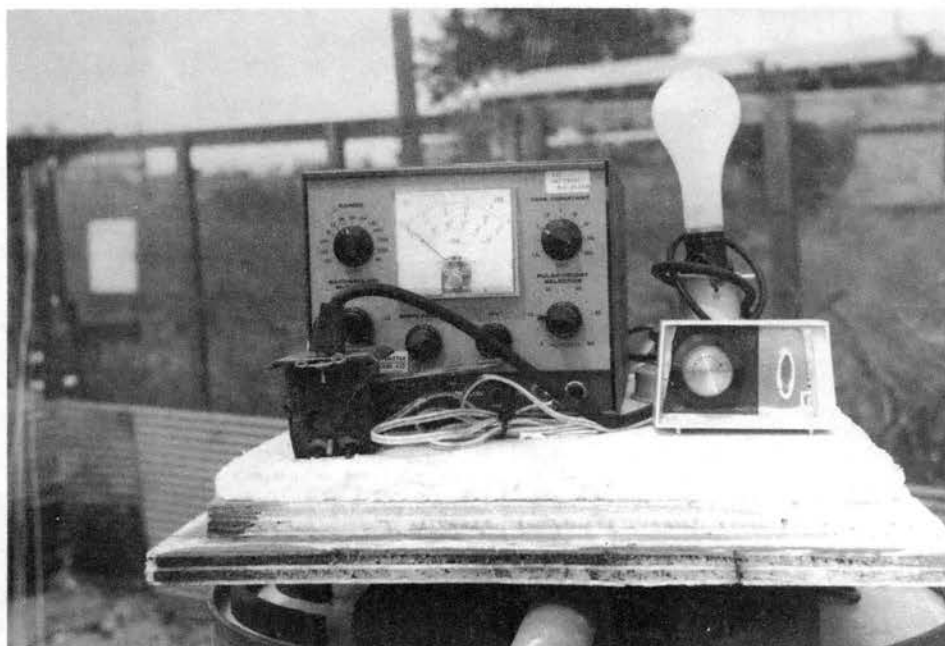


Figure 10. Ratemeter in field situation with cover removed. Light bulb and thermostat provided heat. Cooling unit was mounted on cover.



Figure 11. Apparatus in field situation. Note predator shield wires.

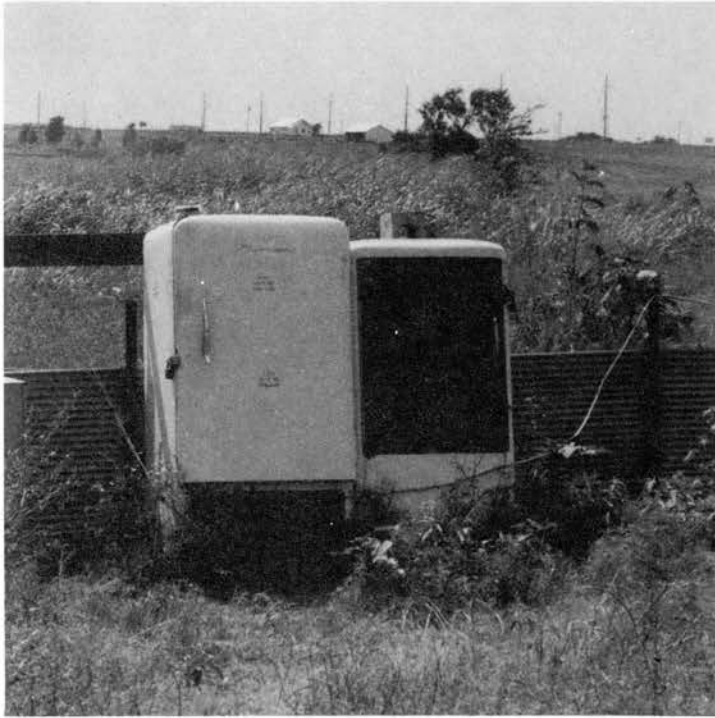


Figure 12. Instrument enclosures in field situation.

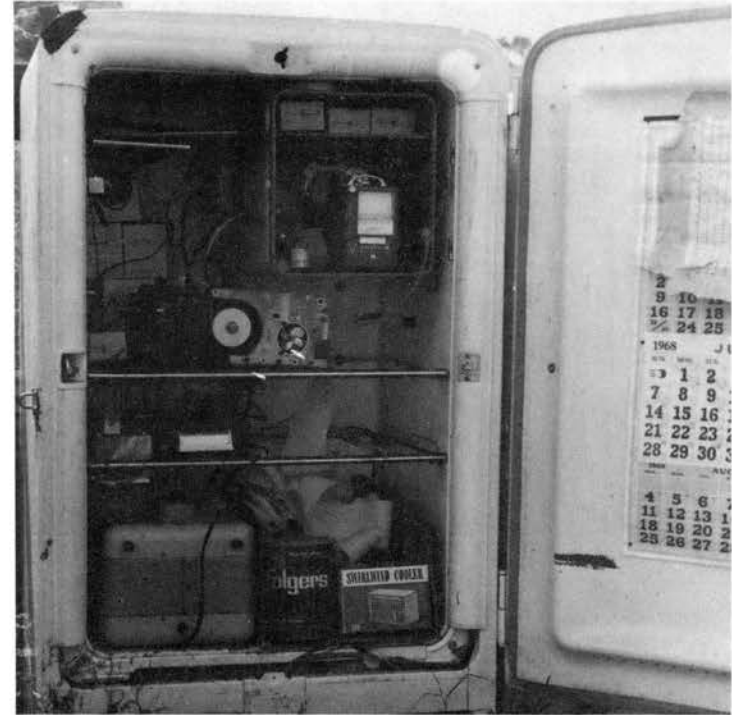


Figure 13. Rustrack recorder in field instrument enclosure.



Figure 14. Onychomys burrowing in nest area of field enclosure. One half of the sand has been removed to show the metal sides.



Figure 15. Trap set for Onychomys.



Figure 16. Southern Plains Experimental Range, Harper County, Oklahoma. Source location of experimental animals.

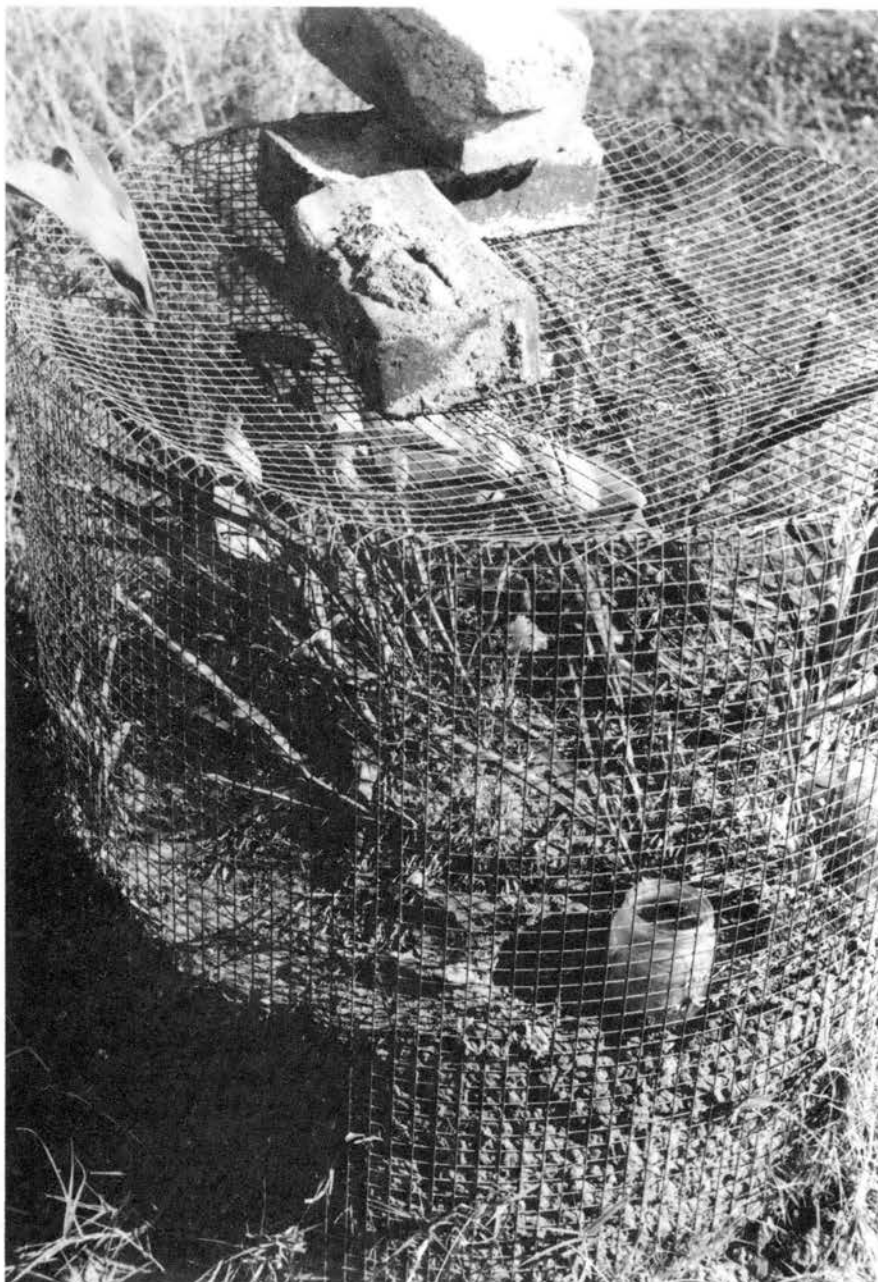


Figure 17. Outdoor holding pen used to hold animals under natural environmental conditions.

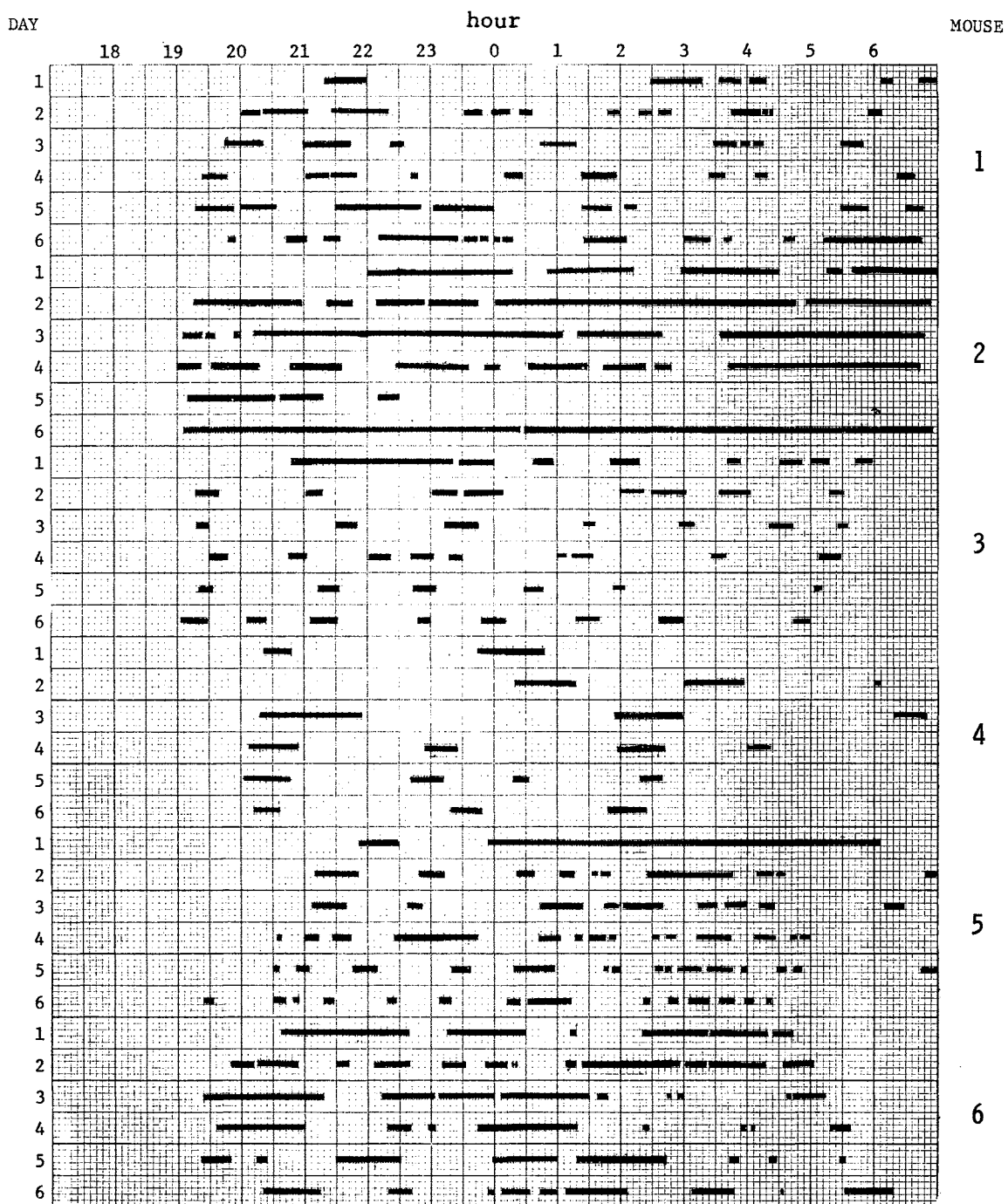
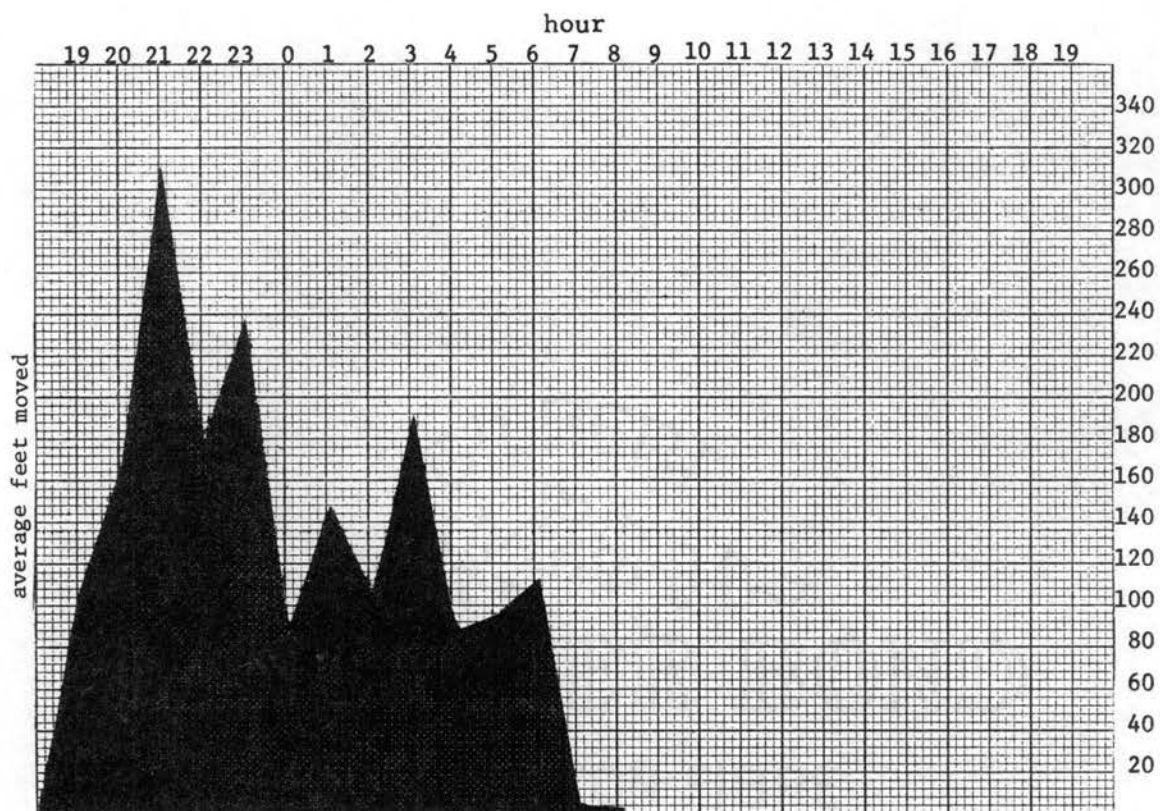


Figure 18. Time of activity for individual mice under 0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900.



Mouse I Q

Figure 19. Amount of activity in average feet moved per hour during the six day interval under 0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mouse 1 (Female).

