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DAILY ACTIVITY PATTERNS IN THE MEADOW VOLE,
Microtus pennsylvanicus

by

William Joseph Graham

A dissertation submitted in partial fulfillment
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Doctoral Committee:

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A B S T R A C T

DAILY ACTIVITY PATTERNS IN THE MEADOW VOLE, MICROTUS PENNSYLVANICUS

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A study was made 1) to define and compare the daily activity patterns of meadow voles under field and laboratory conditions, 2) to determine the amount and extent of day-to-day regularity (synchrony) in activity of individual voles under various test conditions, 3) to determine whether seasonal changes in activity occur in the field and in the laboratory, 4) to determine the relative importance of light and temperature as influences on daily activity, and 5) to ascertain the correlations between vole activity and environmental factors in the field.

To achieve these objectives, the activity of single radioactively-tagged voles was measured for 5-day test periods in 30 ft. diameter field enclosures, and untagged voles were recorded in small activity cages in the field and in similar cages under controlled conditions in the laboratory. The indices of vole activity, which were evaluated for the calendar year 1966, were (a) the percent of time active, i.e. the percentage of recorded 6-minute time units that were classed as active, (b) nocturnal and diurnal activity, i.e. the percentage of the daytime or of the nighttime that consisted of activity periods, (c) the ratio of the number of voles which were primarily nocturnal to the number which were chiefly diurnal, and (d) the proportion of voles which exhibited synchrony in their daily activity patterns over the test period.

1) The activity records obtained in this study support the concept of a physiologically based activity unit consisting of an activity burst

of 1 - 3 hours followed by a 1 - 3 hour period of inactivity. Such a unit characterized the pattern of activity in field enclosures as well as in field and laboratory cages. Voles in enclosures had a significantly diurnal emphasis of activity while those in cages in the field were crepuscular and those in the laboratory were more nocturnal than diurnal. These differences may reflect differences in the amount of cover present in activity cages and field enclosures, differences in the methods of recording activity, and/or differences in the nutritional quality of natural and supplied foods. Voles in field enclosures were significantly more active than were voles in activity cages in either the field or the laboratory. In all test conditions, females were found to be active for a greater part of the test period than were the males.

2) In none of the test situations did all of the voles have significantly synchronous activity; the highest percentage of synchronous individuals (52%) was found in enclosure voles. The percentages of synchronous voles in the field and in the comparable condition in the laboratory (seasonal photoperiod - seasonal temperature) were similar; synchrony decreased as light and/or temperature were held constant.

3) In the field, in both enclosures and activity cages, the percent of time active was greater in the summer than in the other seasons; no seasonal effects in activity were observed in voles recorded in the laboratory.

4) In the laboratory experiments in which light and/or temperature were held constant, light had a greater influence than temperature on the activity pattern of these voles.

5) Vole activity recorded in the field was tested for correlation activity with temperature, humidity, change in temperature, change in humidity, time of day (daytime or nighttime), light intensity, twilight and

rainfall. In field enclosures, the strongest correlation with activity was with time of day; i.e. test voles were clearly more active during the day than at night. The activity of field-caged voles was strongly and positively influenced by twilight. Rainfall apparently had a stronger negative effect on the activity of voles in activity cages than on voles in field enclosures.

The environmental factors measured in the field did not account for more than 30% of the daily activity of these voles. It is likely that the physiologically based activity unit referred to above interfered with the attempt to relate activity to meteorological conditions.

ACKNOWLEDGMENTS

The author is indebted to Dr. Francis C. Evans, who supervised this study and generously contributed much time and effort on details of the project. The other members of my doctoral committee, Drs. William H. Burt, Claude W. Hibbard, and Donald J. Portman, also gave needed assistance in the study and criticism of the manuscript. Dr. Frederick E. Smith helped in designing the statistical test for synchrony. Permission for the use of the study site at the University of Michigan Botanical Gardens was given by Drs. A. G. Norman and W. H. Wagner. The controlled environment chamber in the University of Michigan Museum of Zoology was made available by Dr. Harrison Tordoff.

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INTRODUCTION

Most mammals are strongly nocturnal or diurnal (Park 1940).

These animals have become well adapted to the biological and meteorological features of the habitats in which they are active. A few other mammals are active during both day and night. The latter may have adapted to all of the predators, competitors, and physical factors which nocturnal and diurnal species would encounter, or they may live in a habitat which is rather protected and constant throughout the 24 hours. The latter possibility seems more likely, and it is interesting that the small mammals which live well protected in grass and litter include the groups which are active during both the day and the night. Among these are the shrews (Hamilton, 1940; Osterberg, 1962; and Rood, 1965), and several genera of voles: Clethrionomys, Pitymys, and Microtus.

The activity of these small mammals consists of bursts of activity which alternate with periods of rest (Davis, 1933; Crowcroft, 1954; and Kikkawa, 1964). Although these mammals are active any time of the day, they are often more active in one part of the day than in another. The Scilly shrew (Crocidura suaveolens) is more diurnal than nocturnal in the field (Rood, 1965). Voles of the genus Clethrionomys are generally more nocturnal than diurnal (Kikkawa, 1964; Buchalczyk, 1964) although Brown (1956) described Clethrionomys glareolus as being diurnal when in competition with Apodemus sylvaticus. Pitymys has been considered more nocturnal than diurnal by Smirnov (1962, from Gebczynski, 1964) and as diurnal as it is nocturnal by Langenstein-Issel (1950). There have been conflicting reports about the time of day at which Microtus is most active in the field. In particular, Microtus pennsylvanicus has been described

as (1) mainly nocturnal by Kennicott (1856), Lyon (1936), and Osterberg (1962), (2) mainly diurnal by Jackson (1908) and Emlen et al. (1957), and (3) active during both day and night but with peaks of activity at dawn and dusk (Bailey, 1926; Johnson, 1930; Goodman, 1935; and Hamilton, 1937). Certainly, additional data on Microtus activity in the field are necessary.

Laboratory studies have usually corroborated the field studies. Crowcroft (1954) observed a water shrew (Neomys fodiens) to be active throughout the day without any real peaks in activity; he also (op. cit.) recorded a small peak of activity during the day in a pygmy shrew (Sorex minutus), and found that the patterns of nine Sorex araneus formed a large peak at night and a smaller one twelve hours later during the day. Pearson (1962) and Miller (1955) demonstrated a stronger nocturnal pattern of activity in laboratory studies of Clethrionomys. Gebczynski (1964) classified Pitymys subterraneus, a woodland vole, as nocturnal. Microtus in the laboratory has generally been considered to be more nocturnal than diurnal (Davis, 1933; Calhoun, 1945; and Wiegert, 1961).

Erkinaro (1961) showed seasonal changes in activity of a female Microtus agrestis exposed to natural changes in light. It was largely nocturnal in the summertime and more diurnal than nocturnal in the winter. Similarly, Pearson (1947) recorded more nocturnal activity of two Microtus pennsylvanicus tested in the summer and more diurnal activity in another individual studied in the winter. These results support the suggestion of Getz (1961) and of Wiegert (1961) that the activity patterns of Microtus may be altered by extremes in temperature; they indicate that the meadow vole would be a good experimental animal in which to study the effects of meteorological conditions on mammalian activity.

The conflicting field data on Microtus activity and the indications that meadow voles are active at night in the laboratory suggest that the activity patterns of voles of the genus Microtus are labile. Their activity may vary from one environment to another and from season to season.

This paper reports on a study designed to test Microtus pennsylvanicus in order 1) to define and compare the daily activity patterns of meadow voles under field and laboratory conditions, 2) to determine the amount and extent of day-to-day regularity (synchrony) in activity of individual voles under various test conditions, 3) to determine whether seasonal changes in activity occur in the field and in the laboratory, 4) to determine the relative importance of light and temperature as influences on daily activity, and 5) to ascertain the correlations between vole activity and environmental factors in the field.

METHODS AND MATERIALS

FIELD SITE

This study has considered the effects of several environmental factors on the activity patterns of the meadow vole, Microtus pennsylvanicus, in the field and in the laboratory. The field study site was a level 3.5 acre tract on the Fleming Creek floodplain in the University of Michigan Botanical Gardens. Kentucky bluegrass (Poa pratensis) dominated the vegetation; the major forbs and woody plants included milkweed (Asclepias syriaca), butter-and-eggs (Linaria vulgaris), stinging nettle (Urtica sp.), goldenrod (Solidago spp.), and red-berried elder (Sambucus pubens). A herbicide (2-4-D) was applied twice in the summer of 1963 to the whole tract and once in the summer of 1966 to the activity enclosures to maintain a more uniform bluegrass cover.

The field studies were conducted during the calendar year of 1966. Population levels of Microtus pennsylvanicus in southeastern Michigan and in the study site were low in the summer of 1963, gradually increasing to a high in 1966. A population low occurred in the summer of 1967.

The laboratory studies were performed in the University of Michigan Museum of Zoology.

Study of the daily activity patterns of the meadow vole is hindered by this species' habit of moving about under cover. Activity data collected for animals housed in cages must always be considered with the qualification that the cage may have had some effect on the observed activity pattern. Undoubtedly, small mammals kept in laboratory cages have their activity restricted by the small size of the cage. Brant and Kavanau (1965) constructed a multi-dimensional laboratory

complex with many complicated mazes, each of which was easily explored by a test Peromyscus. One objective of the present study was to compare the effects of different holding cages and environments on the daily activity patterns of Microtus pennsylvanicus. Daily activity was recorded under three different experimental conditions, which were (1) in large field enclosures in which individuals trapped from the study site were radioactively tagged and released into one of two enclosures where their positions could be determined regularly, (2) in small activity cages maintained in the field near the enclosures and recorded during the same test period used for the voles in activity enclosures, and (3) in small activity cages kept in the laboratory under one of several controlled regimes. Following the field test period, voles in field activity cages were taken to the laboratory, acclimated to a particular laboratory regime, and tested further for the activity patterns. No vole was used in a laboratory or a field test more than once.

Another objective of this study was to determine whether a direct correlation could be detected between vole activity and any of the principal meteorological factors operating in the course of the investigation. The factors which were taken into consideration in this connection were (1) temperature, (2) humidity, (3) light intensity, (4) duration of photoperiod, (5) amount of precipitation, and (6) time of rainfall.

1. Temperature was recorded in degrees Fahrenheit on a Bristol Thermo-humidigraph (Model 4069 H) housed in a covered and side-louvered box set in the grass in the study field so that the instrument would be at ground level (Figure 1). Spot-checks of the air temperature in nearby vole runways demonstrated that this was within 2°C. of the temperature

recorded in the instrument shelter and the temperatures in the grass changed in the same manner as it did in the shelter.

2. Humidity was recorded as percent relative humidity on the same Bristol instrument used for the measurement of temperature. The humidity profile in the runways changed in the same manner as it did in the temperature-humidity recording shelter.

3. Light intensity was recorded in gram calories per square centimeter per minute by a Belfort Recording Pyrheliometer (Science Associates Model 653) placed on a stand between two activity enclosures (Figure 2).

4. Duration of photoperiod was calculated from the designations of sunrise and sunset as published by the U.S. Weather Bureau for the Ann Arbor area.

5. Amount of daily precipitation was recorded in inches by a rain gauge (Science Associates Model 508) mounted next to the recording pyrheliometer.

6. Time of rainfall was ascertained by a rainfall detector (Figure 3) which was stationed near the activity cage shelter. Essentially, the detector consisted of two funnels, one over the other, and two copper electrodes. The lower funnel contained a piece of livestock (saltlick) salt set on a thick, plastic-covered mesh. The mesh allowed air circulation around the salt and reduced the amount of moisture dripping from it owing to the hygroscopic nature of salt. Two 12-gauge, solid copper wires were placed under the spout of the lower funnel and connected to one channel of the event recorder. Falling rain was directed through the upper funnel to fall on the salt. Drips from the salt then passed across the two wires and completed the circuit on the recorder channel for

Figure 1. A Bristol Thermo-humidigraph, housed at ground level, provided measurements of temperature and humidity in the field. A hinged lid with a white upper surface covered the recorder when it was in operation.

Figure 2. The pyrlieliometer and rain gauge were located on a stand between two activity enclosures.

Figure 3. The rainfall detector consisted of two funnels, with salt supported in the mouth of the lower one. The two wires were connected to the event recorder used to record vole activity in cages in the field.

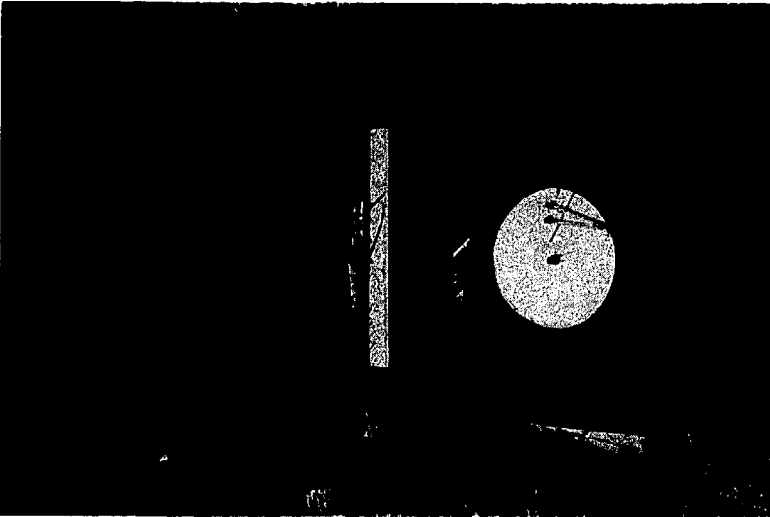


Figure 1.

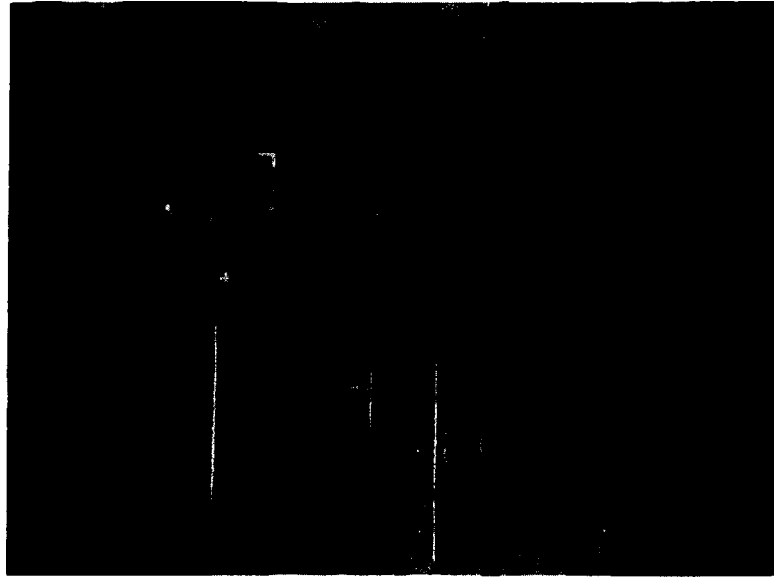


Figure 2.