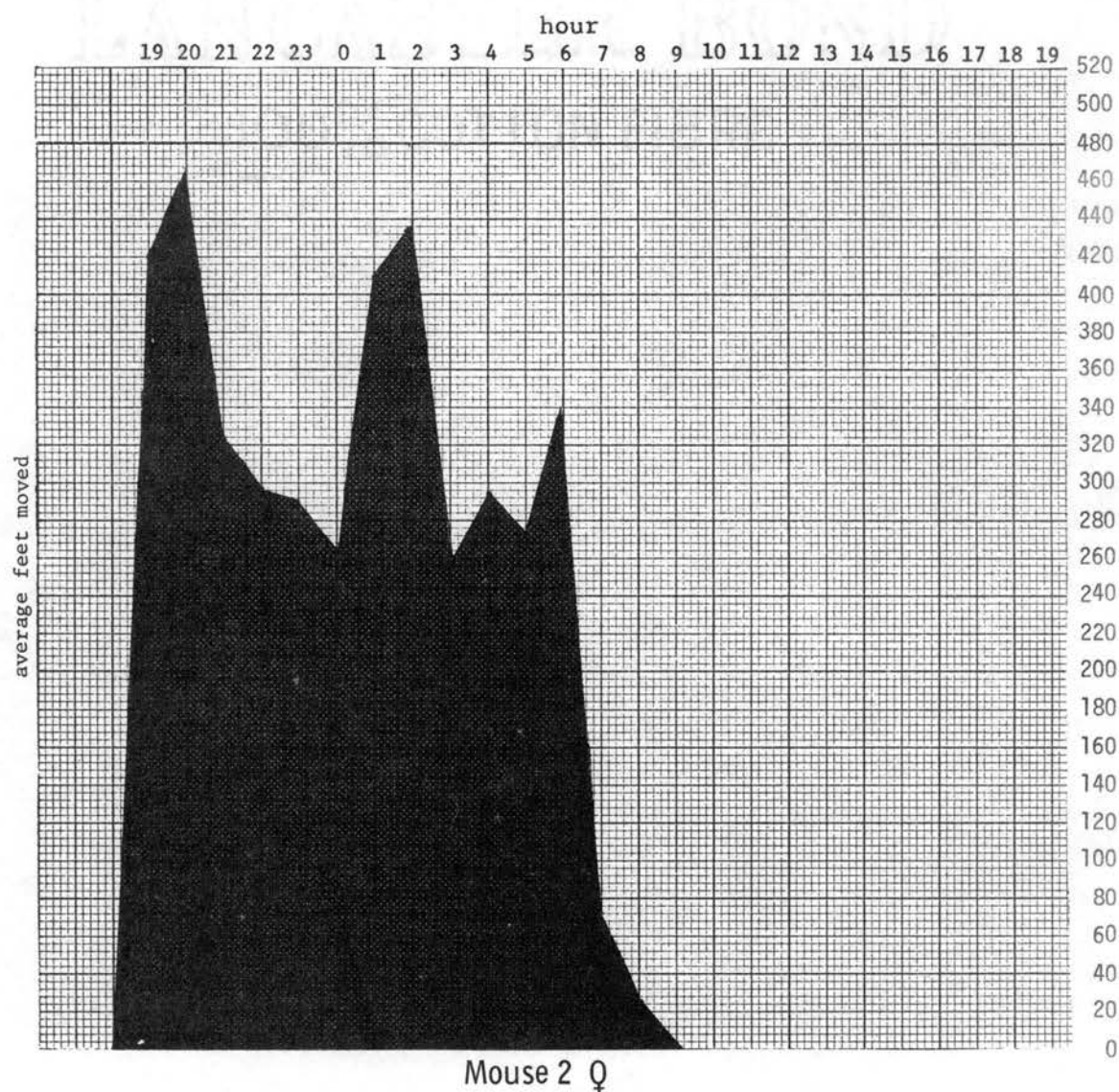


Figure 20. Amount of activity in average feet moved per hour during the six day interval under 0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mouse 2 (Female).

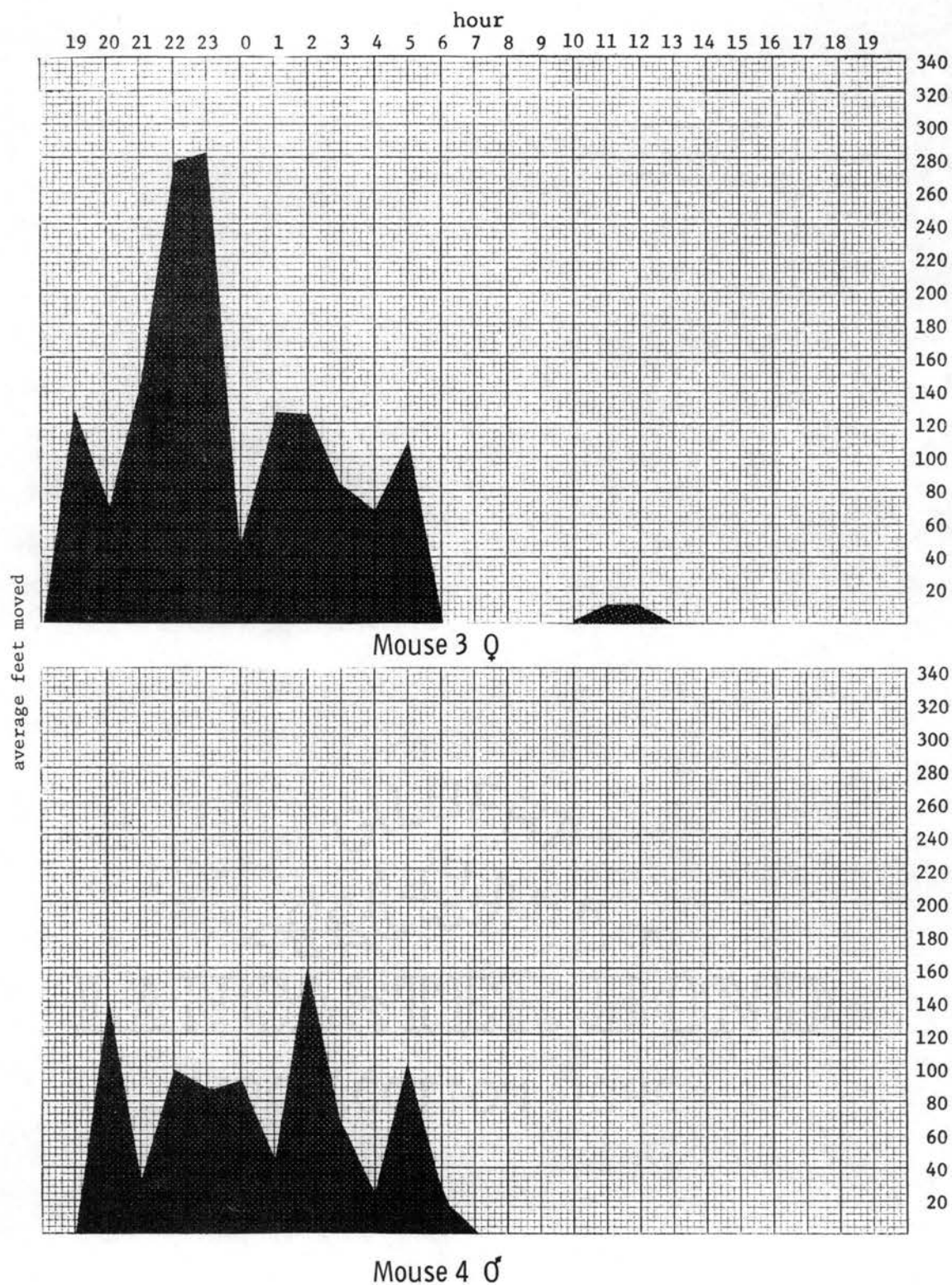


Figure 21. Amount of activity in average feet moved per hour during the six day interval under 0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mouse 3 (Female) and mouse 4 (Male).

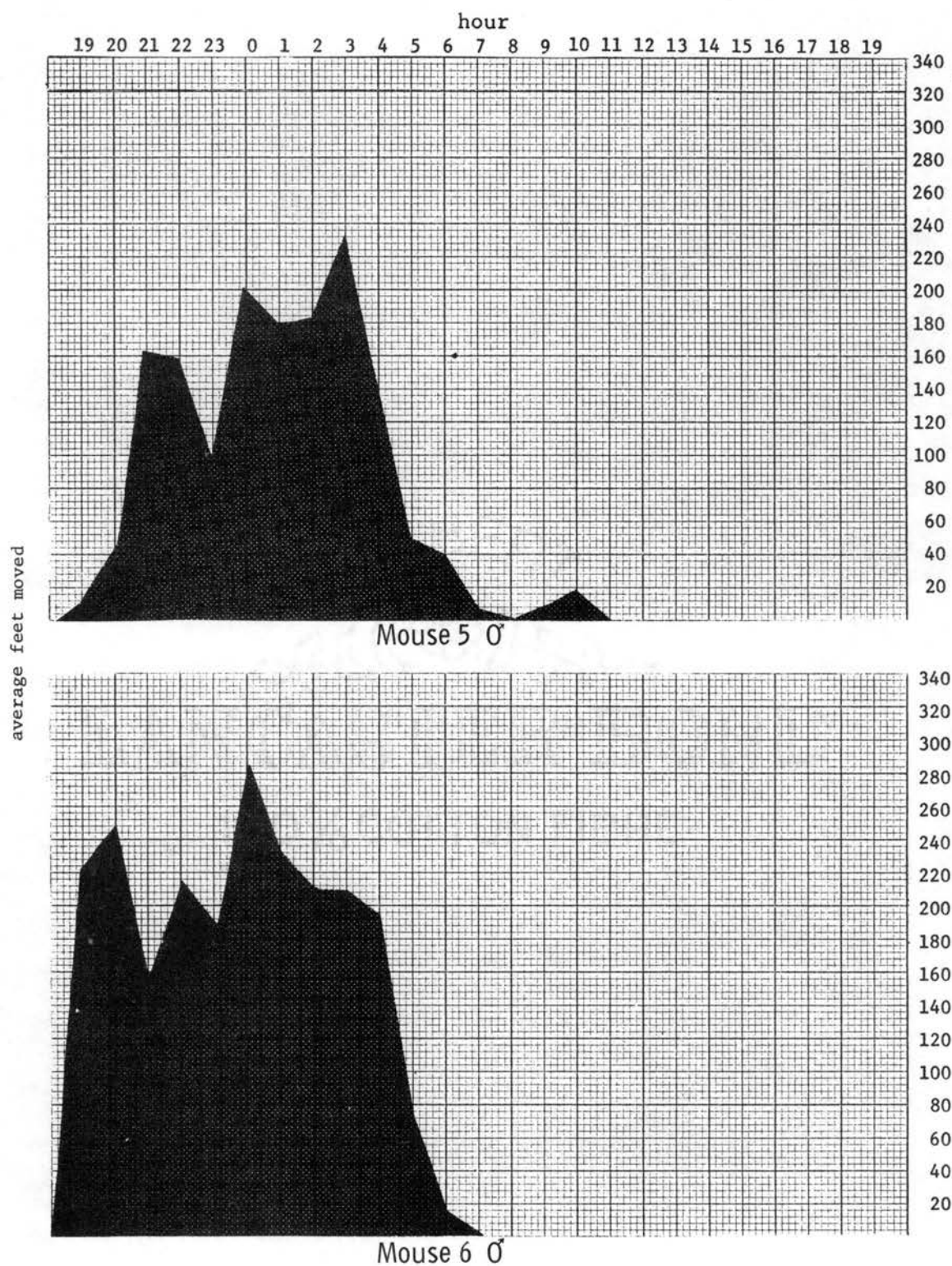


Figure 22. Amount of activity in average feet moved per hour during the six day interval under 0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mouse 5 (Male) and mouse 6 (Female).

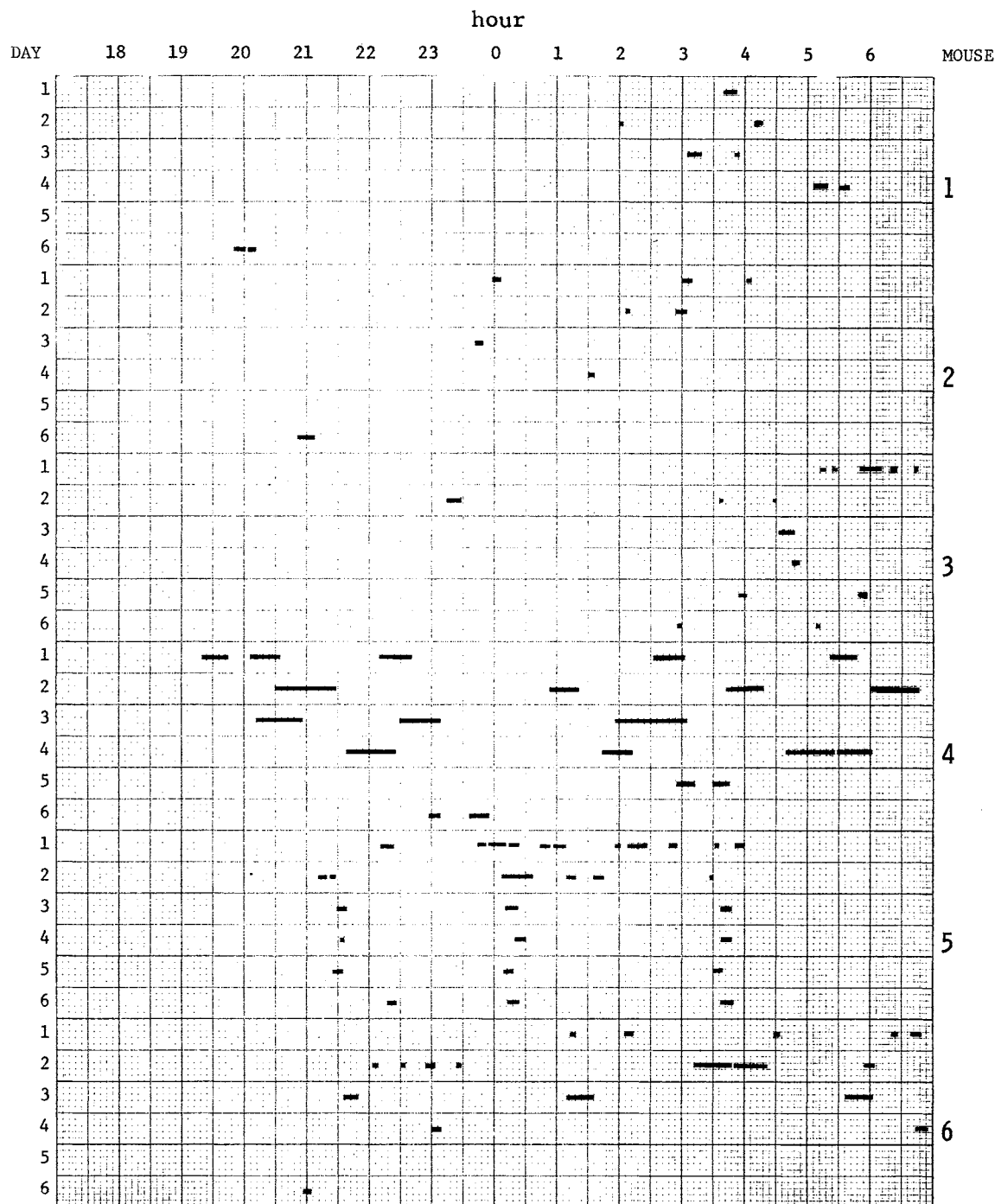


Figure 23. Time of activity for individual mice under 19.5 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900.

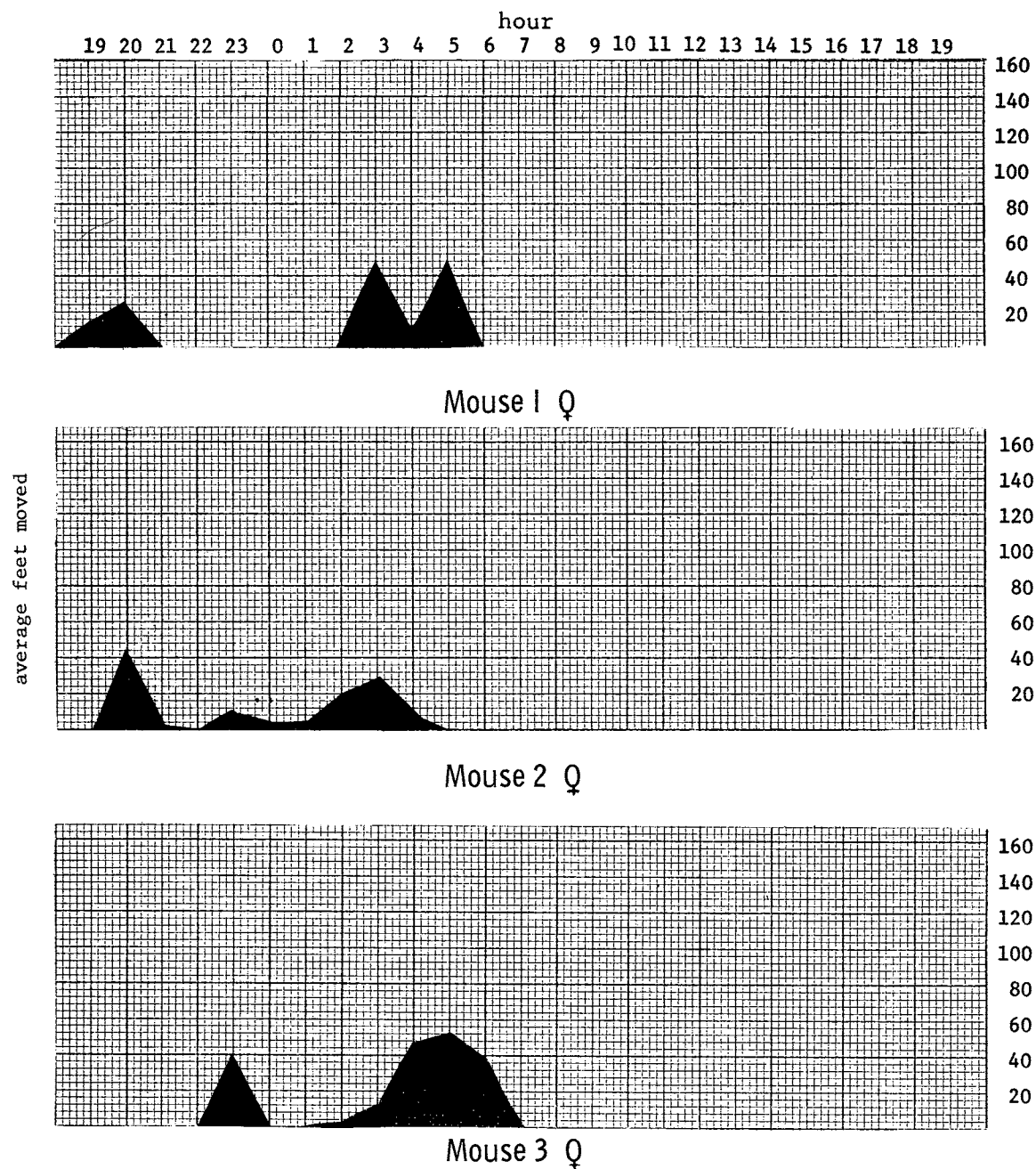


Figure 24. Amount of activity in average feet moved per hour during the six day interval under 19.5 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mice 1-3 (Females).