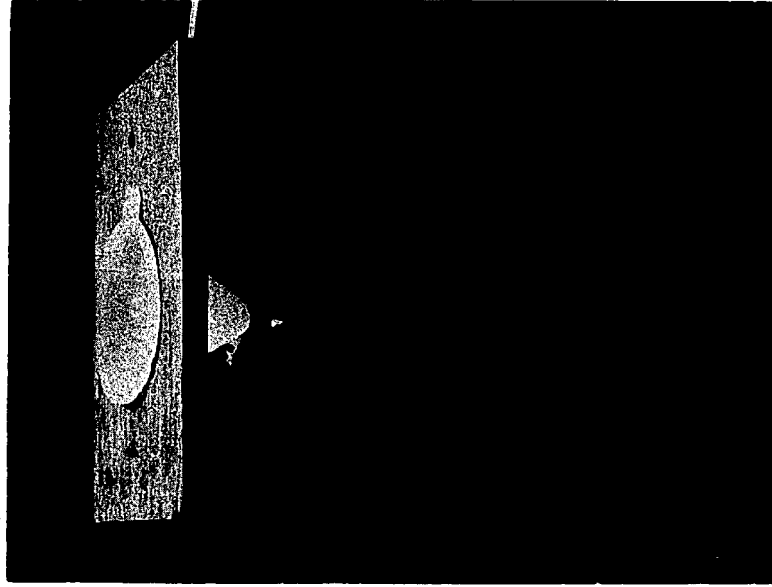


Figure 3.

detection of rainfall. This device gave a qualitative measure of the intensity of the rainfall and also indicated the time at which rain occurred.

The field studies included observations of vole activity in winter, spring, summer, and autumn. These four seasons were arbitrarily limited to the following periods: Winter - December through February; Spring - March through May; Summer - June through August; and Autumn - September through November.

Study of the possible effects of climatic factors on vole activity was extended to the laboratory, where light intensity, duration of photoperiod, and temperature could be controlled within an experimental chamber. The experimental design provided for testing the laboratory voles under three climatic regimes per season; these were: (i) with daily changes in light and temperature to approximate natural conditions (ii) with daily changes in light but with temperature held constant and (iii) with constant light but with daily changes in temperature.

The specific photoperiod and temperature conditions employed for the laboratory experiments were:

	Photoperiod	Temperature
Winter	1. 10L:14D	-4° to +5° C.
	2. 10L:14D	Constant (0° C.)
	3. Constant (2 - 8 foot candles)	Constant (0° C.) - owing to temp. control failure
Spring	1. 12L:12D	5° to 14° C.
	2. 12L:12D	Constant (9° C.)
Summer	1. 14L:10D	15° to 24° C.
	2. 14L:10D	Constant (19° C.)
	3. Constant	15° to 24° C.
Autumn	1. 12L:12D	5° to 14° C.
	2. 12L:12D	Constant (9° C.)
	3. Constant	5° to 14° C.

Light was from two 60-watt incandescent bulbs located near the ceiling of the chamber. These produced a standard light intensity of 2 - 8 foot candles for these experiments, although a gradual diminution and increase of light was provided to simulate conditions of dusk and dawn, respectively. These changes in intensity were achieved by a motor-driven dimmer switch which was automatically turned on and off by a timer, producing 45 minute "twilight" periods at the two ends of the light period. A similar motor-driven device could be used to change the temperature 9° C. each day automatically, with six hours required to change the temperature from one level to another. The temperature regime for a 12L:12D (12 hours of light: 12 hours of dark) test period is diagrammed in Figure 12.

ACTIVITY ENCLOSURE CONSTRUCTION

To learn something of the activity patterns of meadow voles in simulated natural habitat, an elaborate tracking device was constructed in each of several 30 ft.-diameter circular enclosures on the study site (Figure 4). The enclosures had sides of 3' wide galvanized sheet metal sunk 18" into the ground. In the center of each enclosure a 1' x 1' x 2' base constructed of 3/4" plywood supported a rotating platform. Both a Nuclear-Chicago Linear/log rate meter (Model 8731), protected by an insulated plywood box, and a 15 ft. aluminum boom were mounted on this circular platform (Figure 5). As it rotated, the scintillation probe at the outer end of the boom described a circle midway between the edge and the center of the enclosure and 2 feet above the ground. The probe consisted of a 1" x 1" Harshaw thallium-activated NaI crystal (4Pa-4), coupled optically to an RCA 6199 photomultiplier tube

Figure 4. The activity enclosures were placed in a bluegrass field in the University of Michigan Botanical Gardens. The upper box and the boom rotated at a speed of one revolution every 6 minutes. The scintillation probe was installed in the white cylinder on one end of the boom.

Figure 5. The retometer was protected by the insulated upper box (top removed for photo). The thermostat controlled both the heat source (75-watt light bulb) and an exhaust fan mounted behind the retometer. The stationary boom base contained the motor which turned the upper part, the 'commutator' which transmitted power to, and carried signals from the upper rotating section, and a cam-operated microswitch which produced a reference mark each time the probe pointed north.



Figure 4.

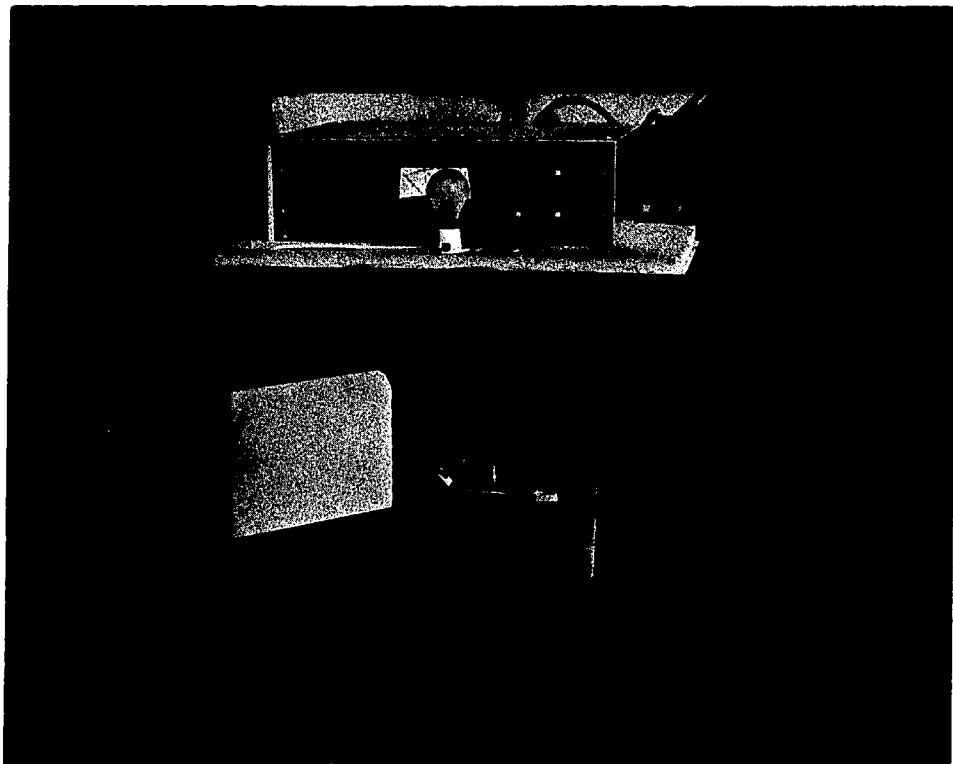


Figure 5.

and sealed in an 8" x 2 1/4" diameter aluminum tube. The platform was rotated by a 3 RPM synchronous motor (Bodine B-2270-600G) through a set of Boston spur gears giving a reduction of 18:1. Thus the boom made one revolution each 6 minutes.

The 60 lb. weight of the platform, boom, ratemeter, and box rested on a Timken roller bearing (3 1/4" diam.). A 3/4" OD pipe attached to the platform passed down through the center of the bearing and carried 4 wires from the ratemeter to the upper half of the "commutator" in the center of the boom base. This device consisted of two 4" x 1/2" plastic discs, the upper one having been attached to the bottom of the pipe and contained 4 heavy plug tips which projected below the disc. Each projecting tip lay in a circular 3/16" x 1/4" mercury-filled groove in the stationary lower disc and thus rotated in its own canal of mercury. In this way, 120 v. 60 cycle power was supplied to the ratemeter and the output signal was carried back to the non-rotating base. This signal activated a 0-100 microampere galvanometer, shunted to reduce its sensitivity, in a Rustrak recorder (Model 146) located outside the enclosure. A cam on the upper rotating disc activated an event recorder in the Rustrak recorder, producing a reference mark each time the boom passed north.

Since the ratemeter was sensitive to both high and low temperatures, a 75-watt bulb in series with the lower stage of a Penn 6219T2X thermostat was installed in the ratemeter box to maintain an ambient temperature of approximately 28° C. Cooling in the summer was accomplished by a small, shuttered Rotron exhaust fan in series with the upper stage of the thermostat. A description of this tracking device and of the enclosures has already been published (Graham and Ambrose, 1967).

Difficulty in preventing voles from burrowing out of one of the three activity enclosures forced its abandonment and the automatic detector was moved to another enclosure; two enclosures were in operation during most of 1966.

ACTIVITY CAGE CONSTRUCTION

Activity cages were constructed by dividing small, 10" x 15" x 7" laboratory cages (Dice, 1929) into nesting and feeding compartments by a 6" x 10" x 1/4" tempered hardboard partition (Figure 6). A 6" x 3 1/2" x 1 5/8" tunnel with sheet metal sides and bottom and a 1/4" mesh hardware-cloth cover joined the two compartments. To get through the tunnel, a vole had to cross a 6" x 1 3/8" hardware-cloth treadle, pivoted at its center. The pivot was a 2" x 1/8" brass rod, soldered across the treadle, with a mercury switch on one end. A spring-steel arm rested against a cam on the pivot rod and held the treadle in one position until the vole moved back across the treadle. When a vole moved from the nesting compartment into the feeding and drinking compartment, the mercury switch closed an electrical circuit connected to one channel of a 20-pen Esterline-Angus event recorder. Movement into the nesting compartment opened the circuit. These data were all recorded at a chart speed of 1 1/2" per hour.

The nest consisted of a one-quart aluminum sauce pan with the handle removed, a mouse-sized notch cut from its edge, filled with Dacron fluff for nesting material and inverted in the rear compartment of the cage. An aluminum trough at the front of the cage was filled with rolled oats for food. Water, with an aqueous vitamin solution added, was available from an inverted 16-ounce water bottle suspended from the front of the cage. During the winter season, in both field and laboratory, the water bottles

were wrapped with waterpipe heating wires to keep the bottles from bursting. During long periods of freezing temperatures in the field, snowballs were added to the cages to provide water when the water spouts on the water bottles froze.

PROCEDURES

ENCLOSURES

Individual voles were trapped from the study site and taken to the laboratory where they were weighed, marked by toe clipping and released into one of the enclosures within 3 days of capture. $^{182}\text{Tantalum}$ was used to tag the voles because (a) most of its emission is high energy gamma radiation with only small amounts of beta radiation, (b) its half-life of 115-120 days makes it ideal for a 3-week study, and (c) it is considered to be biologically inert. A 50-75 microcurie source (1/2" of 18-gauge $^{182}\text{Tantalum}$ wire) was injected subcutaneously into an anesthetized vole. The amount of radiation from the animal (in a wooden trap) was then recorded at the edge of the enclosure, under the probe, and near the boom base for several revolutions, to determine the radiation intensities at known distances in the enclosure. The vole was then released near the boom base to begin the period of acclimation. Records of the vole's position in the enclosure were made during a 5-day test period; the vole was then removed from the enclosure and replaced by another individual. The enclosure was not entered during the recording periods except for occasional, brief maintenance. Nearly all individuals gained weight during the tests and there was no evidence of gross radiation damage to the test animals. Voles which died while tagged or during removal of the radioisotope had only a slight redness in the tissues around the radioactive wire; this might have been caused by local irritation from the wire.

CAGES

Additional mice were trapped in the study field and in other nearby places, brought to the lab, weighed, marked, and taken to the

field for acclimation. These voles were placed, one to an activity cage, near the activity enclosures and their activity was recorded during the same 5-day test period used for the mice in the activity enclosures. The cages were set near ground level under a corrugated, white fiberglass roof, placed about 18 inches above the cages. This shelter generally protected the cages from precipitation and exposed the voles to natural changes in temperature, humidity and light intensity (Figure 7). An electric fence was constructed around the shelter following raids on the cages by a local opossum. Test animals were kept in laboratory cages for 7-14 days for acclimation before being transferred to activity cages for testing. Following the test, these animals were taken to the laboratory for use in one of the seasonal light-temperature experiments.

Voies tested in the laboratory were placed in regular laboratory cages (one to a cage) in a well-insulated 4' x 8' x 6 1/2' Hot Pak environmental chamber (Figure 8) for a period of 7-14 days for acclimation. They were then transferred to activity cages, at least a week before testing. While photoperiod and temperature were programmed for daily variations or constant conditions, humidity was not controlled but was recorded. Humidity varied by no more than 5% relative humidity in each test period. Depending on the temperature conditions, a powerful fan in the test chamber produced either constant or intermittent "white noise." The chamber was entered no more than twice during the test period.

Voies used in all tests were post-juvenals or adults. Four voies used in laboratory experiments were offspring born to females in cages in the field. They were maintained in cages until they were placed in the laboratory for acclimation and testing.

Figure 6. The activity cages were constructed by partitioning a Dice laboratory cage into a nest compartment (left) and a feeding compartment (right). The treadle passed through the partition and the mercury switch was protected by the compartment between the treadle and the edge of the cage.

Figure 7. Voles which were recorded in activity cages in the field were placed in the lower level of the activity shelter where they were exposed to daily changes in temperature, humidity and light intensity. Acclimating voles were maintained in laboratory cages on the upper level.