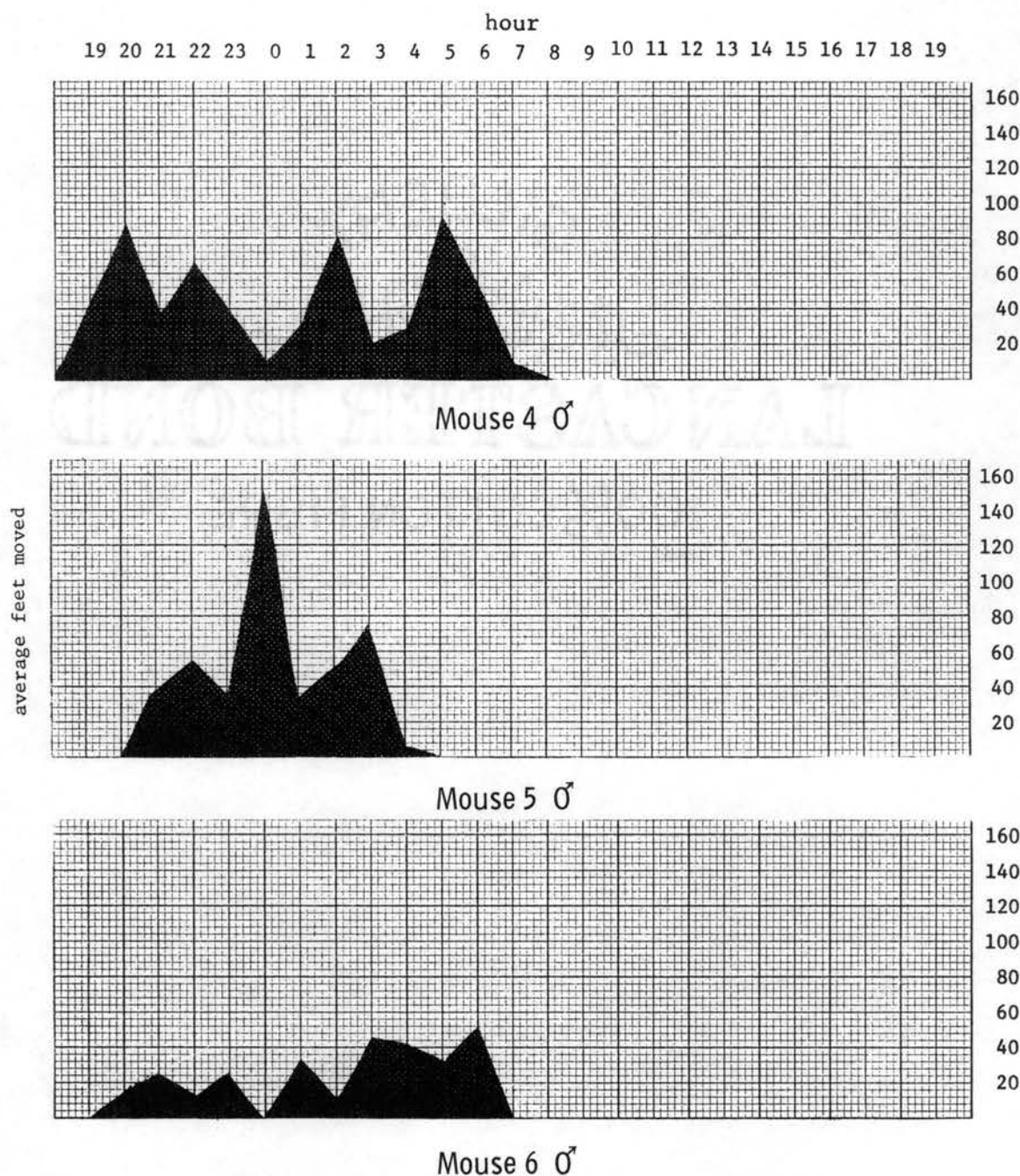


Figure 25. Amount of activity in average feet moved per hour during the six day interval under 19.5 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mice 4-6 (Males).

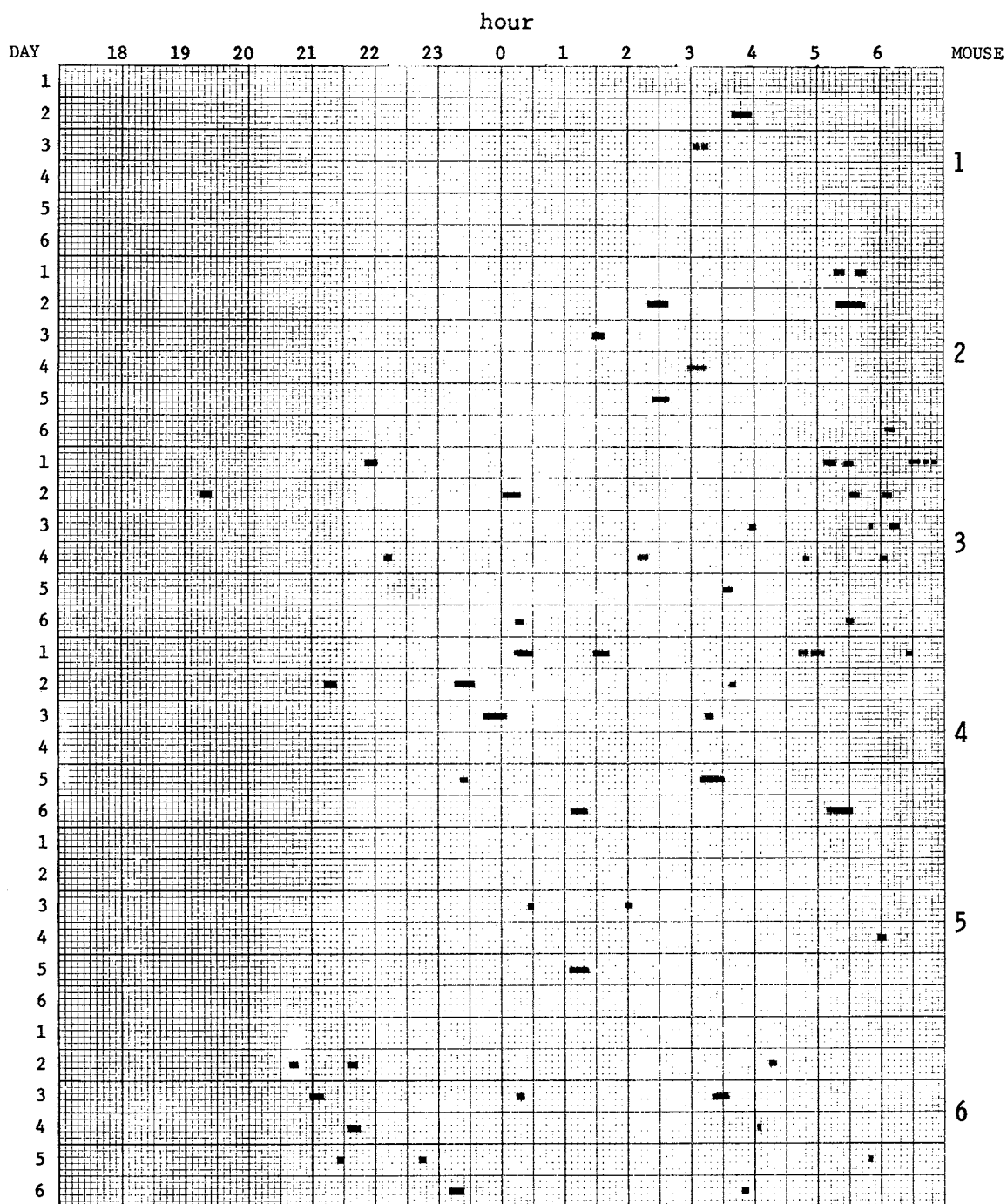


Figure 26. Time of activity for individual mice under 39.0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900.

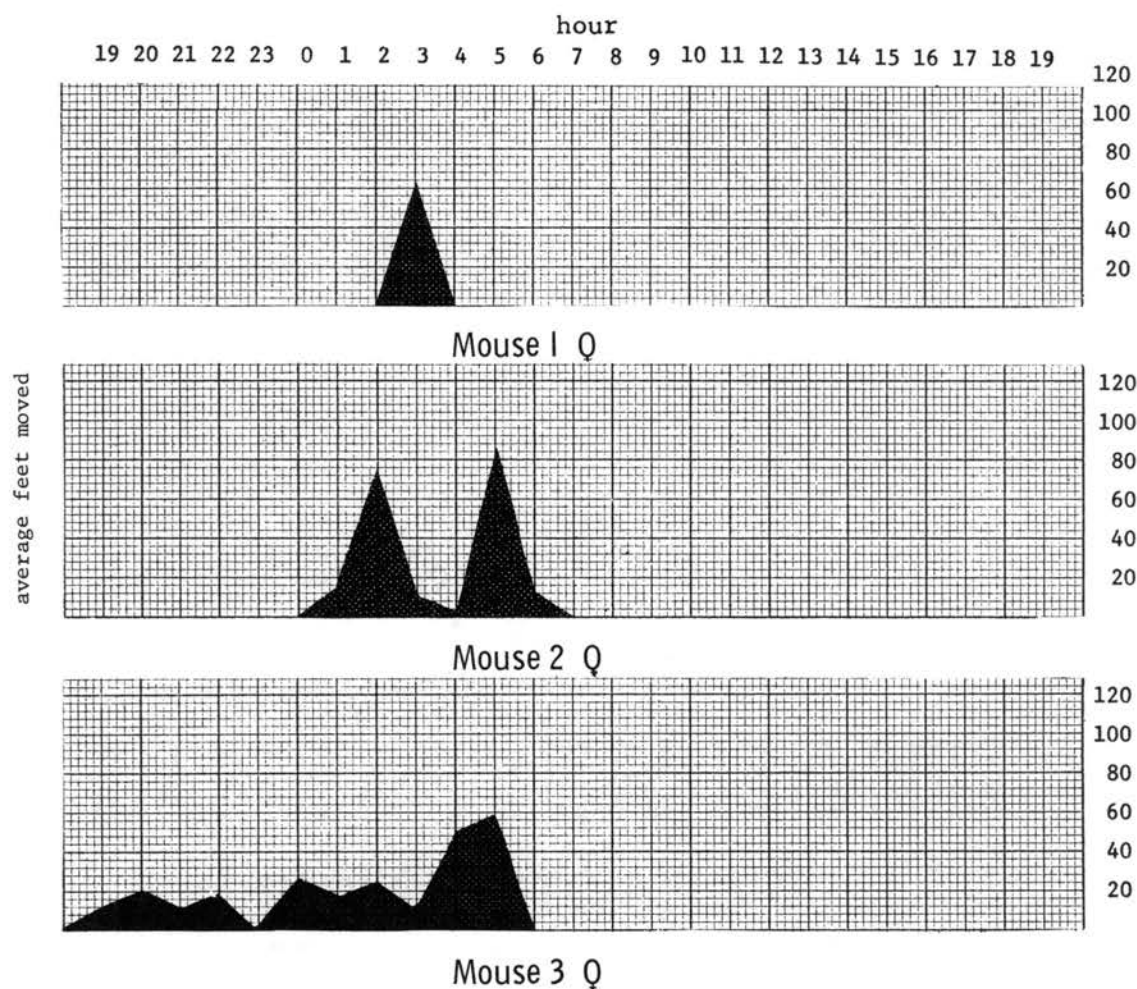


Figure 27. Amount of activity in average feet moved per hour during the six day interval under 39.0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mice 1-3 (Females).

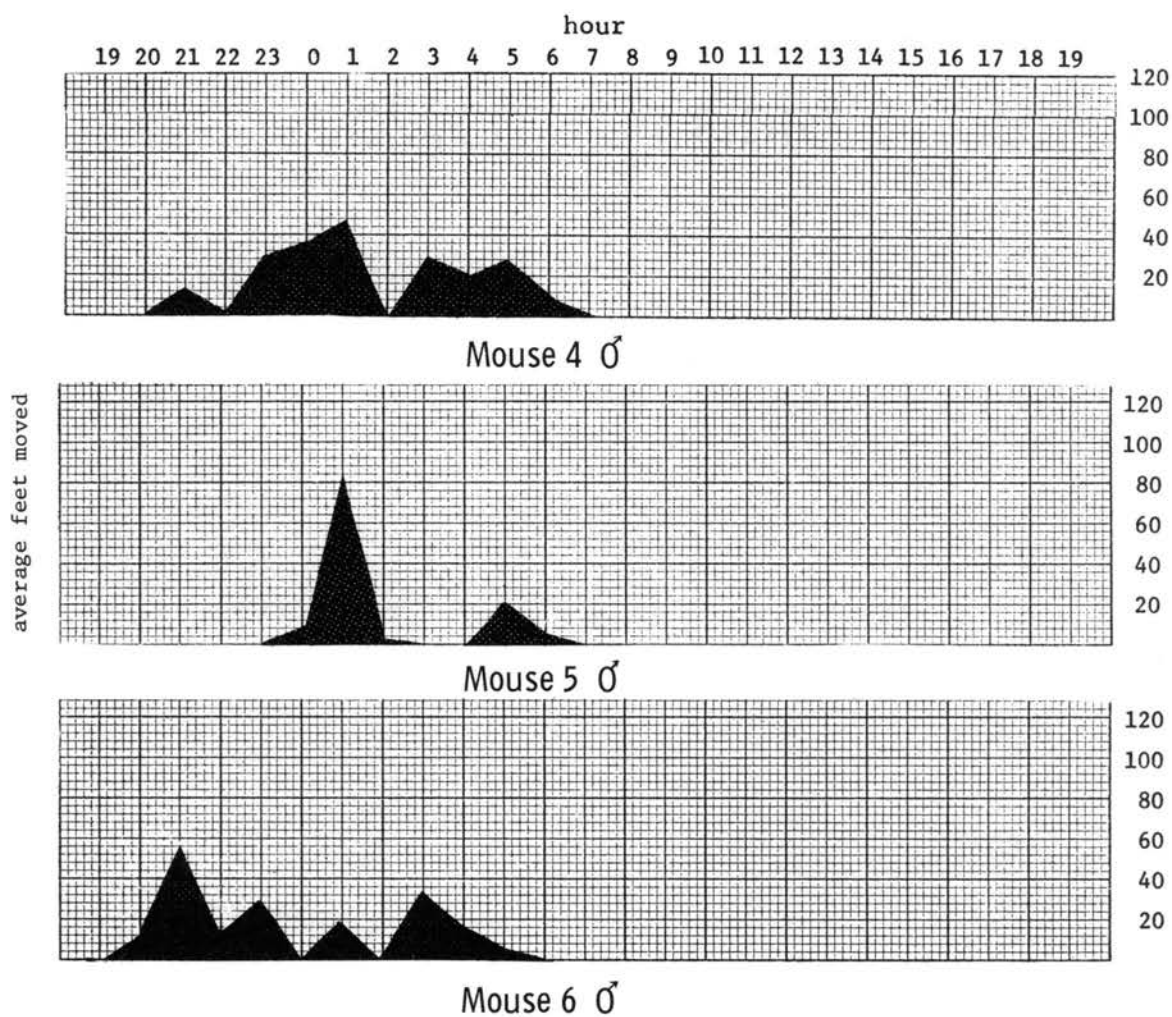


Figure 28. Amount of activity in average feet moved per hour during the six day interval under 39.0 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mice 4-6 (Males).

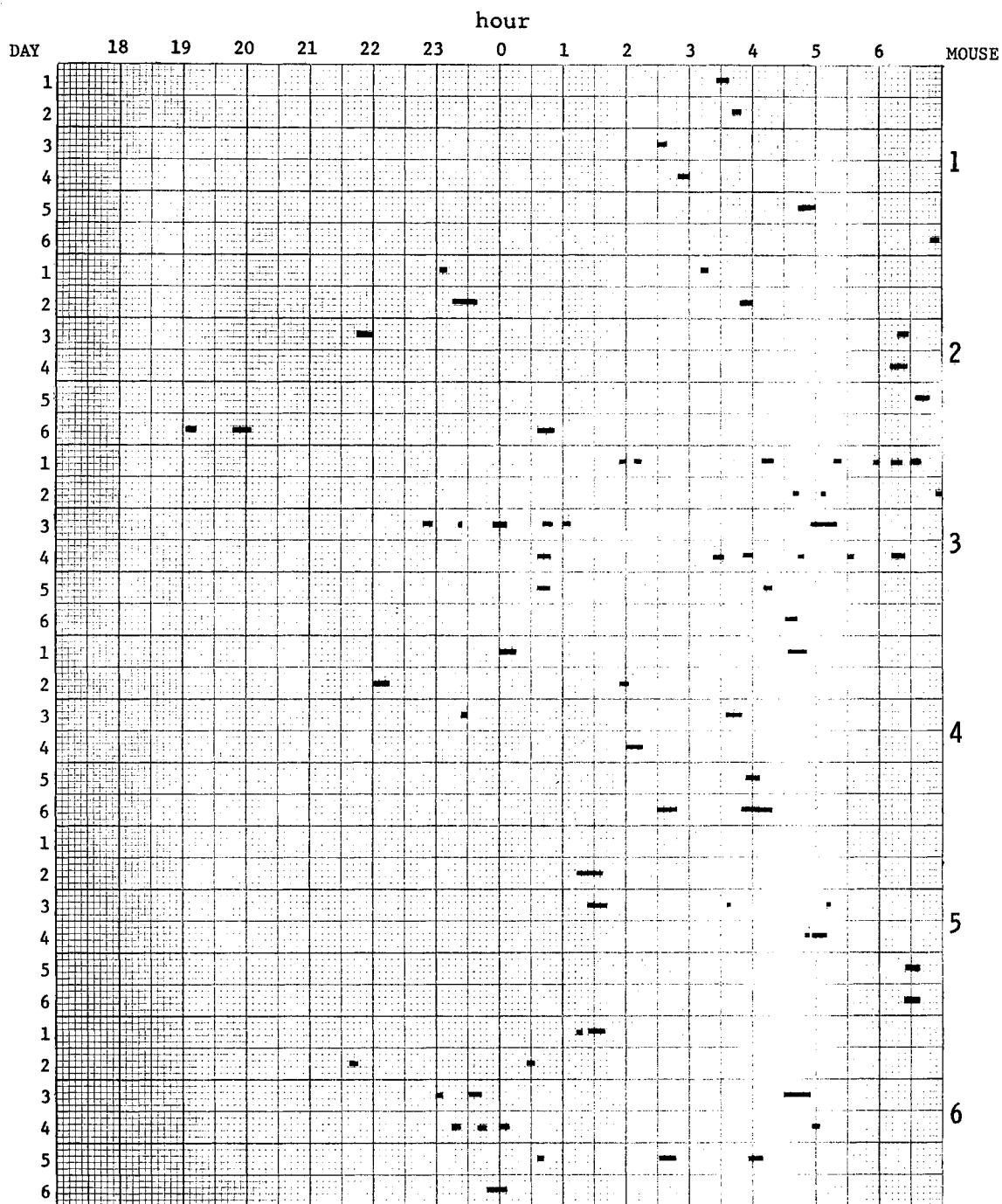


Figure 29. Time of activity for individual mice under 58.5 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900.

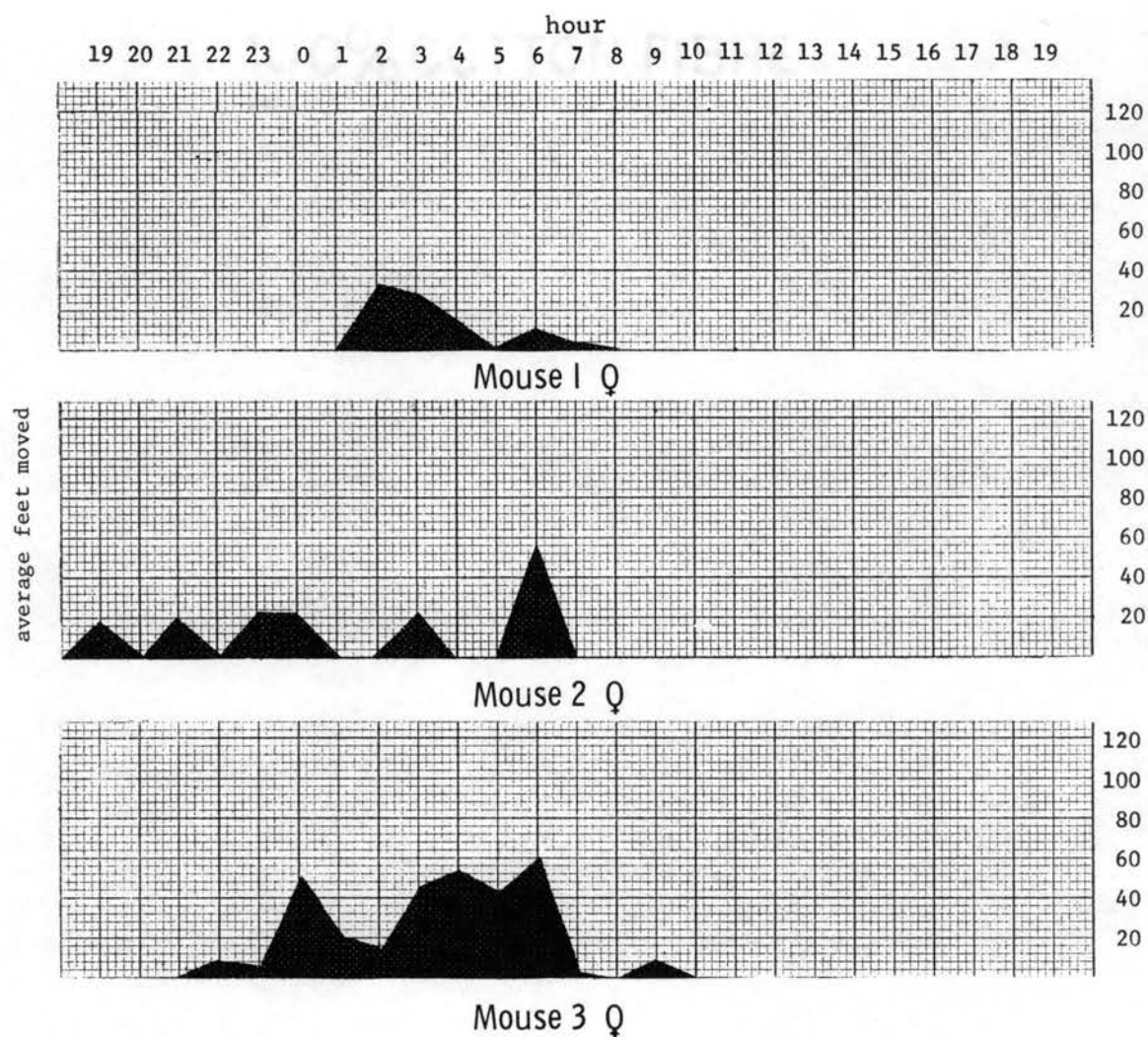


Figure 30. Amount of activity in average feet moved per hour during the six day interval under 58.5 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mice 1-3 (Females).

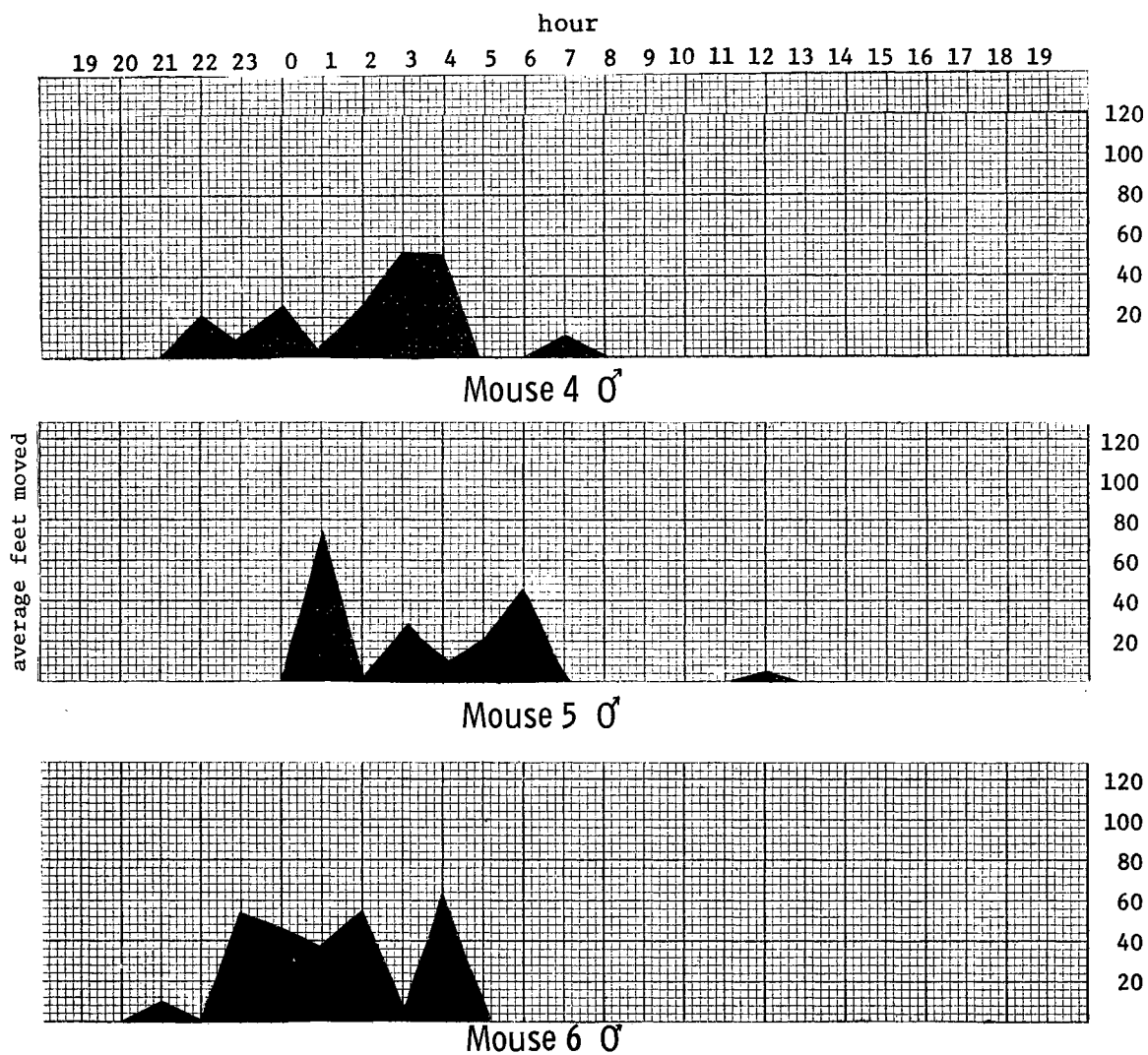


Figure 31. Amount of activity in average feet moved per hour during the six day interval under 58.5 foot-candles from 1900 to 0700 and 78.0 foot-candles from 0700 to 1900 for mice 4-6 (Males).

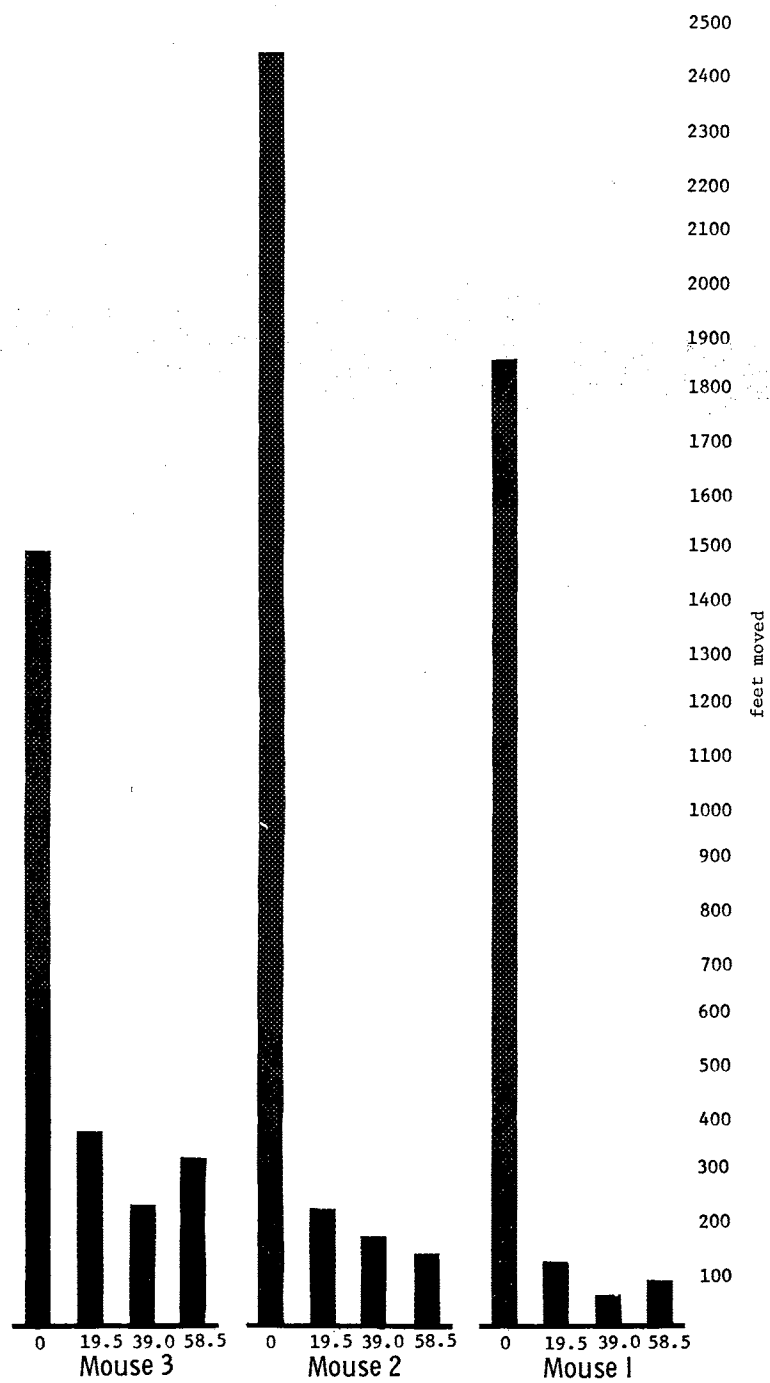


Figure 32. Graphic presentation of amount of activity in average feet moved per day under four conditions of light intensity during the night period for female Onychomys.