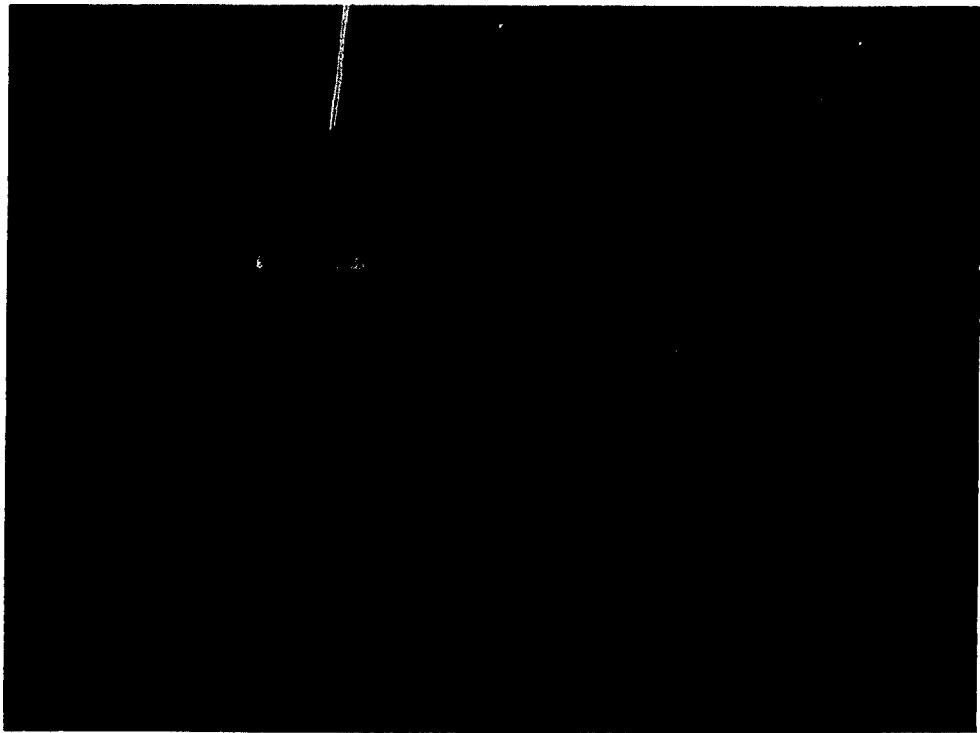


Figure 6.

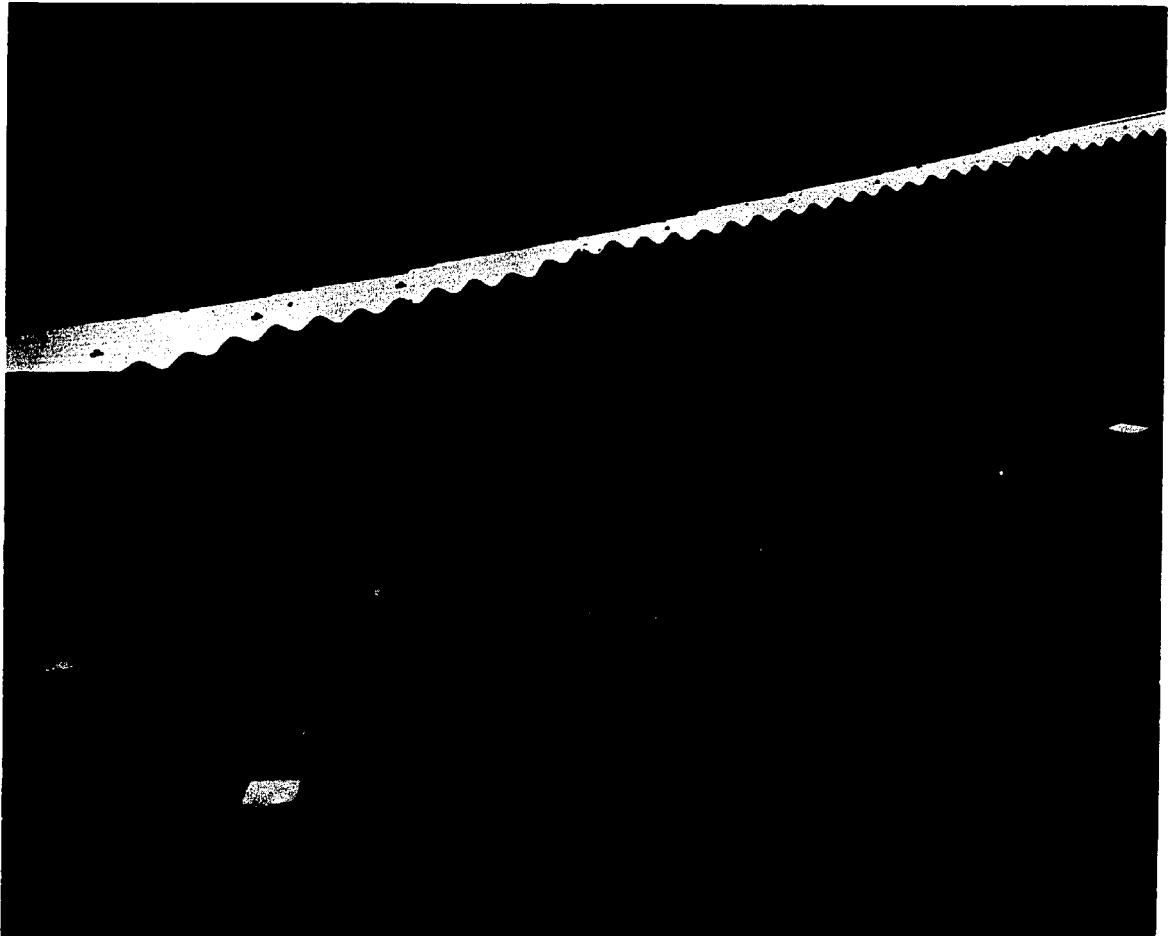


Figure 7.

Figure 8. In the laboratory, voles in activity cages were placed in a Hot Pak environmental chamber. Twilight conditions were simulated by a timer and a motor-powered rheostat constructed in the box on the right.

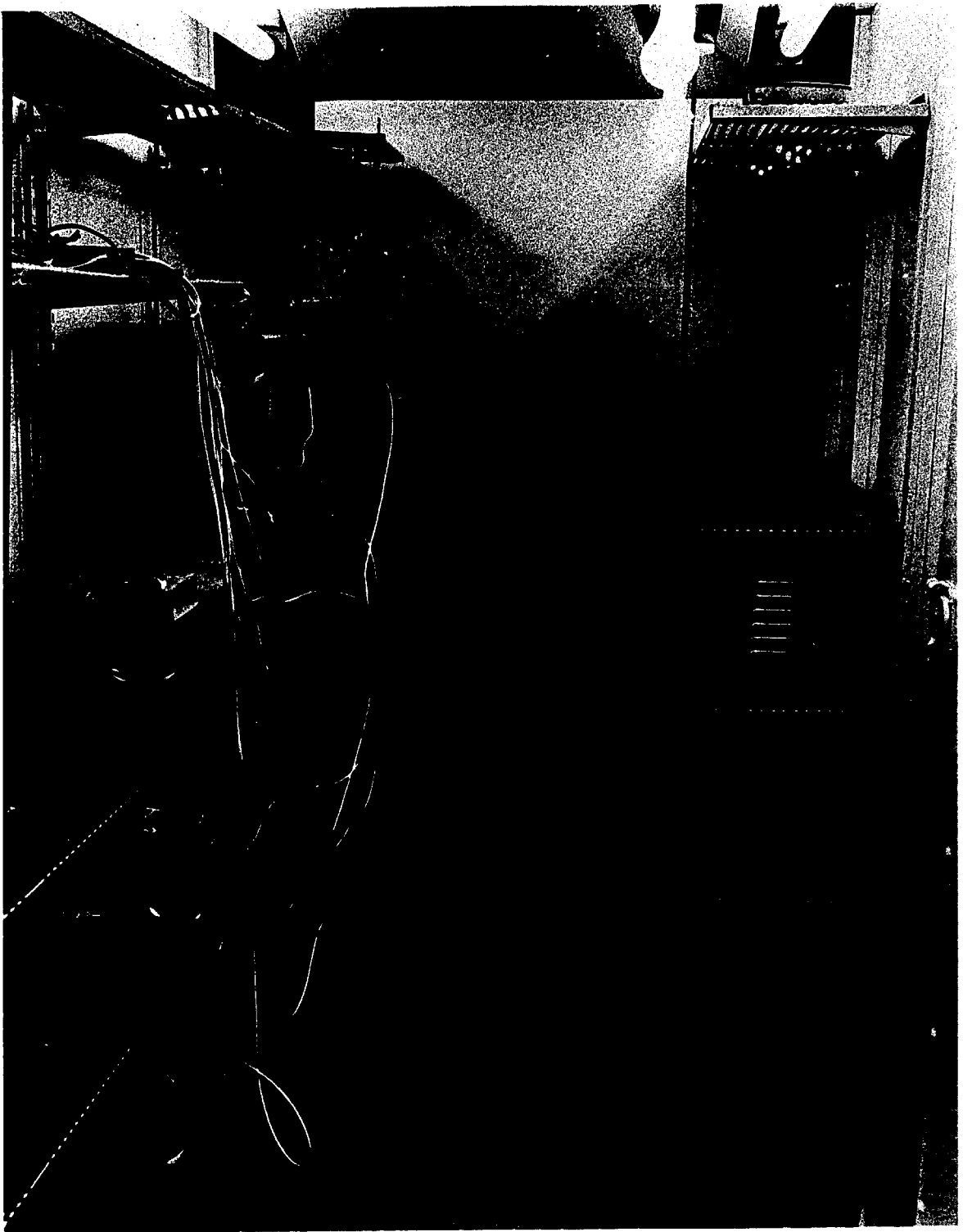


Figure 8.

The order of the laboratory tests is listed on page 9. There were only two test periods in which light was held constant and the temperature changed; constant light and Summer temperature and constant light and Autumn temperature. There was also one period in the winter test group in which both light and temperature remained constant, but this was not a part of the experimental design; it resulted from a failure of the automatic temperature control.

ENCLOSURE RECORD READING

The position of a radioactive vole in the enclosure could be determined from the chart record. The chart paper would appear as in A of Figure 9, if a vole were resting at the south edge of the enclosure, indicated by X. The peak on the chart is exactly midway between the marks which indicate when the boom was pointing due north, showing that the vole was on the 180° radius of the enclosure. The intensity of the radiation from the isotope decreases as the square of its distance from the probe. Since the retometer was operated on the log scale setting, the signal at the recorder changed linearly and proportionally with the distance.

If the vole remained in that spot, the next revolution of the boom would produce a record exactly like the previous one, as in B. If the vole should then move to point Y and remain there during the next revolution of the boom, the chart record would look like C. Likewise, if it then moved to point Z, the next record would look like D. Although points X and Z are almost the same distance from the probe, they can be distinguished on the record by the height of the trough between the peaks. The differences in trough height are due to the differences in radiation intensity detected by the probe when it was on the opposite side of the

enclosure from the vole. Movement of the animal as the boom passed over it resulted in a skewed peak, which did not allow the vole to be located precisely. Despite this, activity of the vole was rather easily determined from the chart record.

ENCLOSURE RECORD ANALYSIS

A test vole in an enclosure was considered inactive if it remained in one spot for 30 minutes or longer; all other periods were considered to be active. Each 6-minute test interval was classified as active or inactive. The active periods for each test day were plotted on 36" long charts for visual comparison and for analysis of day-to-day synchrony.

ACTIVITY CAGE RECORD ANALYSIS

Activity was recorded on chart paper moving at a speed of 1 1/2" per hour. For purposes of chart analysis, a 6" x 14" x 1/4" plexiglass plate was machined with parallel grooves which divided each 1 1/2" portion of the length of the plate into 10 parts. Thus, each part represented a 6-minute interval. The plexiglass plate was placed over each chart record to determine the intervals in which activity occurred during the test period. As in the analysis of enclosure activity, a vole was classified as active or inactive for each 6-minute interval of the test period. The activity cage only detected movements across the treadle and did not reveal activity in the nest compartment. Inactive periods of 20 minutes or less were assumed to be too short for sleeping and were considered as active. Throughout this analysis, the intensity of activity, or the number of movements per time interval, was not considered. This study deals only with timing of activity; that is, with the distribution

Figure 9. The position of a detector and the direction of rotation of the boom in an enclosure is illustrated in the diagram on the left. See text for explanation of the chart record.

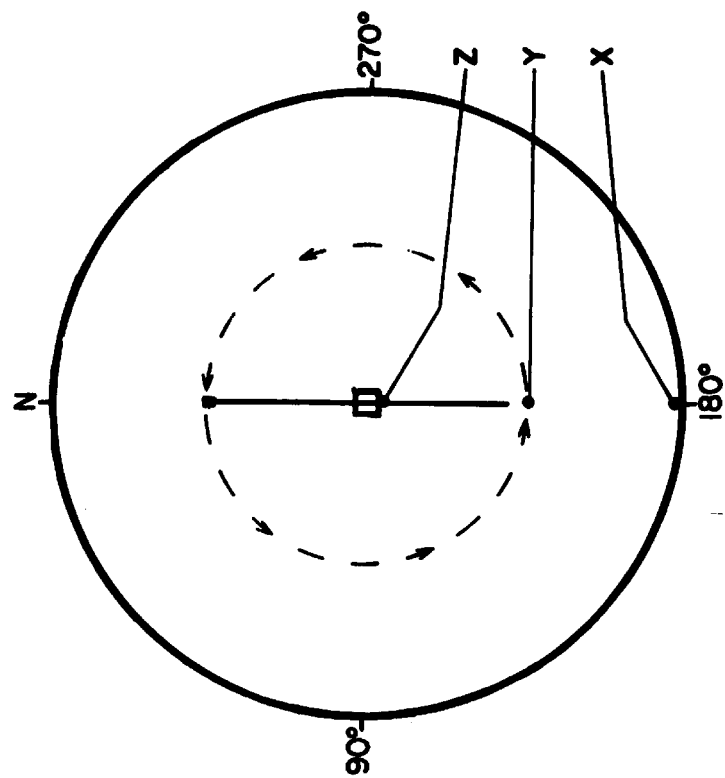
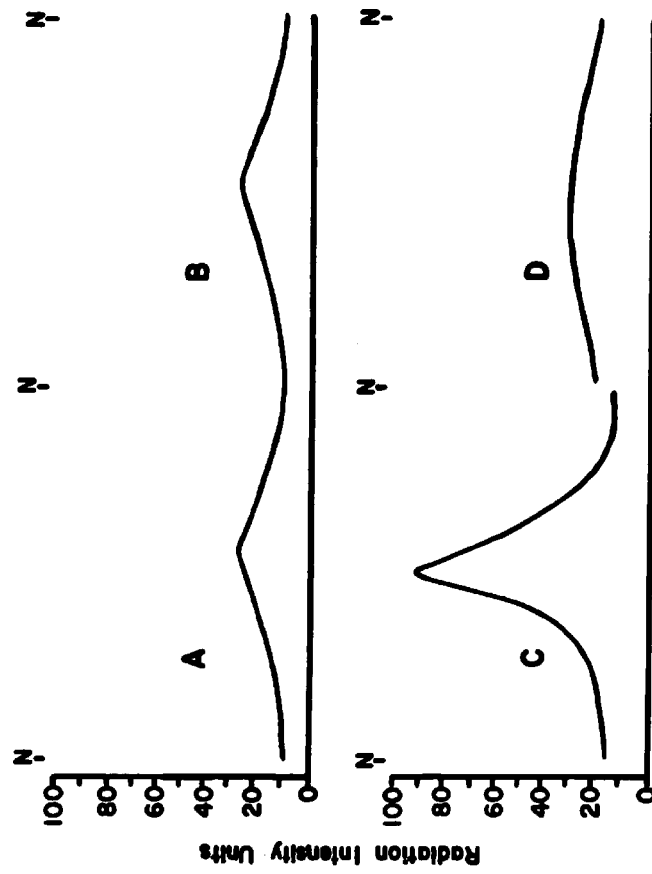


Figure 9.



of the periods of activity during test periods.

ENVIRONMENTAL FACTOR ANALYSIS

Eight environmental variables were tested for correlation with activity in the field study. Temperature, humidity and light intensity were recorded on computer cards in the previously mentioned units of measure. A value for changes in temperature was obtained from a scale of 1 to 20, in which 10 indicated the 2° span of -1° to +1° F. change during an hour. Each other value on the scale also represented a 2° F. unit of change for one hour. Thus, a change of +4° F. would have a value of 12, a change of -10° F. would have a value of 5, etc. This value was used for the entire hour in which that change in temperature occurred. The scale for the change in humidity value was the same as that for change in temperature, with relative humidity figures substituted for temperature figures. Photoperiod (light vs. dark) was recorded as unity (1) between official sunrise and sunset and as zero (0) between sunset and sunrise. Twilight was scored by assigning unity (1) to the interval from 30 minutes before official sunrise to 18 minutes after sunrise and from 18 minutes before sunset to 30 minutes after; zero (0) was used for all other times of the day. Rainfall was indicated by a scale from 0 to 9, with 0 representing no rain and 9 indicating very heavy rain. The number on this scale is equal to the number of drops recorded by the rainfall indicator during each 6-minute interval. Cage activity values for each 6-minute period ranged from 0 to the number of cages being recorded. The value indicated the total number of individuals active during each 6-minute interval. Activity of a vole in an enclosure was unity (1) for activity and zero (0) for inactivity.

These measured environmental factors and the activity records were compiled for each 6-minute interval during a test period. These data were then punched on computer cards and a linear regression analysis was performed by the Regression Analysis Program, University of Michigan Utility Program, Computing Center, University of Michigan on an IBM 7090 computer.

SYNCHRONOUS ACTIVITY ANALYSIS

When 24-hour records of activity were lined up for successive test days, it was evident that some individuals had periods of the day in which activity bursts were likely and other periods in which they were likely to be inactive. The following test was devised to determine whether this was a significant ordering of activity.

The activity record for the test period was diagrammed so that all time periods for each day corresponded vertically (Figure 10). In this way, the 240 six-minute time intervals of the 24-hour day could be compared vertically. In a test period of 5 days, there were 6 scoring possibilities for any 6-minute interval. If the animal was not active during a particular time interval (say from 1006 to 1012) in any of the five test days, that time interval would be scored as a "0." If the vole was active during that time interval on one of the five days, it would be scored as a "1." If the vole were active during that interval on all five days, it would be scored as a "5." All 6-minute intervals from midnight to midnight were scored in this way. The distribution of the scores was then plotted. If there were perfect ordering or synchrony of the activity bursts from one day to the next, the only numbers which would be scored would be 0's and 5's. In Figure 10, the scoring of the observed distribution of activity for q400 for March 2-6, 1966, was: 0 - 63, 1 - 56,

Figure 10. (upper) Activity pattern of vole 400q during its test period.

(lower) The expected distribution of random activity during the 240 6-minute daily time units as predicted by the binomial theorem is shown on the left and the observed distribution is on the right. As activity is more synchronous from one day to the next, the observed distribution more closely approached a "U" shape.

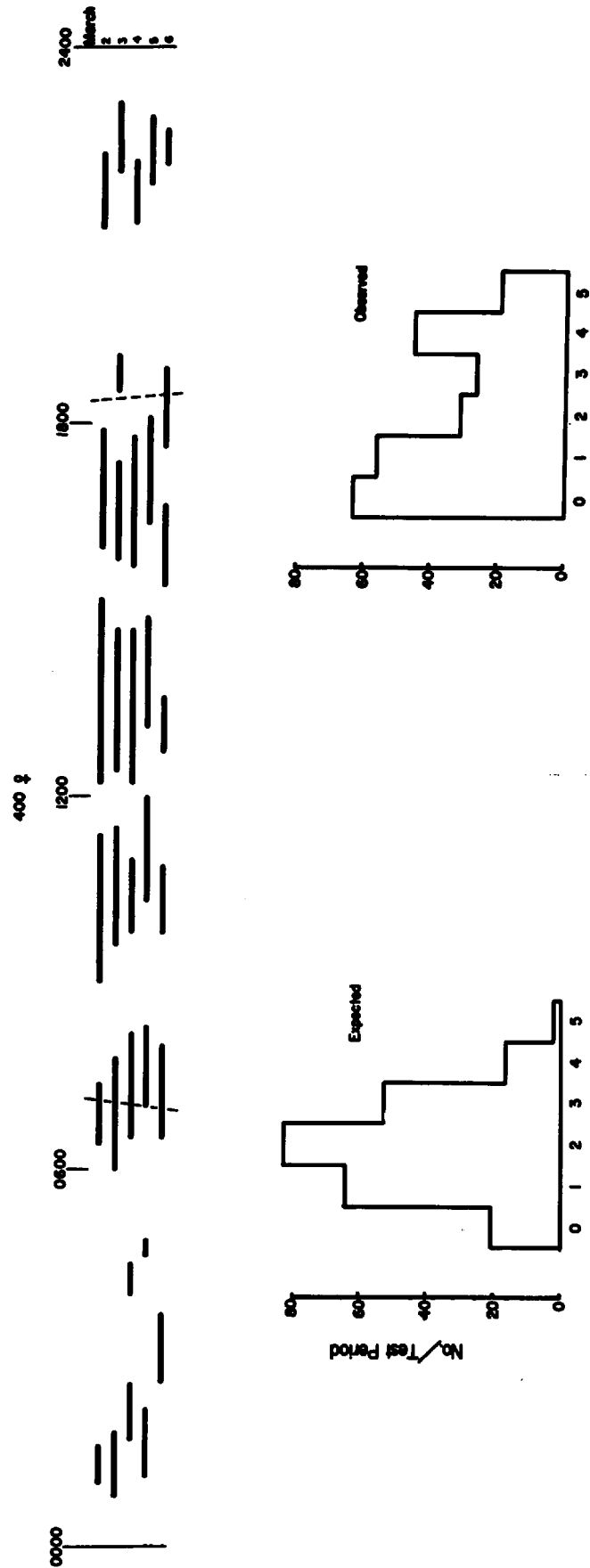


Figure 10.

2 - 31, 3 - 26, 4 - 45, and 5 - 19. The expected random distribution, as predicted by the binomial theorem on the percent of time active, is: 0 - 20, 1 - 64, 2 - 82, 3 - 52, 4 - 17, 5 - 5.

The activity records of all voles tested in enclosures and of five individuals in activity cages in each of the field and laboratory test periods were analyzed in this manner. Their distributions were compared with the expected random distributions predicted by the binomial theorem by means of the Kolmogorov-Smirnov one-sample test (Siegel, 1956) and the significance of deviations from random was determined.

Differences in group means were compared by Student's t-test (Simpson et al., 1960) and sign differences of groups were tested with the Sign Test (Siegel, 1956). The degree of difference between expected and observed nocturnal-diurnal distributions of activity in enclosures was predicted by the Fisher Exact Probability test (Siegel, 1956).

RESULTS

CHARACTERIZATION OF ACTIVITY

Characterization of the daily activity patterns of voles of the genus Microtus is complicated by two basic attributes of this group. As described by Davis (1933) locomotor activity is concentrated in 2-3 hour bursts and is intermittent throughout the day. Secondly, there is considerable individual variation in activity, which means that several voles must be tested at one time to define the pattern and the variance under existing conditions. Figures 11 and 12 illustrate both the recurrent nature of the activity bursts and the amount of variation between individuals recorded under three environmental regimes. As seen in Figure 11, voles in enclosures were generally more active and had more diurnal activity than those recorded in activity cages in the field. Voles in cages in the field responded positively to twilight, with their major bursts of activity occurring around sunrise and sunset. After these voles were acclimated to laboratory conditions (Figure 12), there was a reduction in activity following the onset of light in the morning, and the level of activity generally remained low until the light intensity was again reduced in the evening.

In Figure 12, the sequence of the individual records follows the location of the activity cages in the laboratory, with the uppermost two records belonging to voles on the top shelf and the lower two sets of records being from voles on the lowest shelf (see Figure 8 for shelf positions). Voles on the top shelves were exposed to a light intensity of approximately 8 foot candles (86 lux) during the day while those on the bottom shelf were subjected to about 2 foot candles (21 lux) in the day. While there is a suggestion of a delay in the onset of evening activity of voles held on the top shelf during this test, this was an unusual

Figure 11. Activity records for voles in field enclosures and in field activity cages. The slanted, dashed lines indicate times of official sunrise and sunset. The level of synchrony is indicated by an asterisk. One asterisk denotes synchrony at the $P < 0.05$ level and 2 asterisks indicate a $P < 0.01$ level of synchrony.

FIELD

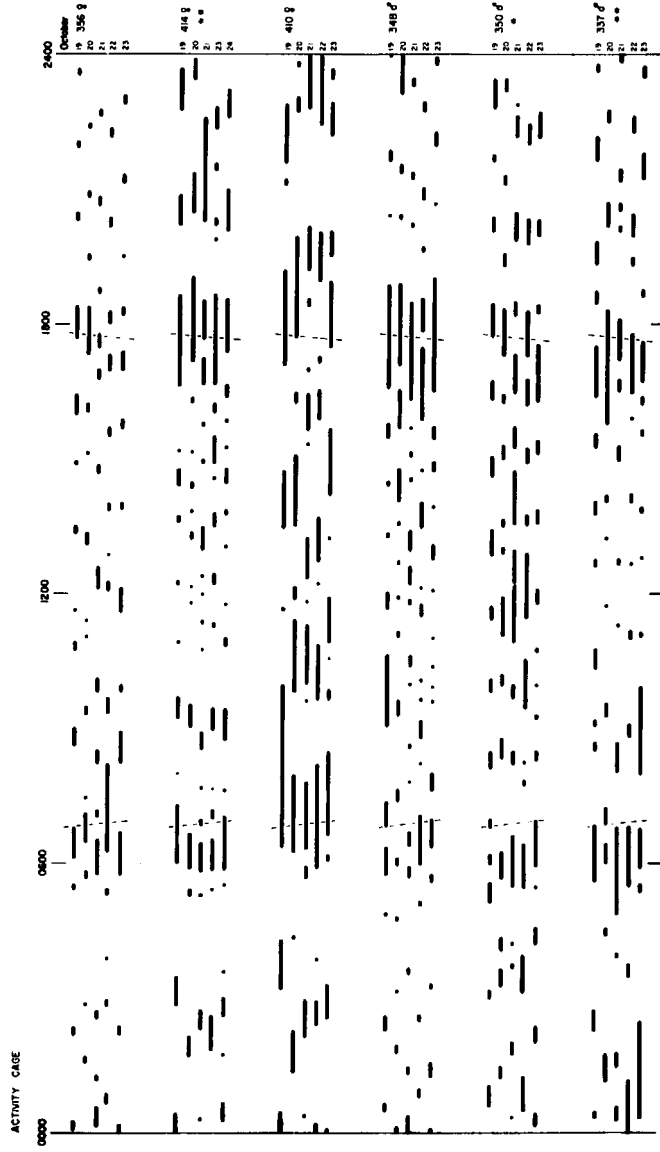
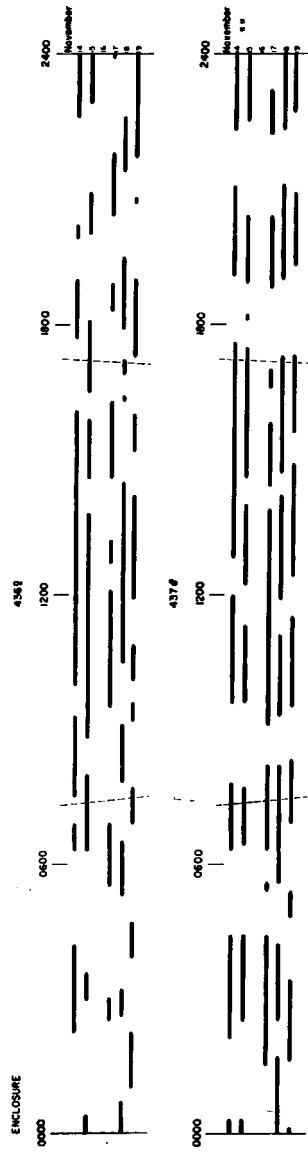


Figure 11.

Figure 12. Records of activity in the laboratory, for voles which had previously (in October) been recorded under field cage conditions. Laboratory test conditions simulated autumn photoperiod and autumn temperature. The lower diagrams indicate the daily light and temperature changes in the environmental chamber during this test period.