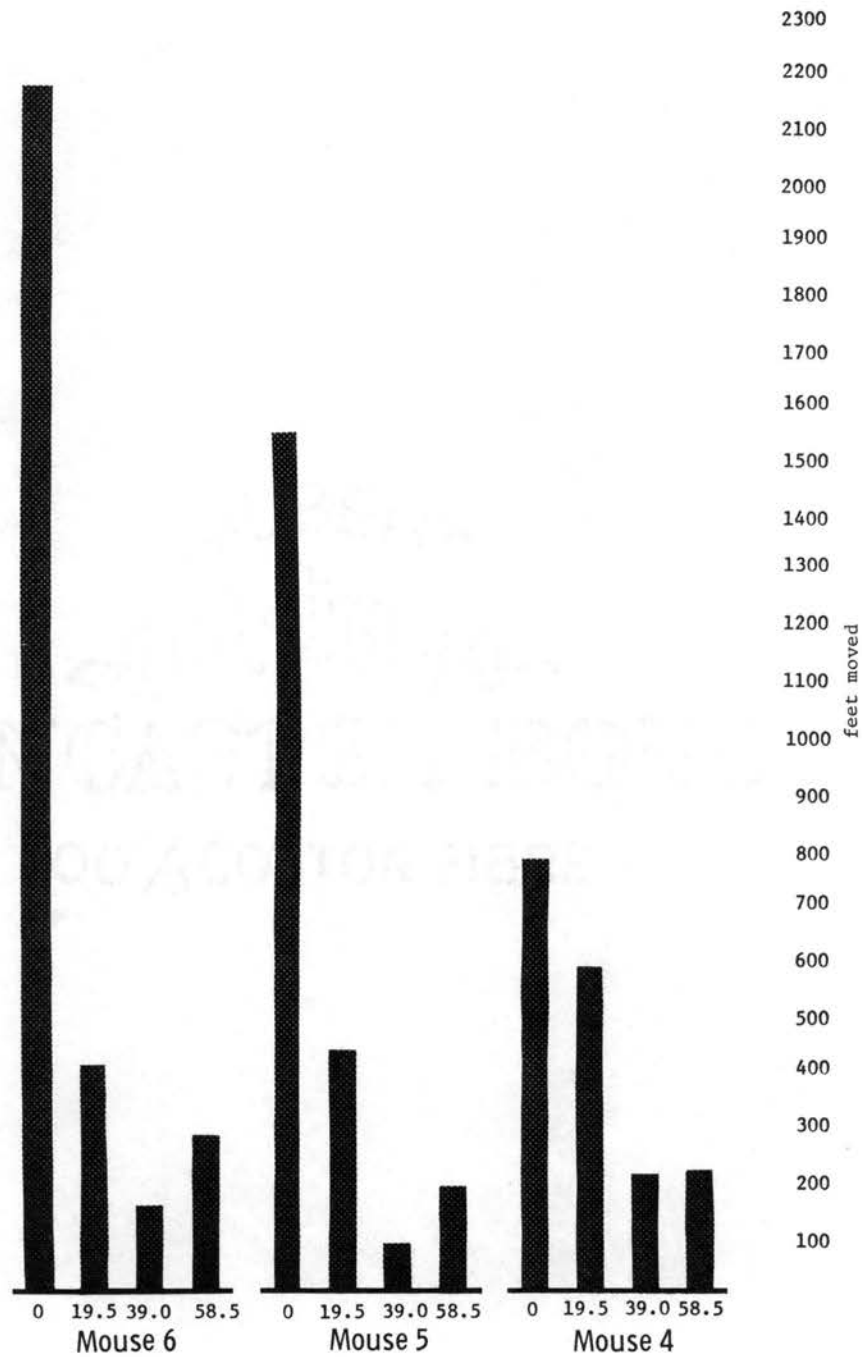


Figure 33. Graphic presentation of amount of activity in average feet moved per day under four conditions of light intensity during the night period for male *Onychomys*.

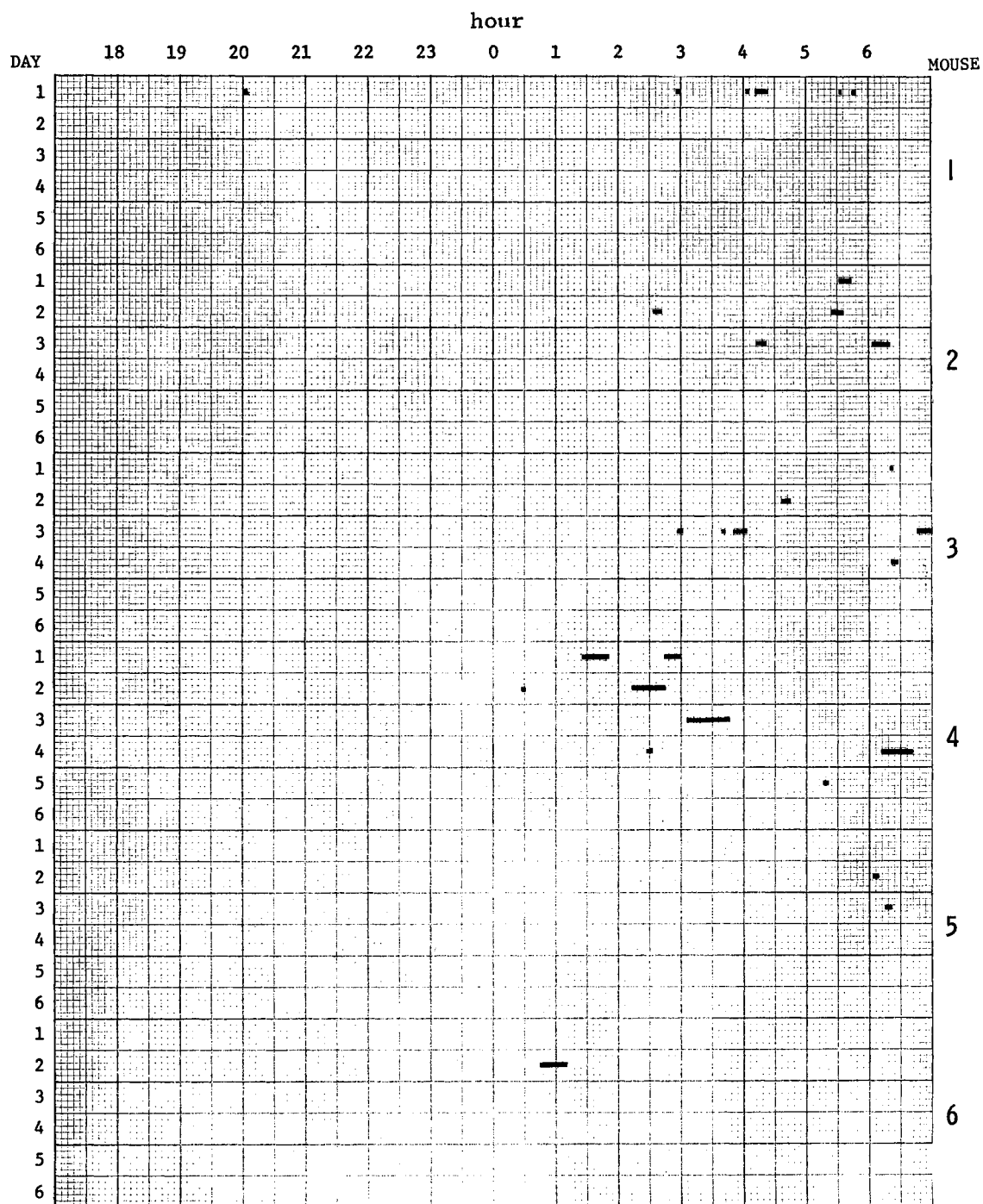


Figure 34. Shift in activity time for individual animals during the six day interval following reversal of photoperiod (1900-0700).

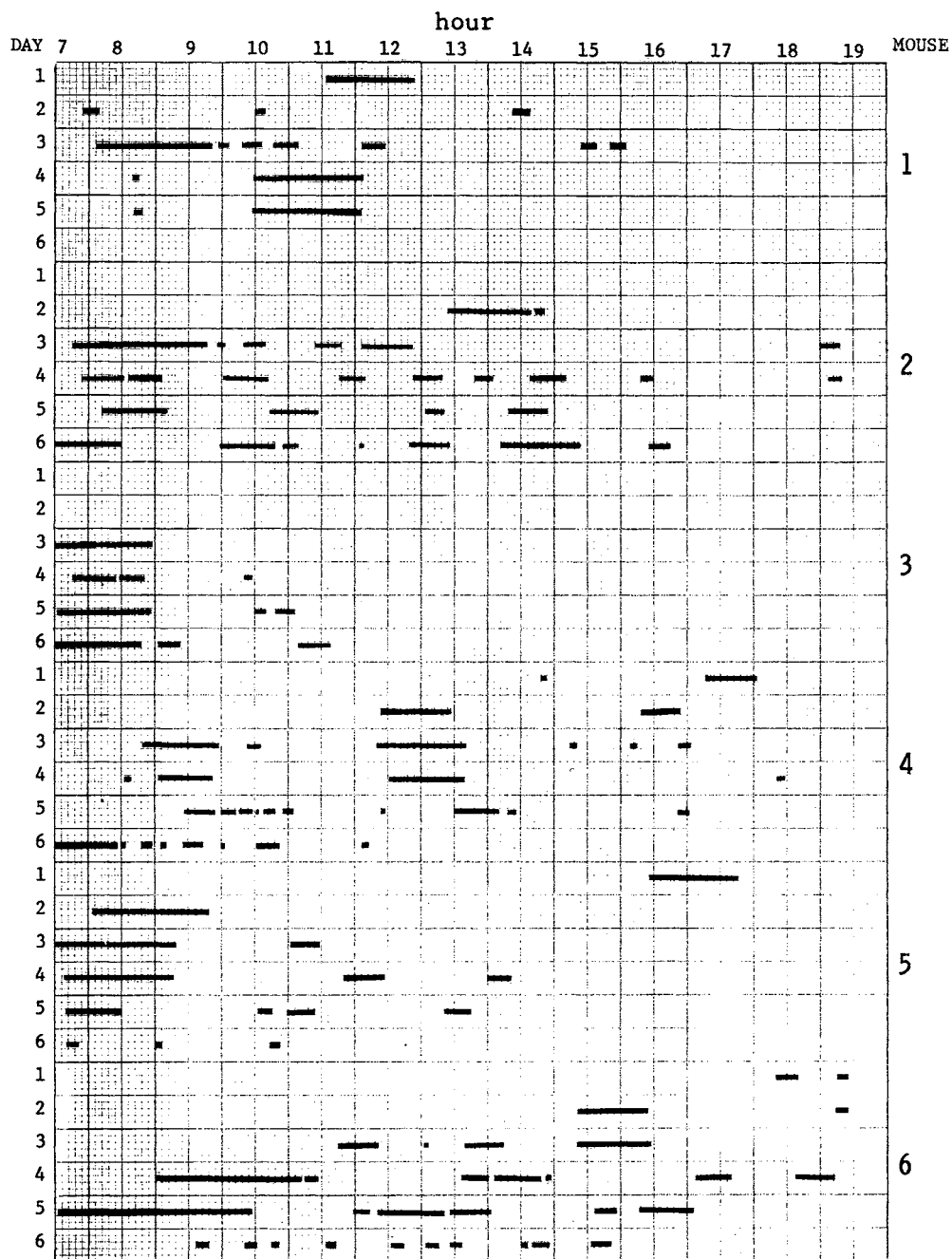


Figure 35. Shift in activity times for individual animals during the six day interval following reversal of photoperiod (0700-1900).

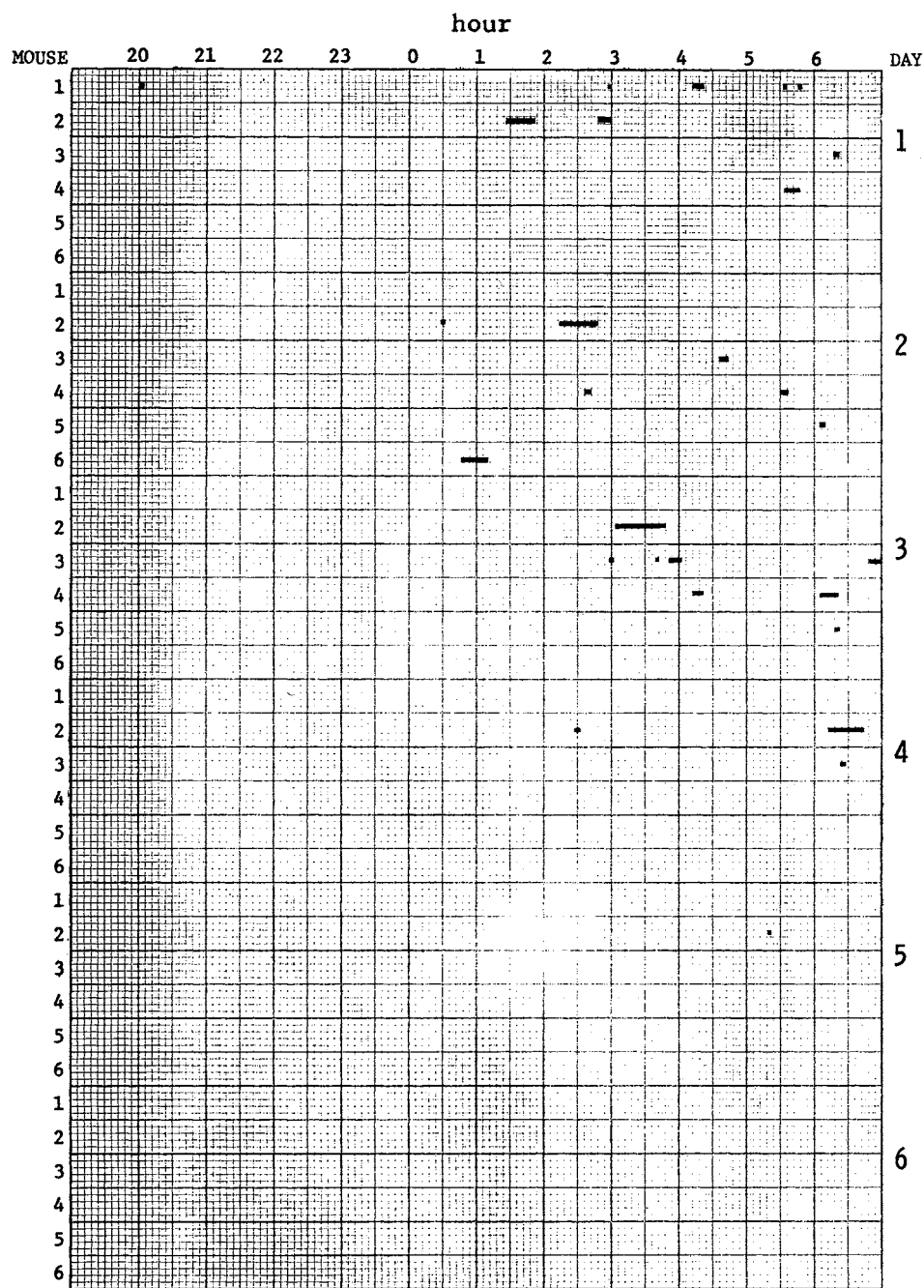


Figure 36. Shift in activity times per day over the six day interval following reversal of photoperiod for all mice (1900-0700).

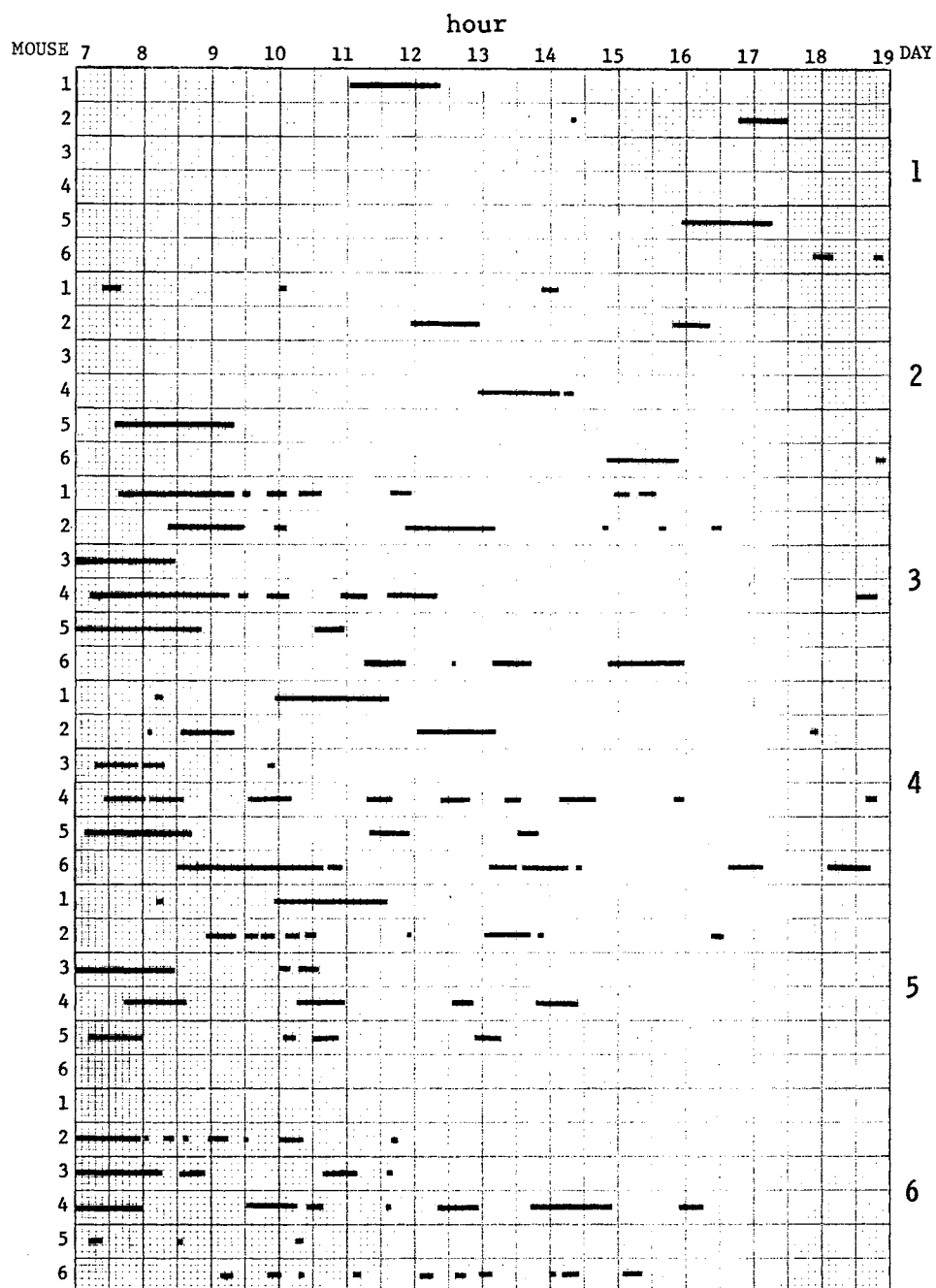


Figure 37. Shift in activity times per day over the six day interval following reversal of photoperiod for all mice (0700-1900).