LABORATORY

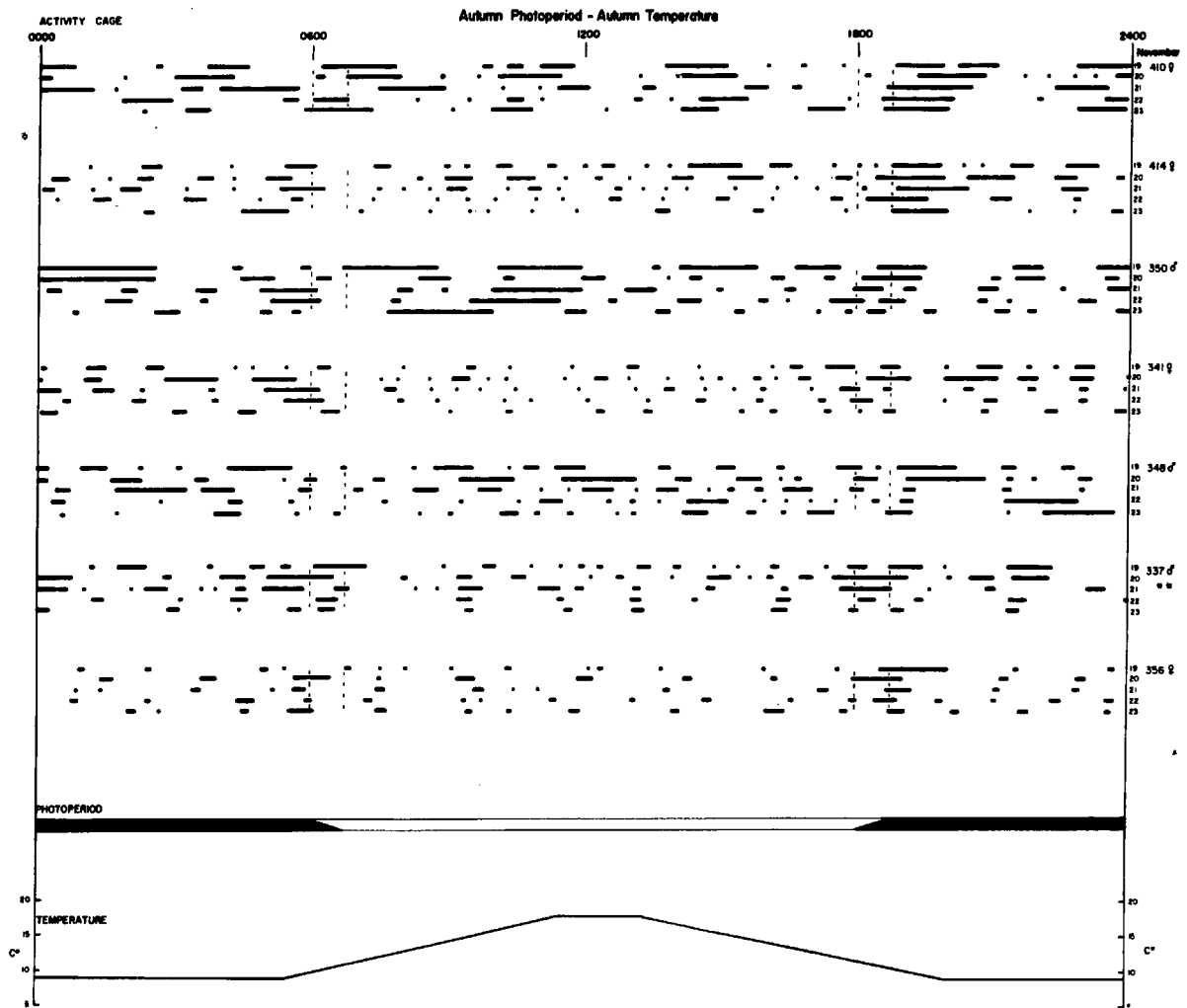


Figure 12.

condition and was not typical of activity patterns recorded during other test periods. ---

The individual variation in activity present in voles exposed to very similar environmental conditions requires the testing of several individuals to characterize the activity of the population. In spite of this variation, it is apparent that there was a general reduction in the level of activity of voles in activity cages in the field and in the laboratory, compared with voles recorded in enclosures. One vole was recorded under both field and laboratory conditions (Figure 13), and this test nicely illustrates some effects of shifting voles from one experimental condition to another. Although crepuscular activity was not noted in this vole when in an activity cage in the field, the activity cage pattern was quite different from either the enclosure or the laboratory records. There was a general reduction in the amount of activity and there was also a shift in emphasis of its activity when it was moved from the field to the laboratory. In order to analyze these activity patterns more objectively, several categories were used to characterize the activity of voles studied during 1966.

PERCENT OF TIME ACTIVE

The records of individual voles under the various environmental regimes were compiled and grouped by test and by season. These data have been listed in Appendices I to VI and are summarized in Figure 14 and Table 1. Each activity record was analyzed for the percent of the total time given over to activity by the vole.

Figure 13. Activity patterns of vole 116♂ in three test conditions. The upper activity pattern was recorded in a field enclosure, the middle was the vole's pattern in a field cage, and the lower pattern was obtained from the same animal in a laboratory cage. The laboratory regime was spring photoperiod and spring temperature.

116 ♂

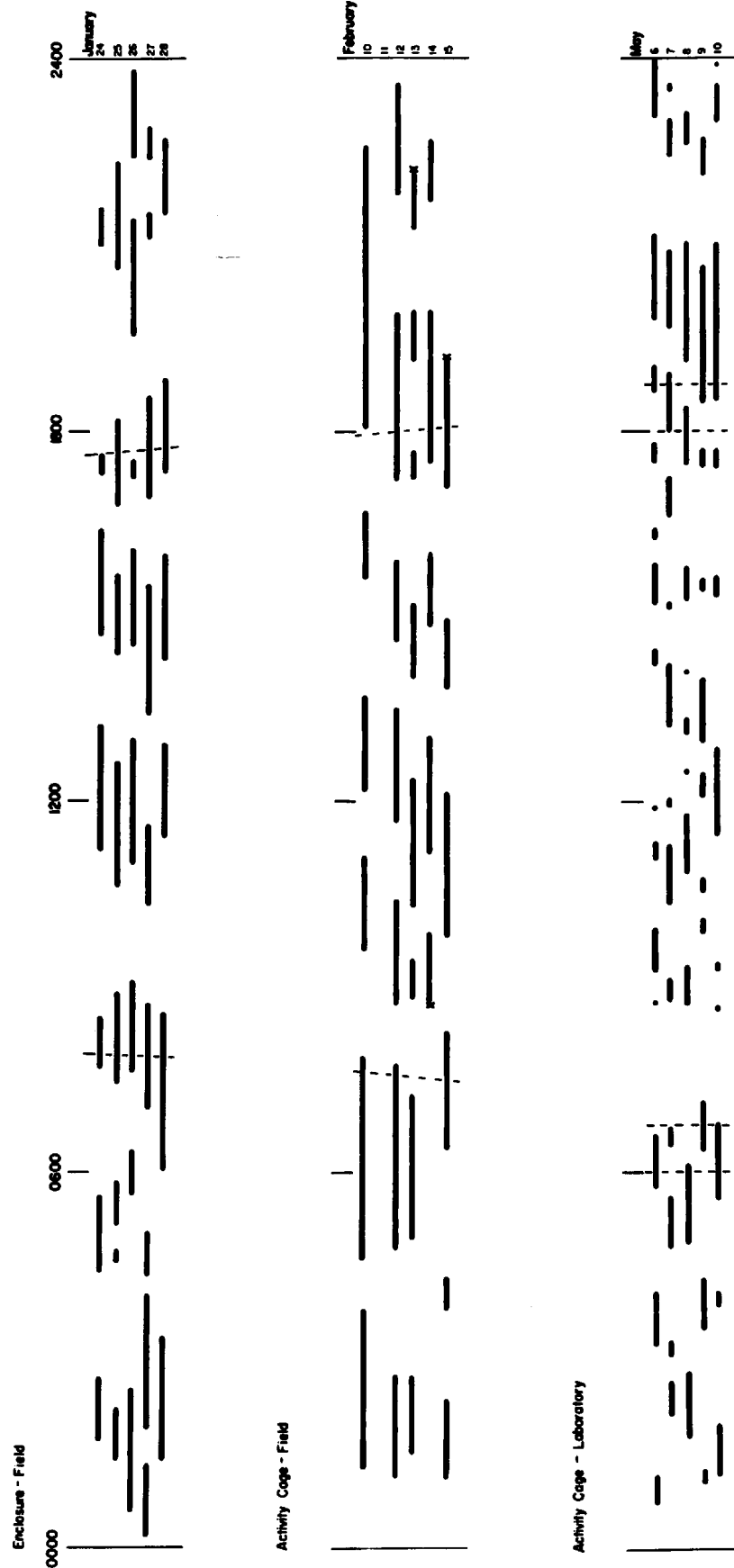


Figure 13.

Figure 14. Levels of activity of voles in different test conditions, grouped by season. The length of the vertical lines indicates the range and the rectangle describes one standard deviation. "Activity in Percent," in this and following figures, denotes the percent of the 6-minute intervals during the test period in which the test voles were classified as active.

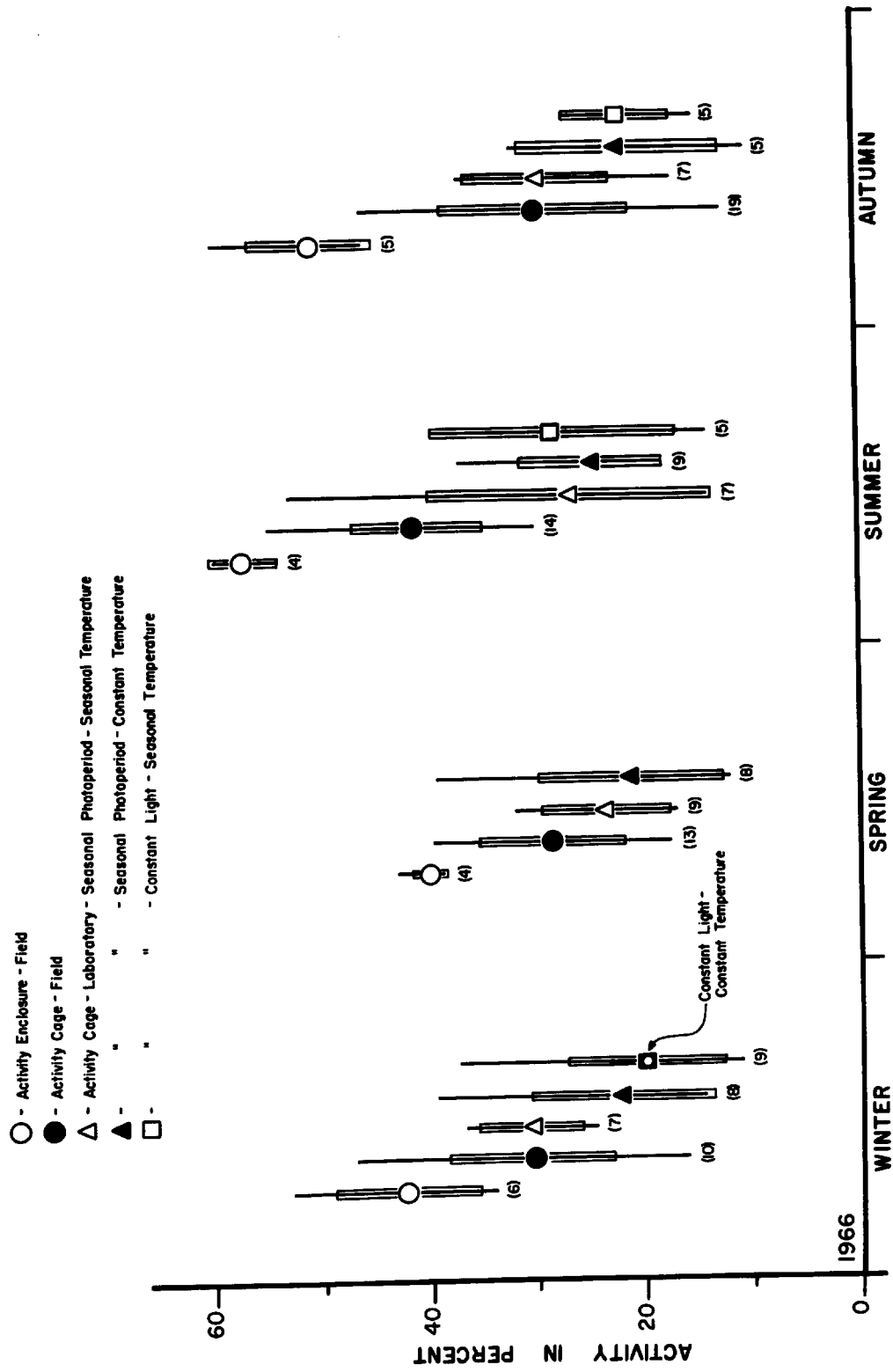


Figure 14.

Table 1. Means of percent of time active grouped by season and by total for year for all test regimes

EXPERIMENTAL CONDITION	SEASON	NUMBER OF VOLES TESTED	SEASONAL MEAN	YEARLY MEAN
FIELD				
Enclosure	Winter	6	42.4	42.5
	Spring	4	40.1	
	Summer	4	56.6	
	Autumn	5	50.9	
	Total	19		
Activity Cage	Winter	10	30.7	32.5
	Spring	14	28.9	
	Summer	14	42.7	
	Autumn	19	29.1	
	Total	57		
LABORATORY				
Seasonal photoperiod- Seasonal temperature	Winter	7	30.6	27.6
	Spring	9	23.6	
	Summer	7	26.7	
	Autumn	7	29.4	
Seasonal photoperiod- Constant temperature	Winter	8	22.1	22.3
	Spring	7	21.1	
	Summer	9	24.5	
	Autumn	5	21.7	
Constant light- Seasonal temperature	Summer	5	27.2	24.4
	Autumn	5	21.6	
Constant light- Constant temperature		9	19.9	
	Total	78		

Total number of voles tested = 154

Differences in total activity within each season - The level of activity of voles in enclosures was significantly higher than that of voles in activity cages during each season, being highly significant in Spring, Summer, and Autumn, and significant ($t = 2.91$ $0.05 > P > 0.01$) in Winter. There was no significant difference in activity between voles in activity cages in the field and those which were exposed to daily changes in temperature and/or light in the laboratory during Winter, Spring, and Autumn. There was, however, a highly significant difference between activity of voles in field cages in the Summer and of voles in a Summer photoperiod - constant temperature regime in the laboratory ($t = 4.29$ $P < 0.001$). Voles recorded in the other two summer environments in the laboratory, including the comparable summer photoperiod - summer temperature regime, were not found to be significantly different by a t-test, probably owing to the large variance within each group. The only significant difference which occurred in the laboratory groups was between winter photoperiod - winter temperature and the constant light - constant temperature test ($t = 2.55$ $0.05 > P > 0.02$). However, this latter condition was not really a seasonal test as the others were, since neither light nor temperature were giving seasonal cues. There was a general reduction in the total activity of the test animals as light and/or temperature were held constant.

Differences in total activity between each season - Total activity of the Winter and Spring group of voles in enclosures was significantly lower than the activity level of the Summer and Autumn group ($t = 3.68$ $P < 0.001$) and was not significantly different within these groups. Voles in activity cages in the field in the Summer were significantly more active than caged voles in the field in the other three seasons

($t = 2.67$ or higher $P < 0.02$). Laboratory voles were remarkably constant, with the only significant difference occurring between constant light - constant temperature and autumn photoperiod - autumn temperature ($t = 2.21$ $0.05 > P > 0.02$). Once again, the 'non-seasonal' condition was the only test environment which provided real differences in activity level from the other laboratory regimes.