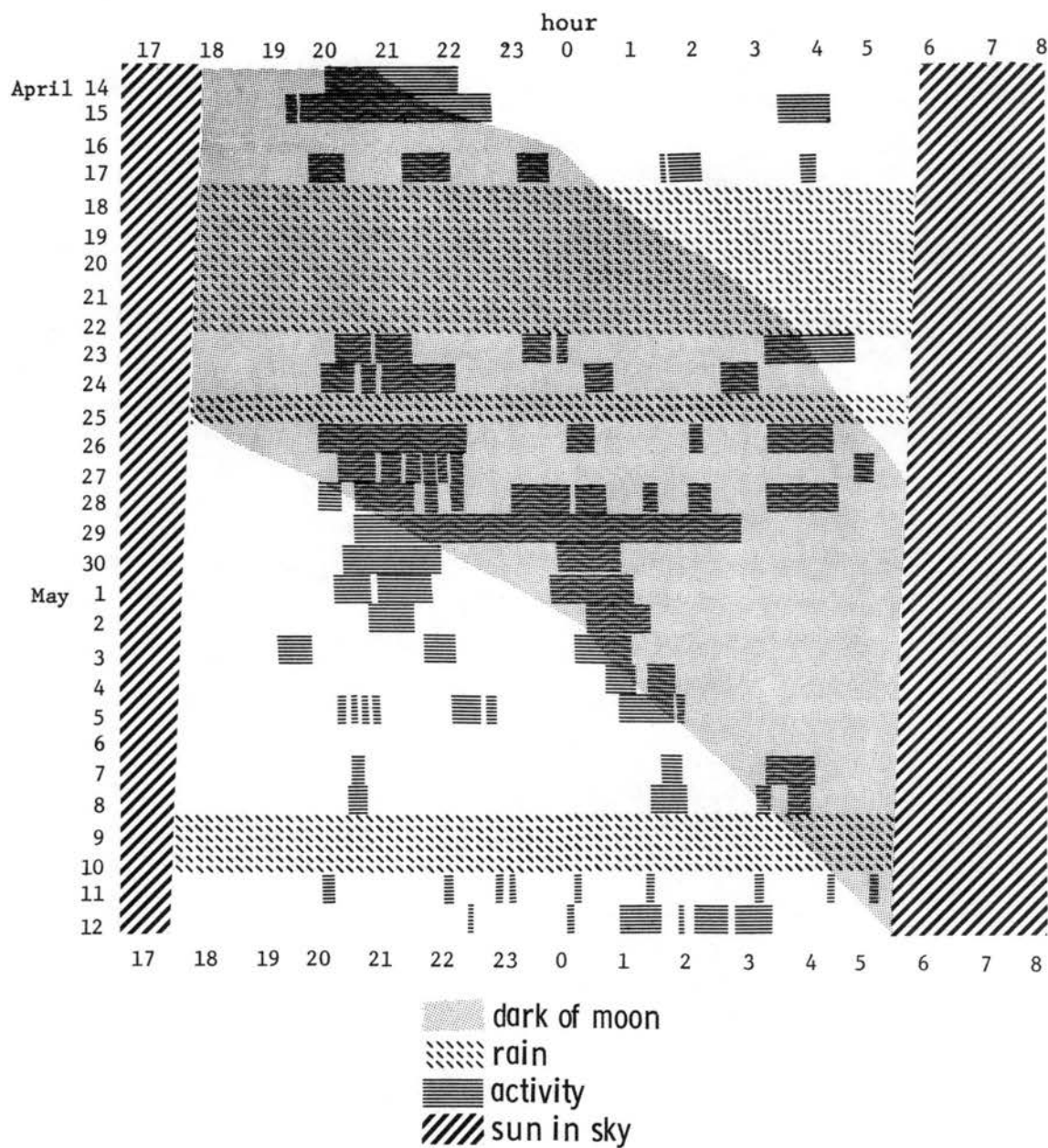


Figure 38. Time of activity of mouse 51 (Female) during the synodical month under natural environmental conditions.

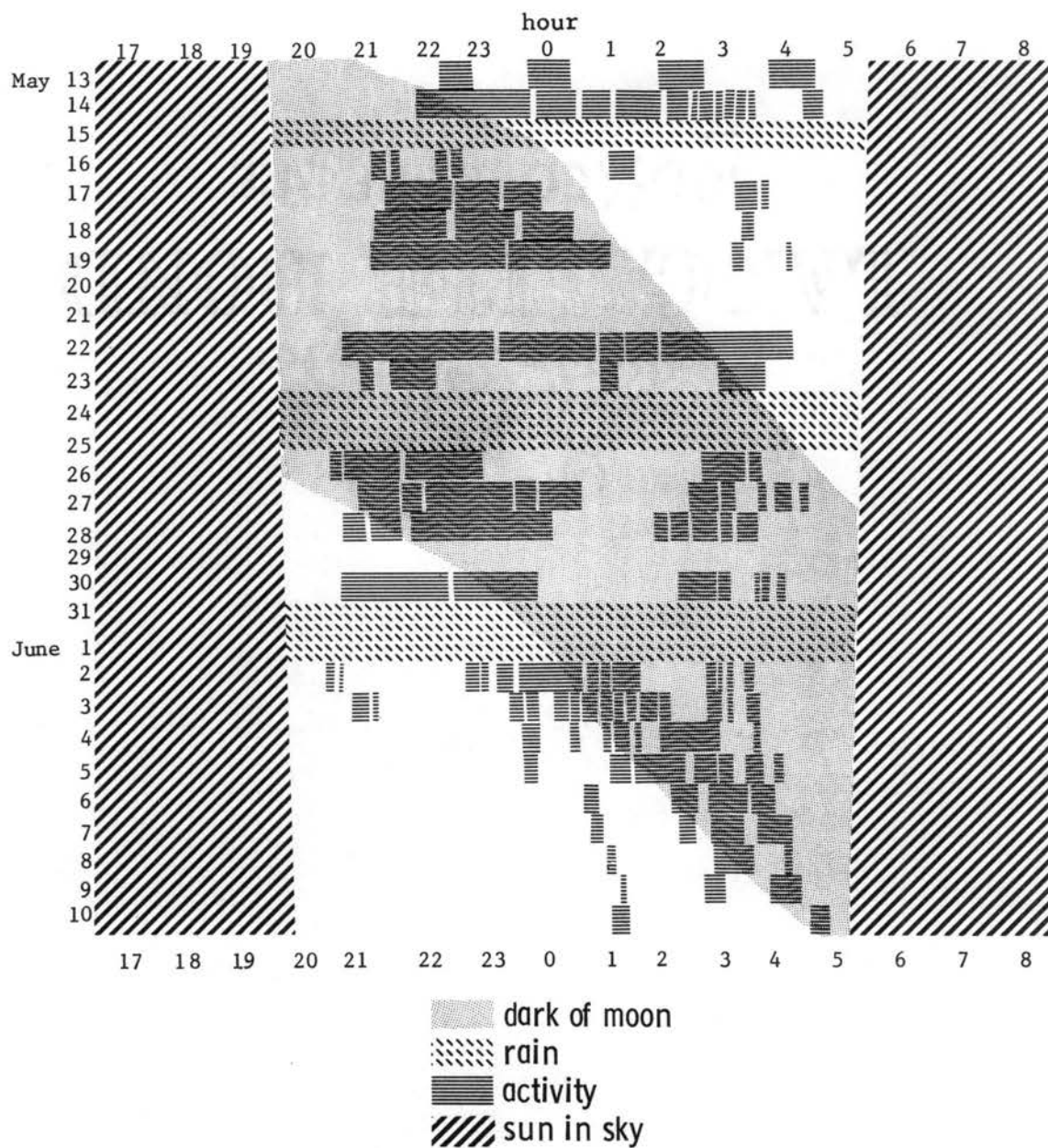


Figure 39. Time of activity of mouse 52 (Female) during the synodical month under natural environmental conditions.

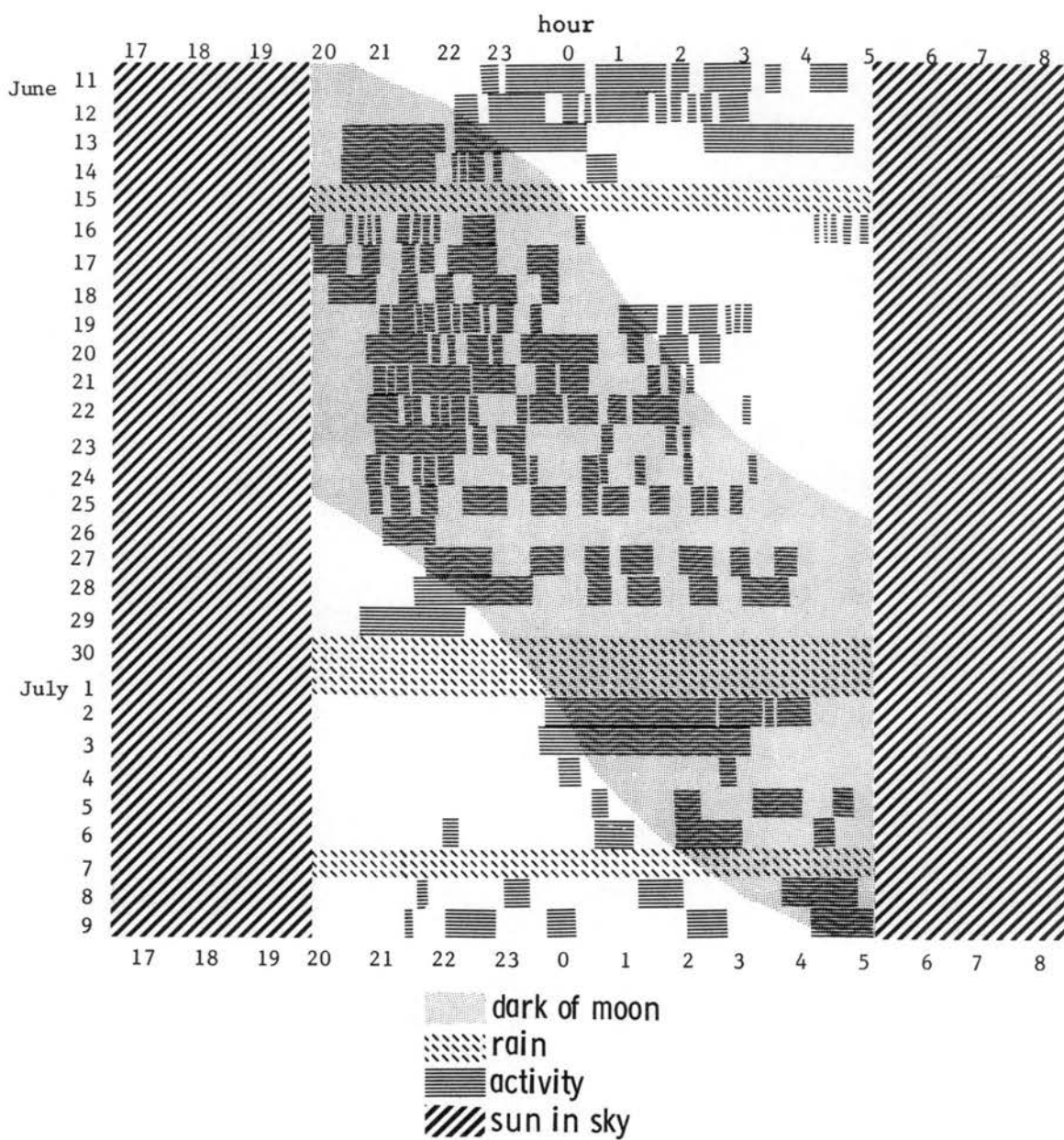


Figure 40. Time of activity of mouse 53 (Male) during the synodical month under natural environmental conditions.

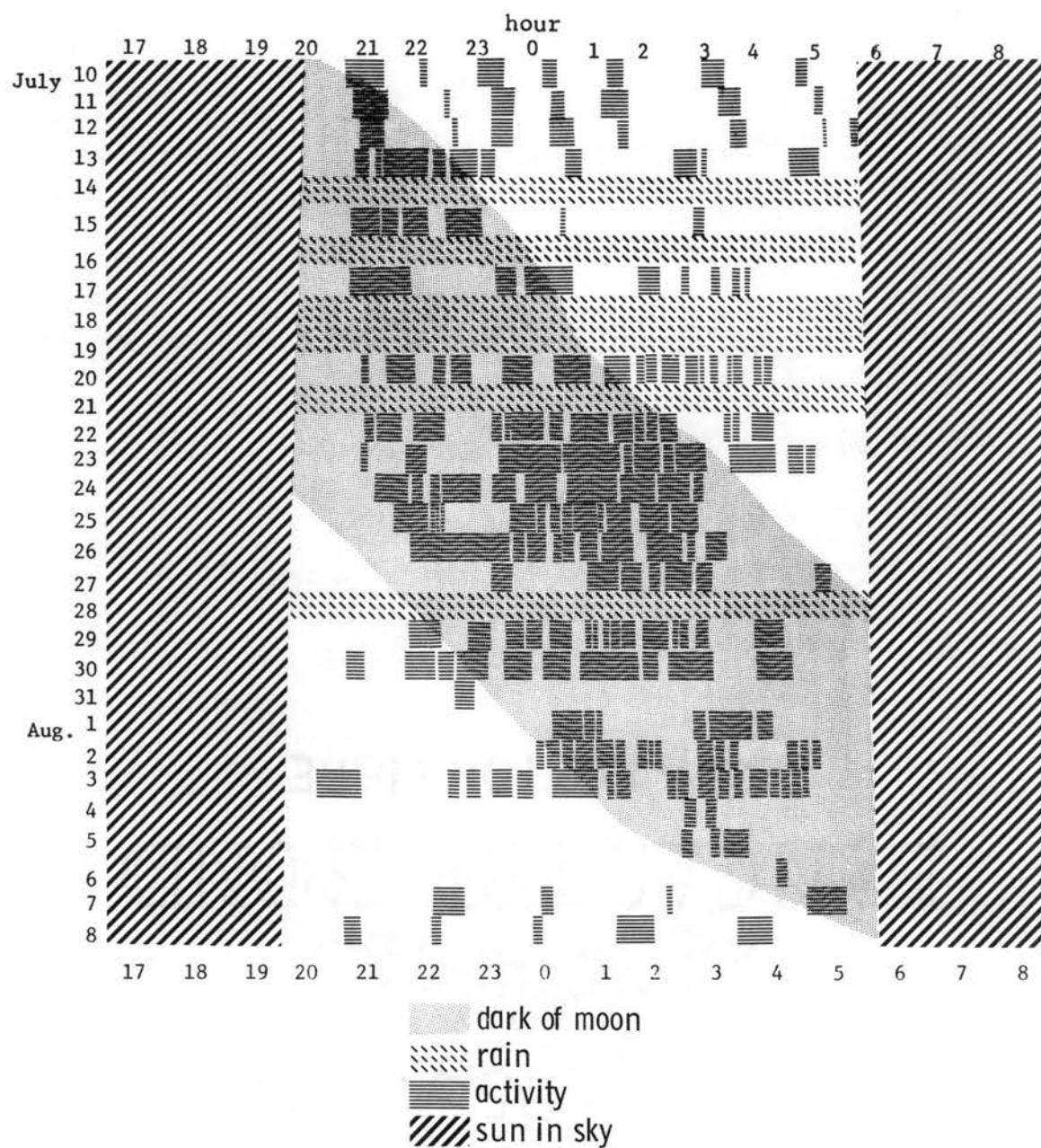


Figure 41. Time of activity of mouse 54 (Male) during the synodical month under natural environmental conditions.