It appears that the Summer conditions in the field provided some stimulation to voles tested there, with significantly larger increases in activity over the other seasons in both enclosures and cages. The constant light - constant temperature regime had the lowest level of activity of the conditions tested.

Grouping the individual test period activity levels permits the analysis of total activity of voles in different seasons, but the sequential changes from one test period to the next are lost by this treatment. The "activity in percent" of individual voles recorded in enclosures and the means of voles in activity cages in the field is plotted in Figure 15. The activity of voles in field cages was lower (except in the June test period) than the activity of voles in enclosures recorded during the same test period. This high value in June may have resulted from the positioning of the activity cages on the upper level of the shelter owing to the presence of a marauding opossum during that week. There was also a general reduction in the amount of activity of the enclosure voles from June through December and of cage voles from July to December.

An unexpected difference in the level of activity between the sexes was observed, with the females having a small but consistently higher percent of activity; that is, they were active more of the time than were males in the same test situation (Table 2). This difference

Figure 15. The activity level of individual voles in enclosures, compared with the average activity of groups of voles in activity cages, in the field in 1966.

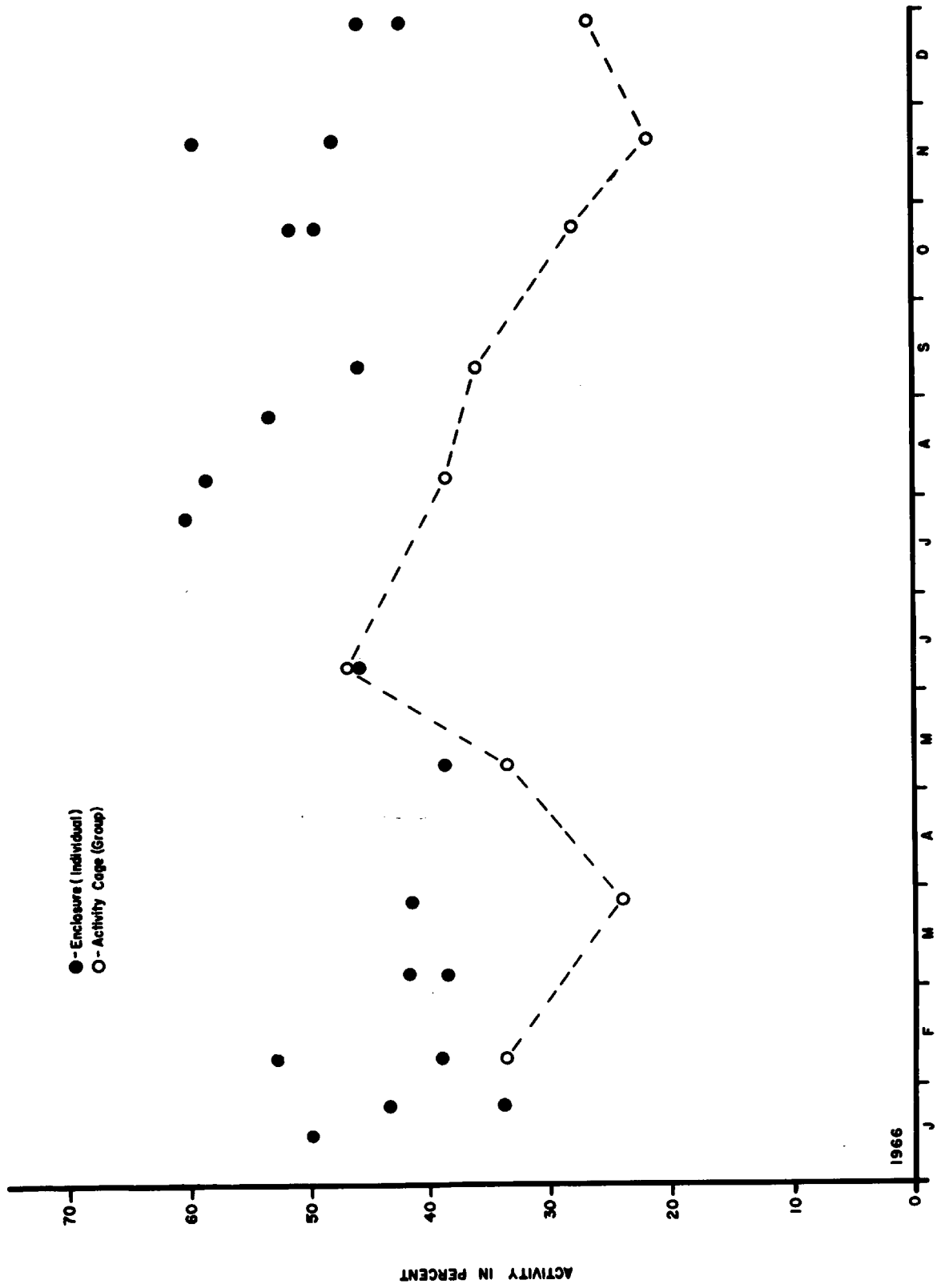


Figure 15

Table 2. Sex differences in the percent of time active in the laboratory and in the field. Numbers in parentheses indicate numbers of voles tested.

EXPERIMENTAL CONDITION	SEX	
	♂♂	♀♀
Field		
Enclosure	45.6 (9)	47.8 (10)
Activity Cage	29.4 (30)	36.3 (26)
Laboratory		
Seasonal photoperiod- Seasonal temperature	25.7 (18)	29.3 (12)
Seasonal photoperiod- Constant temperature	21.8 (13)	22.8 (13)
Constant light- Seasonal temperature	21.5 (5)	28.2 (5)
Constant light- Constant temperature	16.0 (3)	21.9 (6)

is significant (Sign Test $N=6$ $0.05 > P > 0.02$). Most field studies of home range in small mammals indicate that males have a larger home range than females do. It has been generally assumed that males are more active than are the females, but the male Microtus in these test situations certainly were not active as long each day as the females were.

NOCTURNAL AND DIURNAL ACTIVITY

The activity data were further analyzed to determine if there is a nocturnal or a diurnal emphasis of activity in Microtus pennsylvanicus. The level of activity during the day or light hours was compared with that which occurred during the night or dark hours. In the field, official sunrise and sunset were the times chosen to separate day from night. In the laboratory, the day was considered to extend from 15 minutes after the lights began to come on until 15 minutes before they were completely turned off at the end of the light period. The Summer day in the laboratory was 14 hours in length, while Spring and Autumn were 12 and Winter was 10 hours in length. The level of activity was determined by dividing the number of 6-minute intervals of activity of the light or dark portion of the test period by the total number of 6-minute intervals present in that light or dark period, eliminating the seasonal effect of change in day length. These percentages were computed for all test animals and have been listed in Appendices I to VI. From these data each test vole was designated as nocturnal or diurnal. A vole was considered diurnal if the percent of activity in each hour of day was larger than the percent of activity for each night hour, and it was classified as nocturnal if the night activity was found to be larger than the day percent of activity.

A change in the emphasis of the daily activity of test meadow voles

was observed under different environmental conditions, as illustrated in Figure 16. The diurnal activity of voles in enclosures was quite high, producing a strongly diurnal distribution of daily activity. Voles which were tested in activity cages in the field and in the laboratory showed a general decrease in the level of diurnal activity as environmental conditions were held constant. The overall effect was to change the daily emphasis of activity from diurnal to nocturnal. Apparently, the diurnal component of daily activity in M. pennsylvanicus is rather sensitive to environmental changes.

There was also a season-to-season shift in the level of the nocturnal component of the daily activity of voles in enclosures, with an increase in nocturnal activity in the Summer and Autumn groups compared with the Winter and Spring groups. It was this increase in nocturnal activity which accounted for the significant difference in total activity previously seen between the Winter-Spring and the Summer-Autumn seasons.

The diurnal or nocturnal activity classifications have been summarized in Appendix VII and totaled in Table 3. Table 3 gives further evidence of the shift in emphasis of activity from the enclosures to the cages. Voles in enclosures were significantly diurnal (Sign Test $N=19$ $P < 0.005$), with only one of 19 animals having more activity at night than during the day. These voles were free to move about within the enclosure, construct runways and nests, and feed on the natural vegetation in the enclosure. Voles housed in activity cages in the field were exposed to similar daily changes in meteorological conditions as were those in enclosures, but they were more restricted in their movements, their diet was oats rather than natural herbage, and

Figure 16. Seasonal means of diurnal and nocturnal activity in the field and the laboratory, plotted as percent of activity in light and in dark periods.

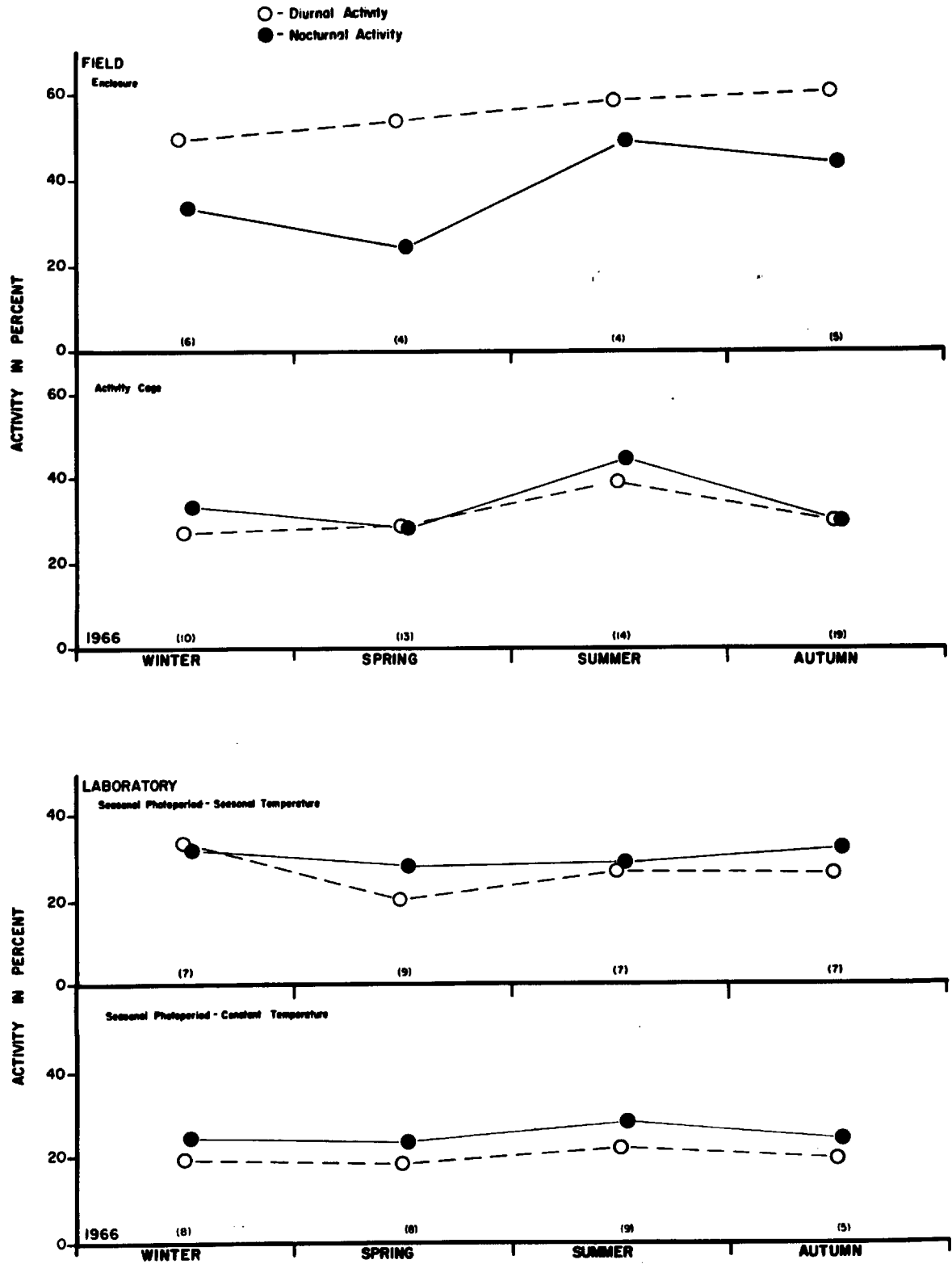


Figure 16.

Table 3. Numbers of voles showing diurnal or nocturnal activity patterns under various kinds of field and laboratory conditions.

EXPERIMENTAL CONDITION	Activity classified as:	
	DIURNAL	NOCTURNAL
Field		
Enclosure	18	1
Activity Cage	24	32
Laboratory		
Seasonal photoperiod- Seasonal temperature	10	20
Seasonal photoperiod- Constant temperature	7	23

they were not immediately surrounded by natural cover. Although the daily changes in meteorological conditions were probably similar in activity cages and the enclosures, the absolute values of the conditions in activity cages above the ground and in enclosure runways surrounded by bluegrass were undoubtedly different.

Voles in the field cages were not significantly nocturnal or diurnal; the percent of nocturnal activity was nearly equal to that of diurnal activity. This activity distribution evidently resulted from the strong crepuscular activity of caged voles in the field, as their major activity bursts overlapped sunrise and sunset rather precisely (Figure 11). There was a real difference between the nocturnal-diurnal distribution of vole activity in enclosures and that of voles in activity cages in the field (Fisher's Exact Prob. Test $P < 0.0001$). As the activity of voles in the laboratory was more nocturnal than that of voles in activity cages in the field, the difference between nocturnal-diurnal activity distribution was even greater.

When the activity of voles under the two constant light - seasonal temperature regimes was analyzed with regard for high and low temperature conditions, there was found to be slightly more activity per hour during the warmer part of the day (26.5%) than in the cooler part (23.1%). This suggests that the constant light condition may eliminate the cue which tends to channel laboratory activity into the dark period of the day.

The winter photoperiod - winter temperature regime was the only laboratory treatment which had a higher level of diurnal than of nocturnal activity. It also had more individuals classified as diurnal than nocturnal. In comparing this test period with the winter test periods in

the field cages, it is worth noting that the voles in the laboratory were exposed to a low ambient temperature of -4°C . for 9 hours each day of the acclimation and test periods. This temperature was lower than the lows recorded on 9 of the 10 test days which make up the winter group in the field. If Microtus has some sensitivity to these low temperatures, it would seem reasonable that the voles would shift their activity emphasis from the 'normal' laboratory (nocturnal) pattern to a diurnal emphasis as a result of consistent and predictable low temperatures.

Another shift in daily activity appeared during another period of temperature extremes. Five voles recorded in activity cages in the field during a hot and humid test period from August 5 to 9, 1966, reduced their activity during the day and become more nocturnal (Figure 17). The noon temperatures for August 6, 7, 8, and 9 were 93° , 90° , 88° , and 82°F ., respectively; the corresponding relative humidity readings were 60%, 50%, 94%, and 88%. The high temperature seems to have been quite effective in reducing the amount of movement of the voles in the activity cages, for a shift in emphasis of activity was evident by August 7 when the humidity was at its lowest point during the test. Analysis later in the paper will indicate that temperature has a greater effect on daily activity in Microtus pennsylvanicus than does humidity.

Although light-associated factors appear to have most strongly influenced activity in these voles, temperature may also shift the emphasis of their activity during the day, particularly at their limits of tolerance. These findings support the suggestions of Getz (1961) and Wiegert (1961) that Microtus pennsylvanicus modifies its daily

Figure 17. Activity patterns of five voles maintained in field cages in summer, grouped by day. The vertical dashed lines indicate sunrise and sunset. The voles recorded were (from the top): 354♂, 333♂, 50♂, 346♀ and 351♂.

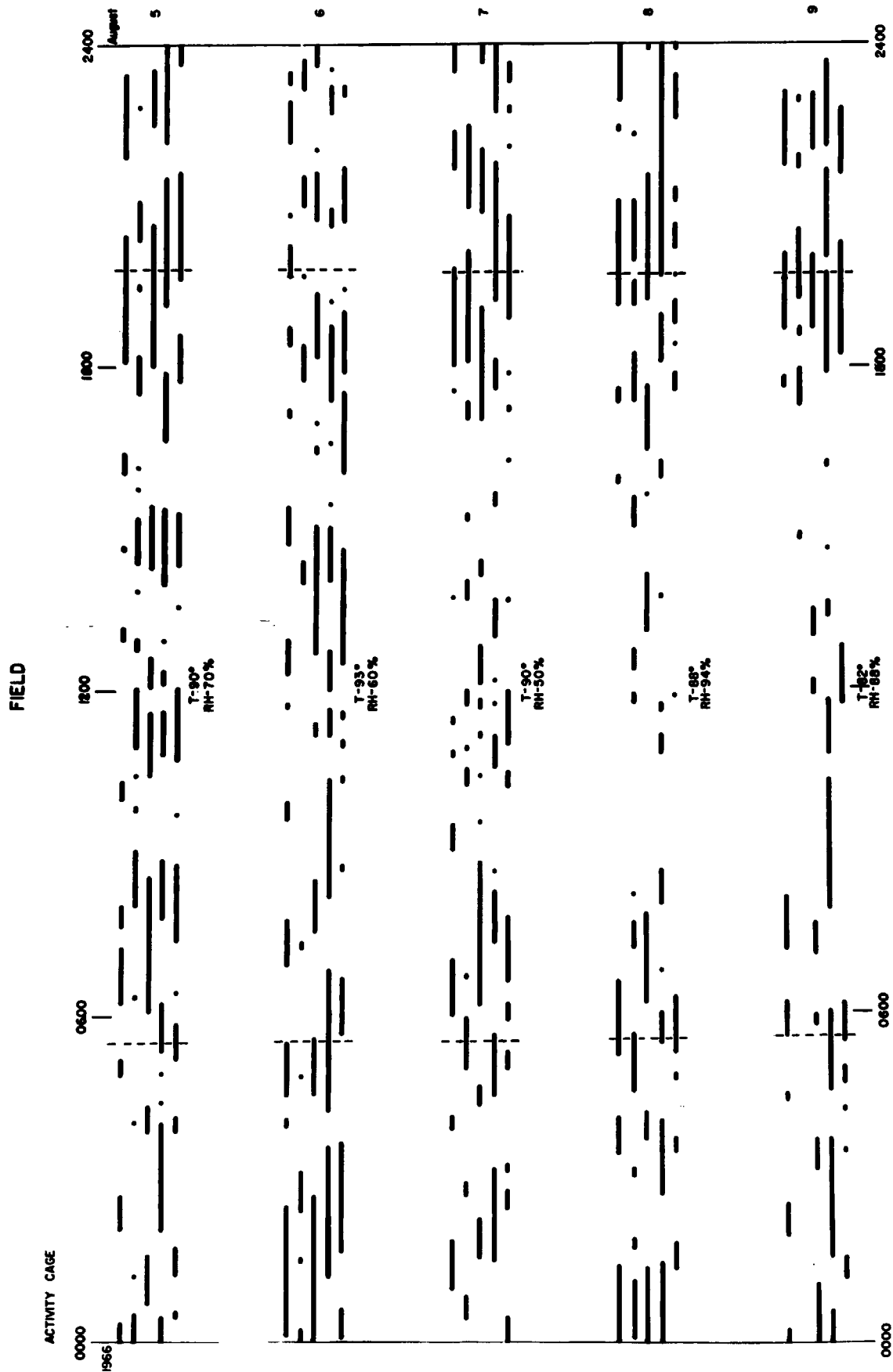


Figure 17.

activity during periods of extreme temperature stress.

SYNCHRONY

The third characterization of vole activity to be considered in this paper, synchrony, describes the regularity of a vole's periods of activity and inactivity from one day to the next. The synchrony tests used in this paper can also describe the synchrony of a group of voles for a one-day period, but the present analysis will be limited to tests of individuals during their test period. Synchrony which is statistically significant is a reflection of the interaction of the physiologically based activity pattern and some cue or set of environmental cues that results in a non-random distribution of activity and inactivity during the day. Voles can also exhibit synchrony in total darkness and constant temperature (Graham, unpubl. data), but this is probably an expression of the endogenous Zeitgeber or physiological timekeeper (Aschoff, 1951) operating without light or temperature cues. This study is concerned with the proportion of the voles under a certain set of conditions which are responding to one or more environmental cues such that an individual's activity is synchronous. A comparison of the proportion of voles which are synchronous under different conditions should provide evidence for the strength of an environmental factor as a cue for a vole's daily activity pattern.

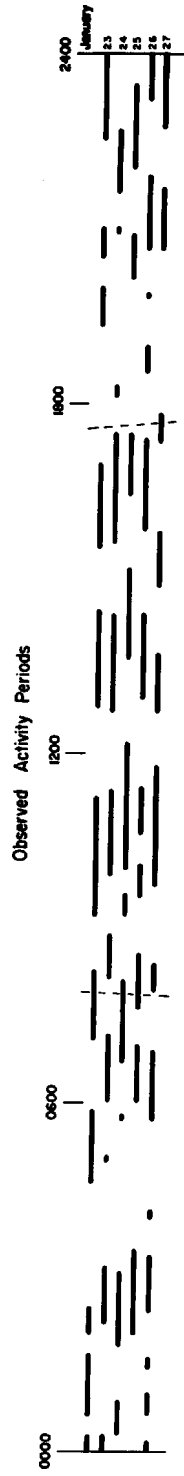
The procedures for determining synchrony have been described on page 27. By this technique, the record of a vole (Q101) with an activity pattern that barely achieved the level of statistical significance ($P < 0.01$) was analyzed (Figure 18). The histogram showing the distribution of the observed activity indicates an increase of both the 0's (inactivity at the same time each day of the test period) and the 5's

Figure 18. (Top) Observed daily activity pattern of vole 101q in test period.

(Middle) Pattern produced after randomizing the activity and inactivity periods of the observed record.

(Bottom) Distributions of activity (from left to right) (1) as predicted by the binomial theorem, (2) resulting from randomizing the observed pattern and (3) the observed distribution.

101 ♀



Randomized Activity Periods

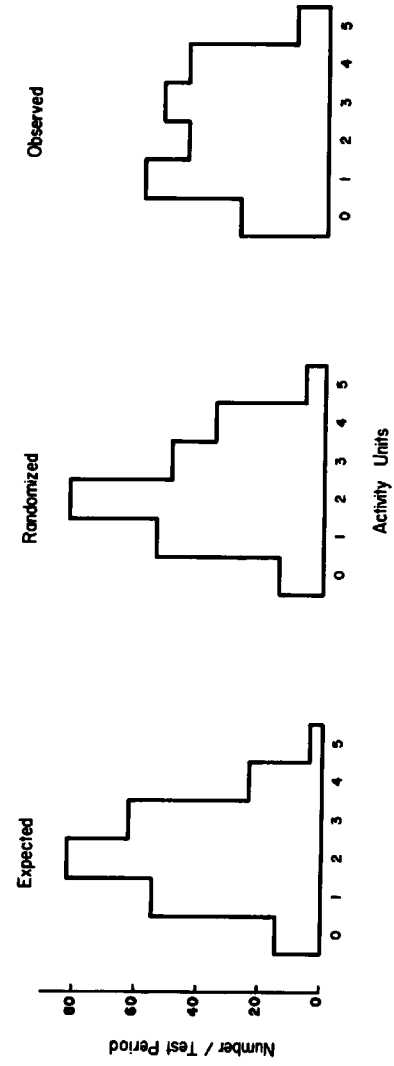


Figure 18.

(activity at the same time each day) over the distribution one would expect by chance; hence there is a flattening of the observed distribution compared with the expected.

A test was devised to determine whether this statistical procedure actually distinguished between synchronous and random activity. The length of each period of activity and inactivity was measured and both the inactive and active periods were then assorted by reference to a table of random numbers. The new, randomized pattern was then diagrammed (Figure 18) and tested for synchrony. The D value of the Kolmogorov-Smirnov test of the randomized activity was found to be 5.60 (a value of 9.24 would have been necessary for significant synchrony at the $P < 0.05$ level). Randomizing the periods of activity and inactivity evidently destroyed the patterning by which vole 101q had grouped activity in a significant manner. A visual comparison of the histograms for the randomized and the expected distribution predicted by the binomial theorem shows but little difference between them; the observed activity distribution differs from both. It appears that this synchrony test is a valid test of the regularity of activity and inactivity from one day to the next.

The activity of pairs of synchronous and nonsynchronous individuals diagrammed in Figures 11 and 12 was grouped into 30 minute portions and plotted in Figure 19. The distribution of activity during the day for both synchronous and non-synchronous voles is similar, but the peaks and troughs of the graph are more pronounced in the synchronous animals, indicating clumping of activity and inactivity periods. Figure 19 also shows the shift from diurnality in the field to nocturnality in the laboratory. Voles in field activity cages had a

Figure 19. Distribution of activity of 6 voles in field and laboratory for entire test period. Voles on left were non-synchronous and those on the right were synchronous at the $P < 0.01$ level.

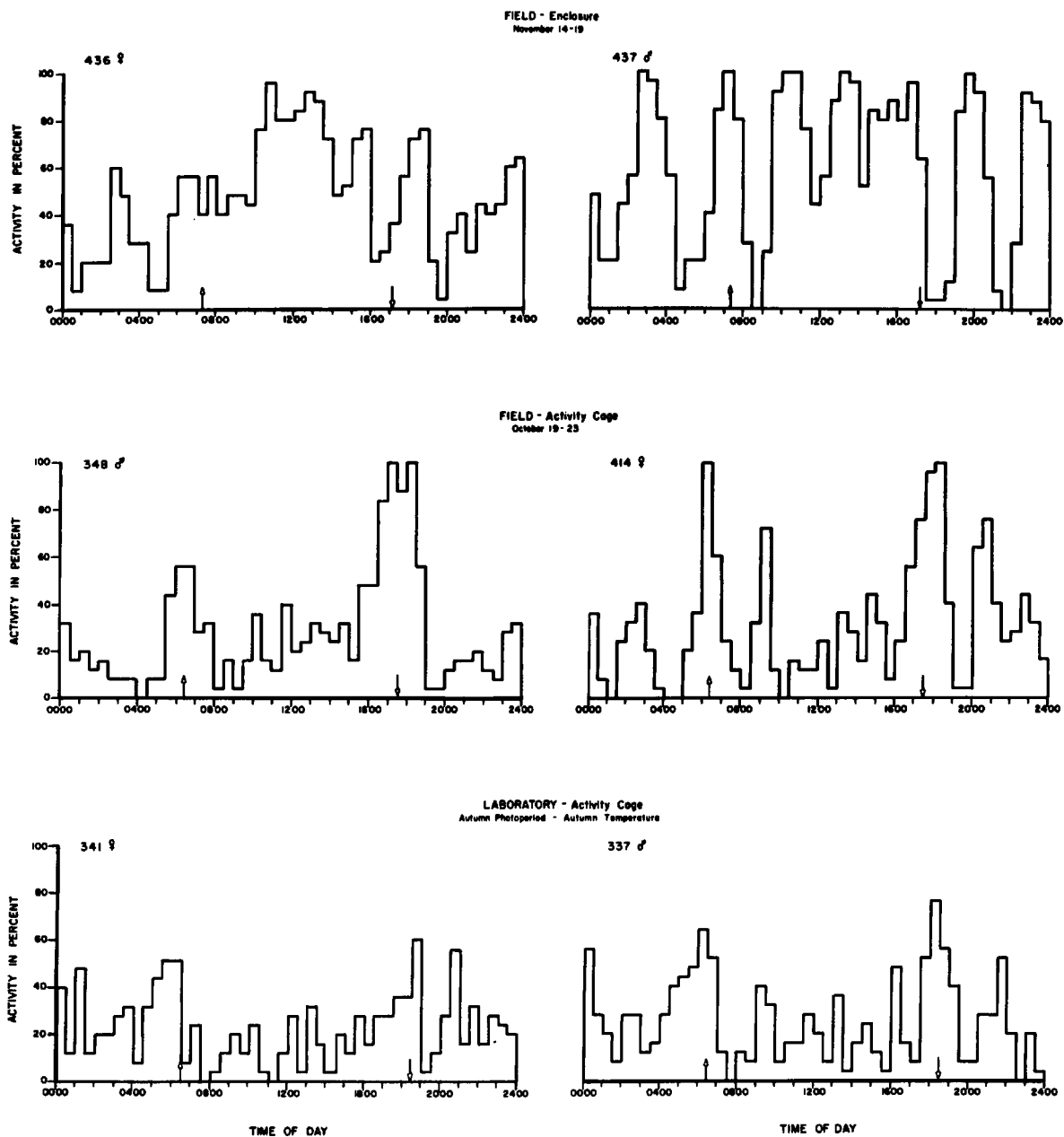


Figure 19.

strongly crepuscular pattern of activity.