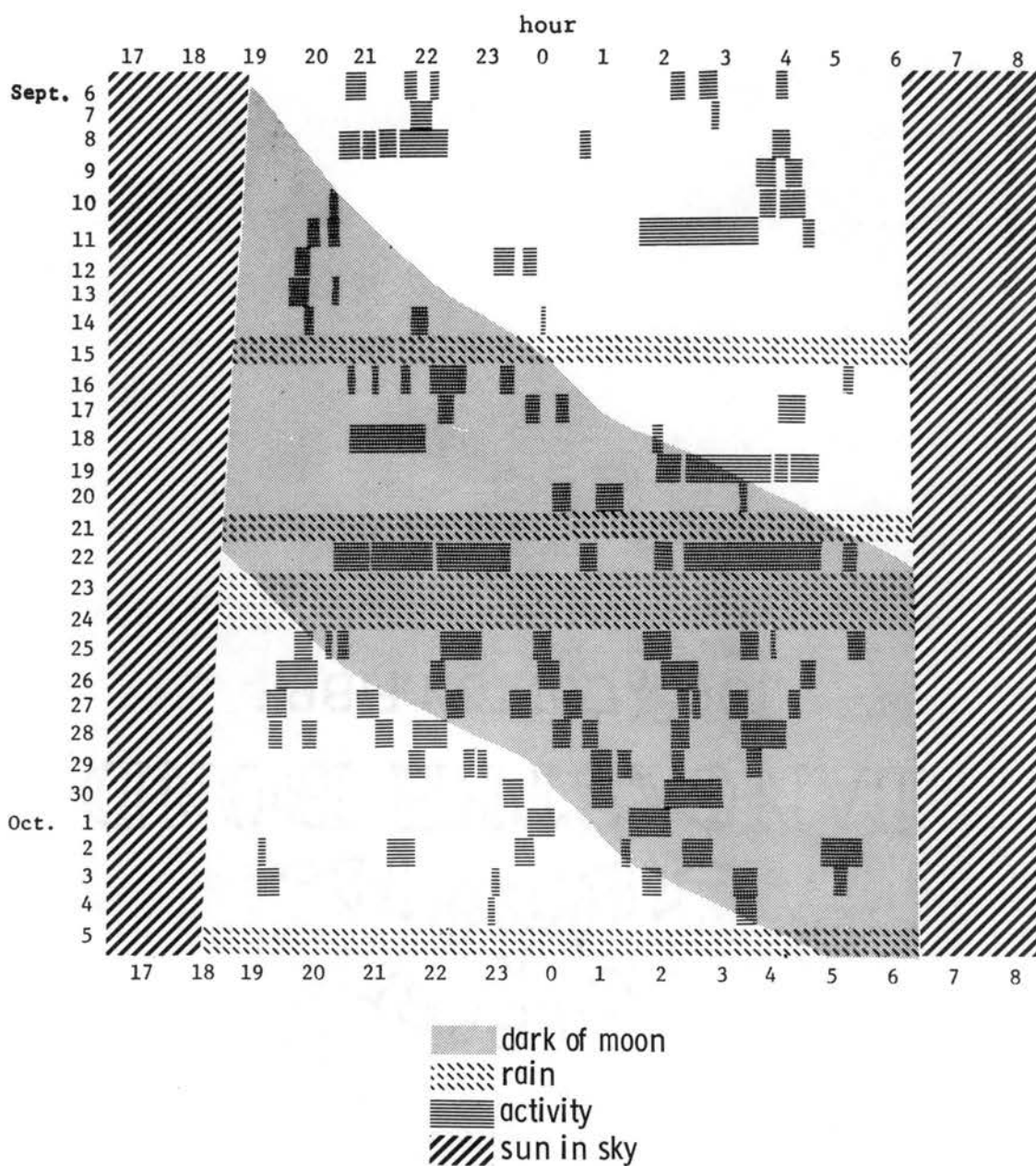


Figure 42. Time of activity of mouse 55 (Female) during the synodical month under natural environmental conditions.

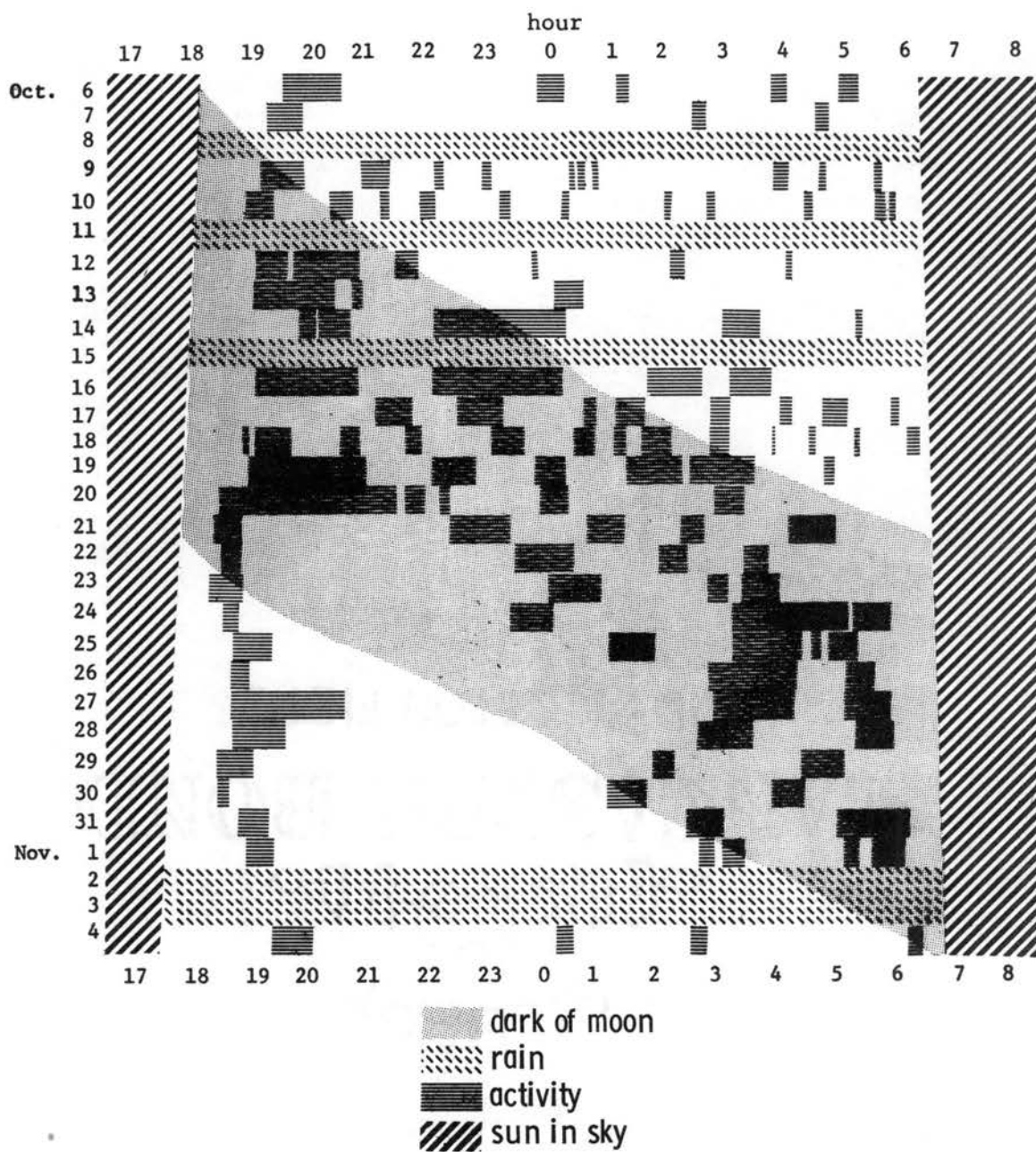


Figure 43. Time of activity of mouse 56 (Male) during the synodical month under natural environmental conditions.

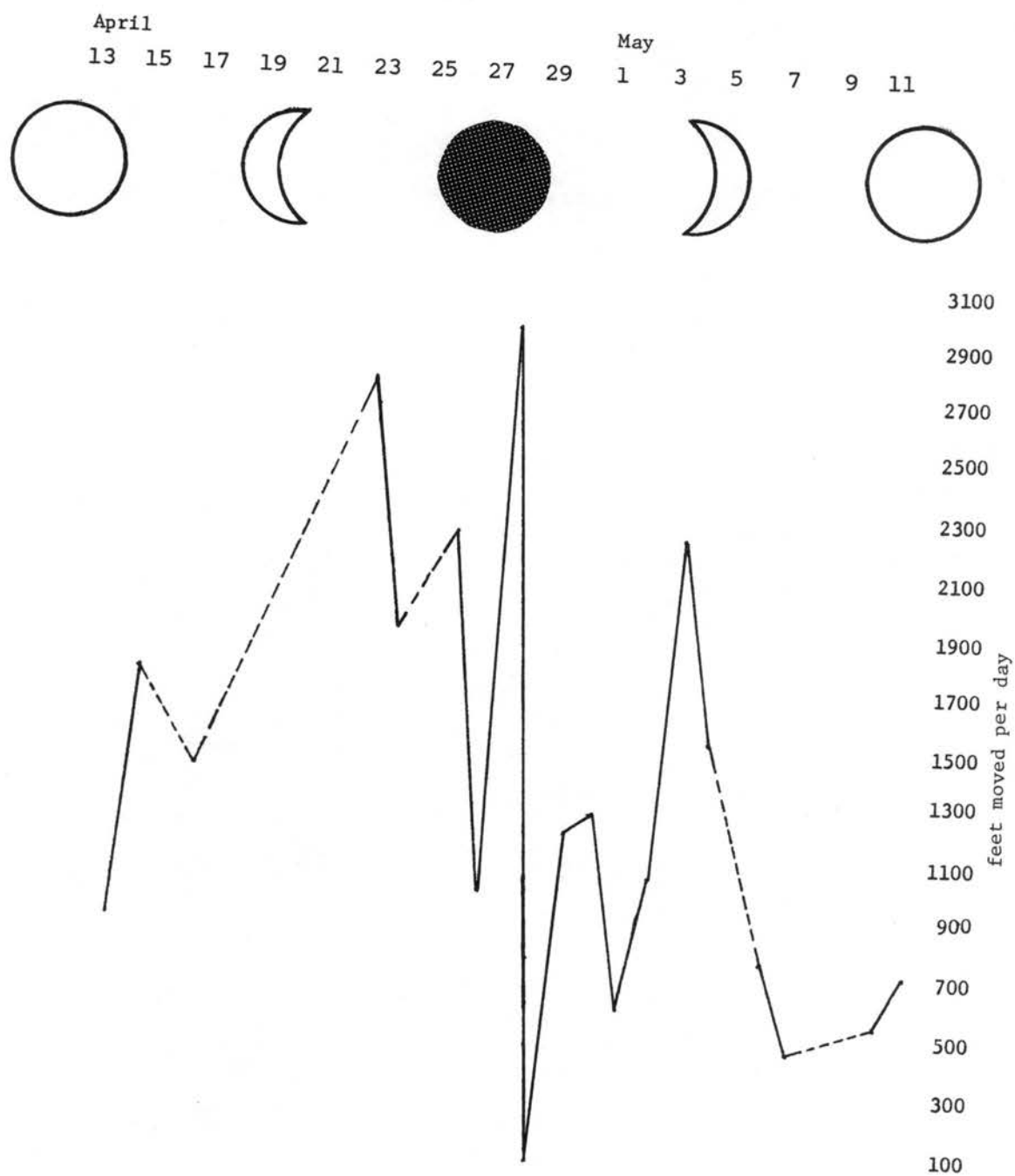


Figure 44. Amount of activity of mouse 51 (Female) in feet moved per day during the synodical month under natural environmental conditions.

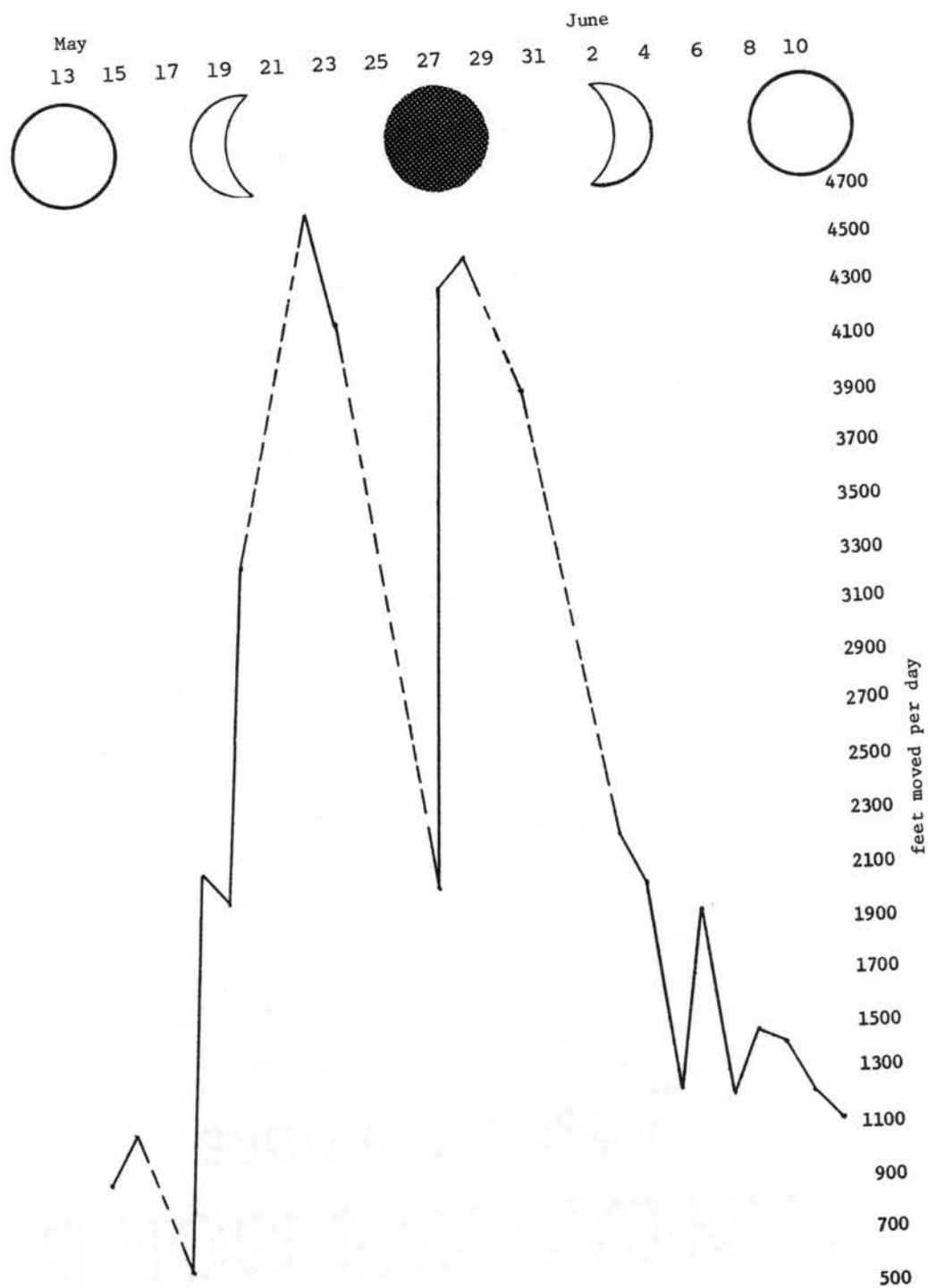


Figure 45. Amount of activity of mouse 52 (Female) in feet moved per day during the synodical month under natural environmental conditions.

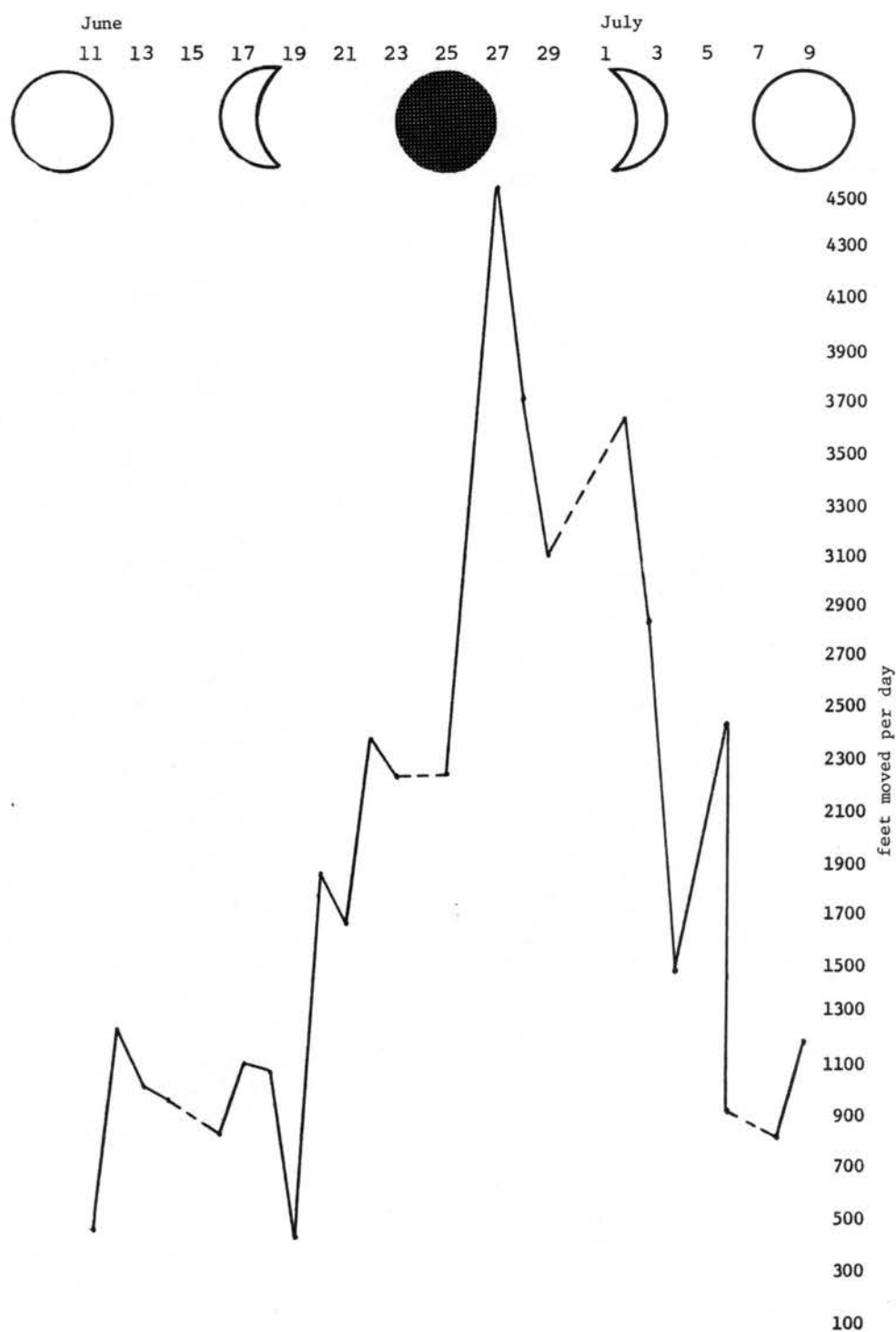


Figure 46. Amount of activity of mouse 53 (Male) in feet moved per day during the synodical month under natural environmental conditions.

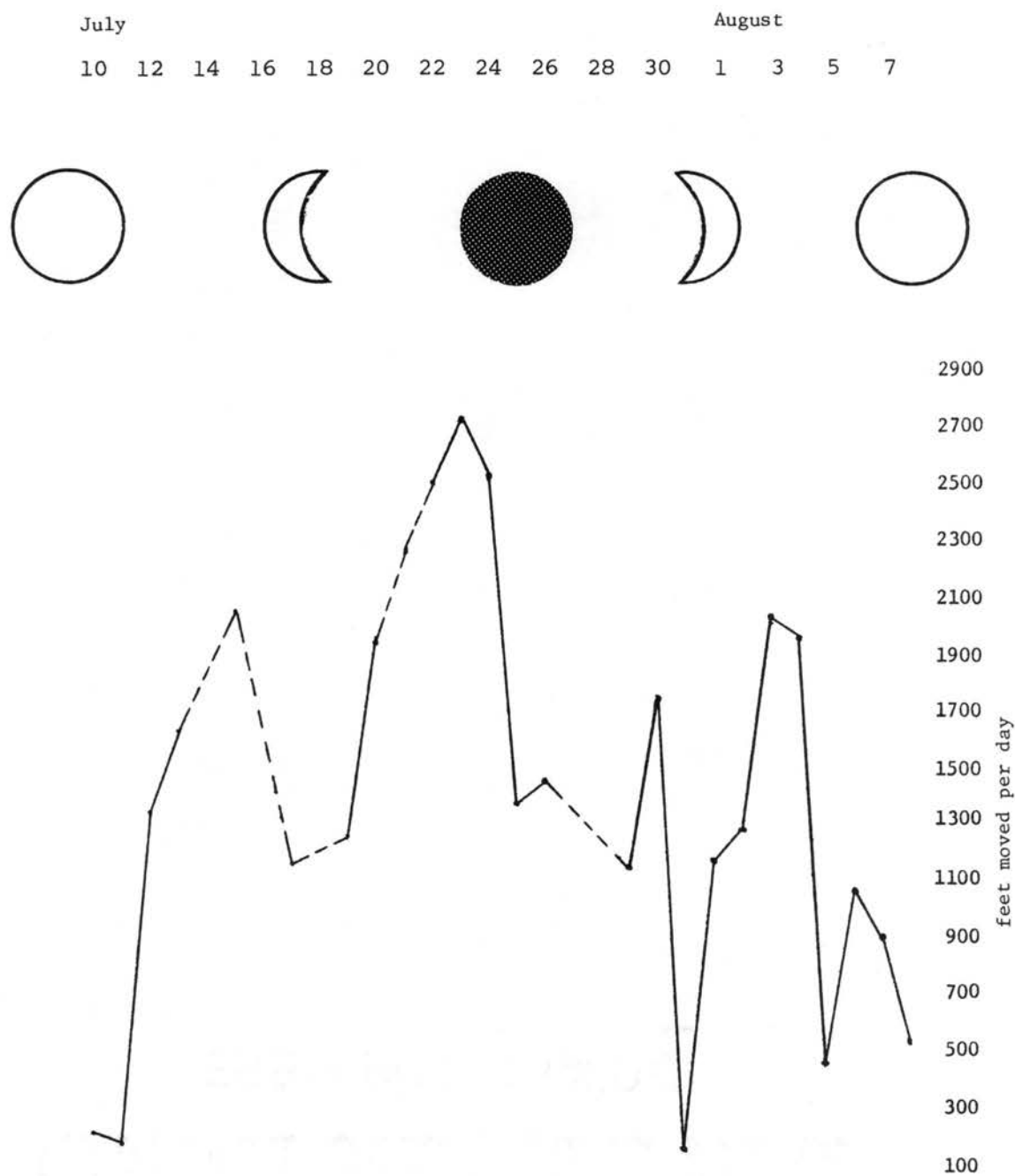


Figure 47. Amount of activity of mouse 54 (Male) in feet moved per day during the synodical month under natural environmental conditions.

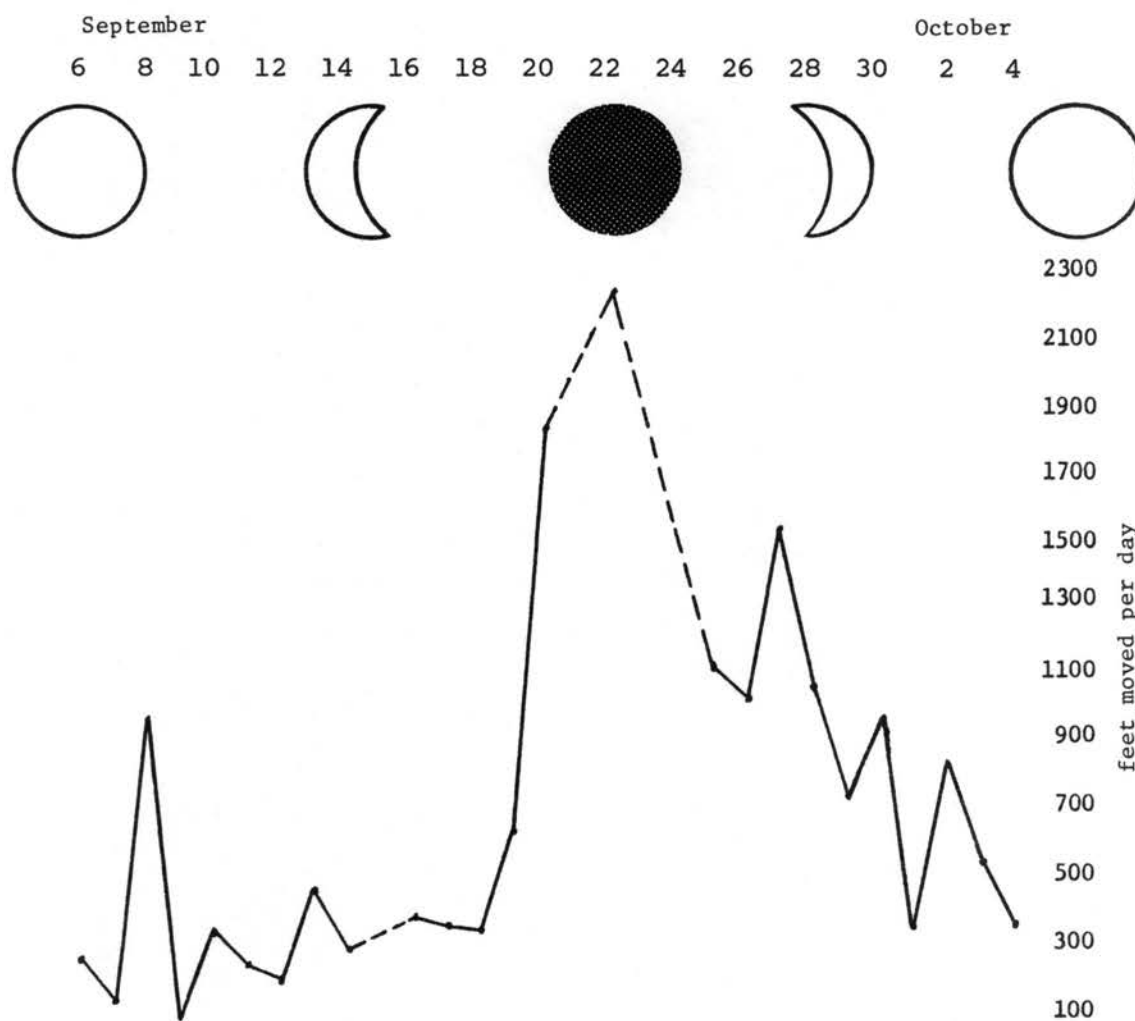


Figure 48. Amount of activity of mouse 55 (Female) in feet moved per day during the synodical month under natural environmental conditions.

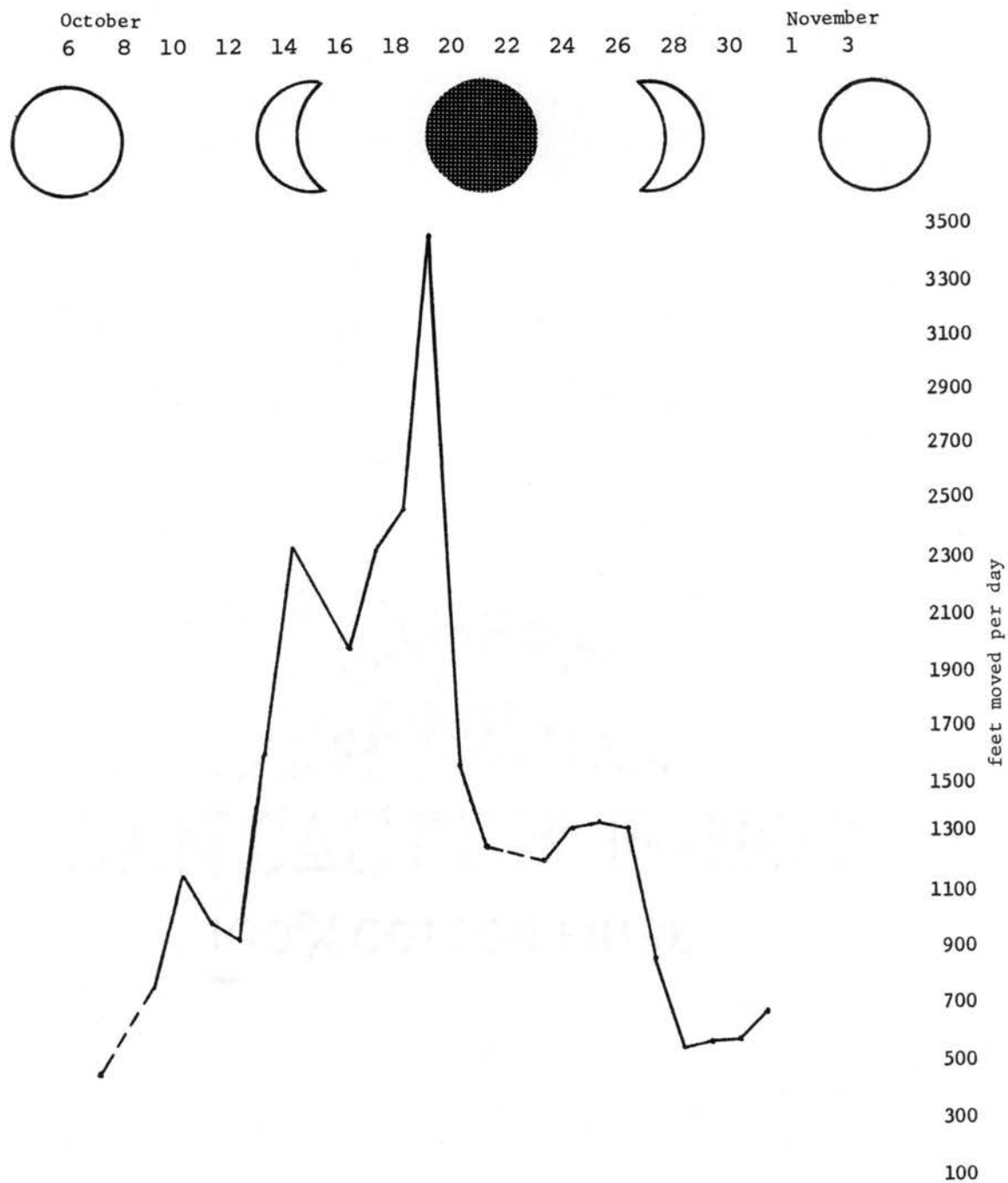


Figure 49. Amount of activity of mouse 56 (Male) in feet moved per day during the synodical month under natural environmental conditions.

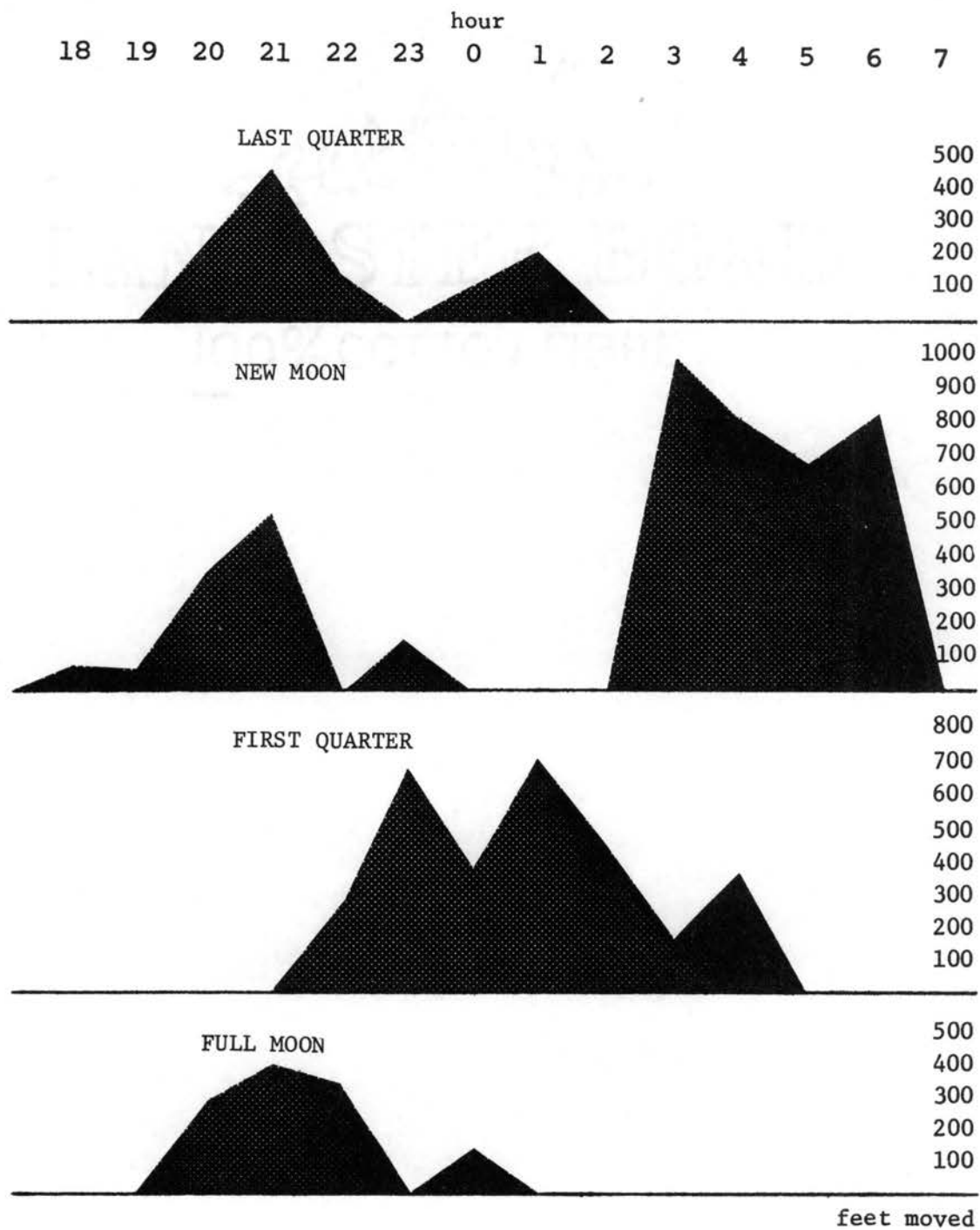


Figure 50. Activity for Mouse 53 in feet moved per hour during the four phases of the moon.

VITA }

John Curtis Jahoda

Candidate for the Degree of

Doctor of Philosophy

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