Tests for synchrony were performed on a total of 154 different vole-environment combinations (some voles were used in both activity cages in the field and in the laboratory). These results are summarized in Table 4 (the details appear in Appendix VIII). Voles in enclosures had the highest percentage of synchrony; those in the constant light - constant temperature regime appeared to have little if any synchrony. The data in Appendix VIII suggest that changes in photoperiod have a greater effect in maintaining synchrony than do daily changes in temperature. There was a sharp decrease in the percentage of synchronous individuals when voles were placed in activity cages as opposed to those recorded in enclosures.

In the summer of 1966, even though additional sheet metal was forced into the ground next to the enclosure walls, some voles were able to tunnel under the walls. When test voles were trapped out of the enclosures following a test period, other meadow voles or short-tailed shrews (Blarina brevicauda) were occasionally trapped out as well. In four of the five test periods in which a non-test vole was present, the test vole was determined to be synchronous. Thus, other voles may have contributed to synchrony in the test vole. Short-tailed shrews were also trapped out at times, but only two of four voles were tested as being synchronous when Blarina were present during the test period. There was no apparent relationship between the presence of voles or shrews and the level of activity of the test animals. It would be interesting to know if the voles in a natural population have synchronous activity, with some social factor serving to stimulate synchrony. Presently, there is no way of telling how universal synchrony

Table 4. Frequency of synchrony of daily activity in the laboratory and in the field

Experimental Condition	Number of voles tested	Number of voles significantly synchronous	Per cent significantly synchronous
Field			
Enclosure	19	10	52.6
Activity Cage	57	20	35.1
Laboratory - Activity Cage			
Seasonal photoperiod- Seasonal temperature	30	10	33.3
Seasonal photoperiod- Constant temperature	29	8	27.6
Constant light- Seasonal temperature	10	2	20.0
Constant light- Constant temperature	9	0	00.0
Totals	154	50	

is in a natural population. Nor do we know if the enclosure itself may restrict some individuals and prevent them from being active in such a way as to be classified as synchronous.

There was no relationship between the weight of the test vole and synchrony nor between the sex of the vole and synchrony. However, a positive relationship between the length of the acclimation period and the degree of synchrony was suspected after working up the first few records from field enclosures. It was then decided to give each vole an acclimation period of 7-10 days before beginning the test period. Longer acclimation periods were planned for the rest of the test periods, and acclimation periods for 1966 tests are listed in Appendix IX. Although voles which tested as synchronous had been acclimated in the enclosures for longer periods than the non-synchronous individuals (11.6: 10.8 days), the difference was not significant. There was a tendency for the number of days of acclimation and the level of activity to be inversely related, but it was not significant.

CORRELATION OF VOLE ACTIVITY AND ENVIRONMENTAL FACTORS

The activity of voles in the field was recorded simultaneously with the measurement of temperature, humidity, change in temperature, change in humidity, light vs. dark (which compares levels of activity in the day with activity levels at night), light intensity, twilight, and rainfall as described on pages 5 and 26; correlations were looked for by means of a linear regression program. The correlation coefficients of the measured environmental variables and vole activity in enclosures and vole activity in activity cages are summarized in Appendices X and XI, respectively.

Voles in enclosures - During 1966, voles in enclosures generally had strong positive correlations with light vs. dark, light intensity and temperature. Lower positive correlations were exhibited with change in temperature and twilight. The enclosure voles had generally negative correlations with humidity in the spring and positive correlations with humidity in the autumn. A weak negative relationship between activity and change in humidity was seen in these voles.

Voles in activity cages - Voles in activity cages in the field had high positive correlations of activity with twilight and lesser correlations with rainfall, light intensity, temperature and change in humidity. Small positive correlations were generally found between activity and light vs. dark. The often strong negative correlations between activity and light intensity from June to December resulted from the concentration of activity at twilight periods, when light intensities were low.

Multiple correlation coefficients of the interaction of the eight environmental factors on activity were also calculated (in Appendices X and XI). The square of the multiple correlation coefficient is the coefficient of determination, which describes the percent of the variability in the activity which can be accounted for by the variability in the environmental factors. The coefficients of determination for voles in enclosures and in field activity cages are listed in Appendices XII and XIII, respectively, and summarized in Figure 20. For voles in enclosures, the values of the coefficients of determination increased during the spring and then dropped and stayed at a low level during the rest of the year. Voles in activity cages in the field had values which remained relatively low during the spring and summer, rose and declined again in the autumn.

Figure 20. Coefficient of determination of individual voles in enclosures and of voles in activity cages in the field in 1966.

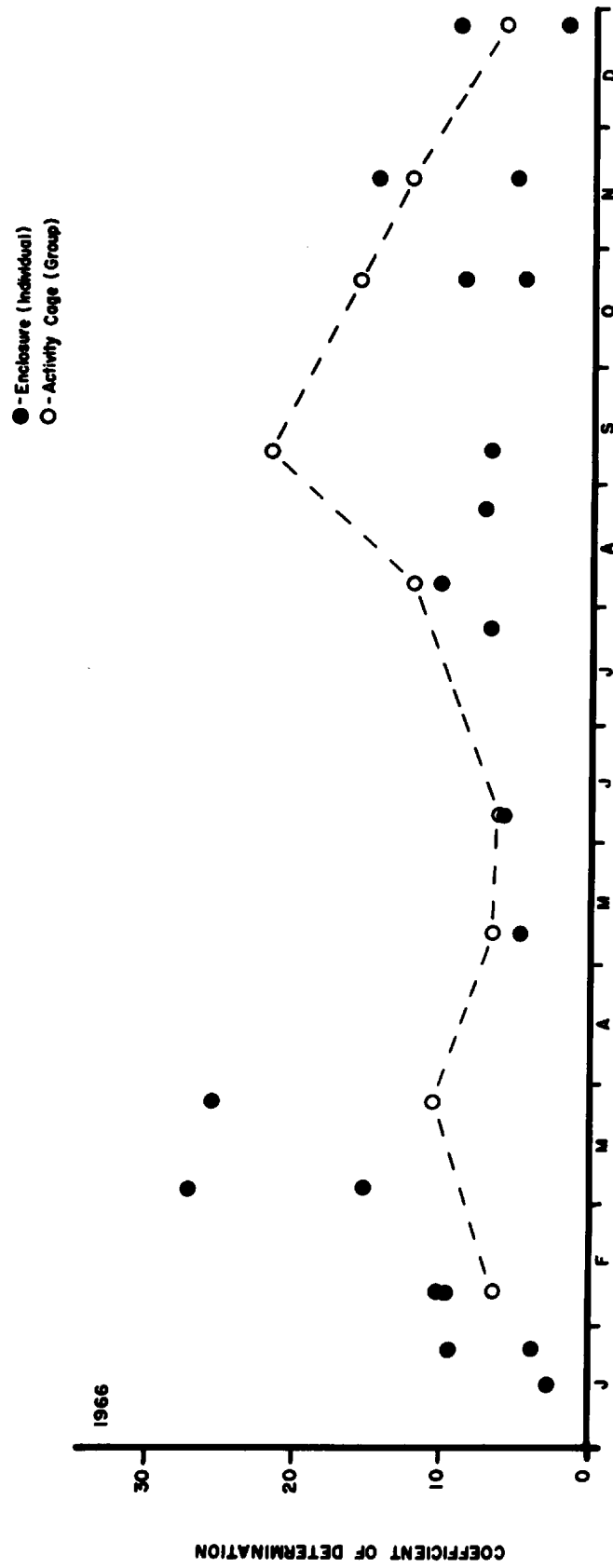


Figure 20

The effect of the environmental factors on vole activity varied through the year and at no time did these factors explain or account for more than 30 percent of the variation in the daily activity of the test voles. The amount of 'explained' activity would have approached 100 percent if Microtus pennsylvanicus were as nocturnal as Peromyscus species are; the physiologically based short-term activity bursts preclude a direct relationship with one or several of the measured environmental factors, which are basically of a 24-hour cyclicity. Even so, in each test condition at least two of the measured environmental factors had a statistically significant ($P < 0.01$) effect on activity, indicating some response of the test voles to these conditions. The order of importance of the significant factors for each test animal or group of animals has been listed in Appendices XII and XIII. The light vs. dark condition had the greatest effect on voles in enclosures, since they were largely diurnal. Voles in field cages responded most strongly to twilight conditions.

Percentages of influence were calculated by dividing the number of times that a factor had a significant effect on activity by the number of times the relationship was measured. These percentages are listed in Table 5. The order of importance of the major factors influencing vole activity in enclosures was light vs. dark, twilight and temperature, while twilight, rainfall, light vs. dark and temperature were most important in influencing the activity of voles in cages in the field. After summing temperature and humidity factors, light factors and rainfall, it is evident that light factors (cueing elements of the environment) produce more real effect on the activity of voles than do temperature and humidity (which can be biologically stressful factors).

Table 5. Percentage of influence of measured environmental factors on activity of voles in the field in 1966

	Temperature	Change in Temperature	Humidity	Change in Humidity	Light Intensity	Light vs. Dark	Twilight	Rainfall
Enclosures	45.0	25.0	35.0	35.0	35.0	75.0	50.0	25.0
						53.3		25.0
Activity Cages	44.4	11.1	11.1	33.3	22.2	44.4	100.0	80.0
						59.3		80.0

Rainfall seemed to have a generally negative effect on the activity of voles in field cages but little detectable effect on the activity of those in enclosures. The voles in the cages responded to the sound of rain on the shelter and/or to immediate meteorological changes associated with the rainfall; voles in the enclosures, however, were able to feel the rain as well as to hear it and they were exposed to similar meteorological conditions as those in cages. The small number of significant correlations between rainfall and activity of voles in enclosures may be real or may have resulted from insufficient data.

DISCUSSION

FIELD STUDIES

Few previous field studies of Microtus activity have systematically evaluated daily activity for as long as one year. Some seasonal modifications in the daily activity pattern of Microtus pennsylvanicus were anticipated, but the patterns remained remarkably similar from season to season. Diurnal activity of voles in field enclosures in summer was high, when a reduction in activity, owing to high daytime temperatures, should have been observed (Getz, 1961). This may have resulted from the high moisture content in the soil; the protective vegetation was in good shape during all of 1966. However, voles in field activity cages in a summer test period (Figure 17) concentrated most of their diurnal activity in the morning and were inactive in the afternoon. Voles in activity cages were not living in a thick, protective cover of bluegrass and were both physiologically and psychologically "exposed." It is not known whether the increased morning activity was some sort of compensatory response to the individual's reduced activity on the hot afternoon of the preceding day, a conscious shifting of activity to the cooler part of the day, or was caused by an increased consumption of water in the morning hours. Pearson (1960) found that Microtus californicus were active during the day and night in the autumn, winter and spring; in summer they were very active during the early morning hours and were generally inactive in the afternoons. He proposed that the presence of dew accounted for the high level of activity he observed in Microtus californicus in the mornings and that high temperatures reduced their activity in the middle of the hot, dry summer afternoons.

During 1966, enclosure voles in this study were active from 35 to 60 percent of the time available to them, as revealed by constantly monitoring their location in the activity enclosures. Pearson (1960) used a photographic device to record movements of individual Microtus californicus in their runways. Estimates of the amount of above-ground activity of marked voles indicated that they were active above ground for 1 to 2 percent of the time available to them. The habits of the two species of vole account for some of this discrepancy, as M. californicus spends much of the day in underground burrows, whereas M. pennsylvanicus nests and moves about above ground in the fall and spring, with some time spent in burrows in summer and winter. There is also the possibility that some of the excursions by the California voles went undetected by Pearson's photographic device.

Sexual differences in daily activity were noted in this study. Female Microtus pennsylvanicus were significantly more active than were the males when six experimental regimes were compared. Among mammals, the home range of the male is commonly larger than that of the female, and most investigators have assumed that males are active for longer periods than are the females. The implication from these data is that the males have more intense activity when they are up and about but that they rest more than do the females. Pearson (1960) reported similar results in the California vole, as the average male vole used the runways more frequently than the average female, but the time of the average excursion by a female was longer than that recorded for the average male.

Pearson also found that daytime excursions for California voles of both sexes were longer than those at night. This pattern, reflected

in the longer activity bursts during the day as compared with night-time, was observed for the meadow vole and suggests that the California vole, as previously reported by Grinnell (1908), is more diurnal than nocturnal.

Voles recorded in enclosures began a daily sequence of activity bursts from one-half to one hour before sunrise and, generally, four activity bursts were spaced through the daylight hours. The end of the last burst of activity in daylight hours usually occurred about one hour before sunset. It was also found that the voles in enclosures were significantly diurnal. These findings corroborate results obtained in an extensive field study by Hamilton (1937). He found that the number of baits removed from specific field sites was greater in the day than at night. His snap-trap capture data showed there were twice as many snap-trap captures of Microtus pennsylvanicus in each hour of daylight as in each hour of darkness, regardless of season. He reported peaks in live-trap captures after dawn and before dusk; these roughly correspond to the results of this study, as he defined dawn as the time one can safely turn the car lights off and dusk as the time it is prudent to turn them on (Hamilton, pers. comm.).

LABORATORY STUDIES

In this study, voles caged in the field and in the laboratory were not significantly diurnal or nocturnal, but all test voles recorded in the laboratory were more nocturnal than diurnal, whether they were exposed to lighting conditions which simulated twilight or to abrupt changes from light to dark (Graham, unpubl. data). Calhoun (1945), Pearson (1947), Grodzinski (1960) and Wiegert (1961) also recorded Microtus

as more nocturnal than diurnal in the laboratory. While this pattern of activity appears to be widespread, a vole maintained in the laboratory for long periods under natural (daylight) illumination and constant temperature was more diurnal than nocturnal (Durup, 1956). It is not known at the present time whether artificial light represses diurnal activity or whether some quality of natural illumination may favor a diurnal emphasis of activity in Microtus. Certainly, the level of nocturnal activity remained relatively constant in these studies, and diurnal activity decreased when voles were put into cages and brought into the laboratory.

A striking shift in the distribution of the daily activity of the meadow vole was found in this study. They were strongly diurnal in the field enclosures and more nocturnal than diurnal in the laboratory. In another study in which the activity of a small mammal was recorded in the field and in the laboratory, Rood (1965) found that the Scilly shrew (Crocidura suaveolens) was more active during the day in the field and more active at night when they were brought into the laboratory. This pattern of a shift in the daily emphasis of activity may be common in Microtus and present in some of the shrews. Additional data are necessary before further statements may be made about the universality of this pattern in short-cycle small mammals and the behavioral implications of this phenomenon.

SEASONAL SHIFTS IN ACTIVITY

Significant seasonal shifts in daily activity pattern were anticipated in the planning of this experimental study, but little seasonal change in the daily activity pattern of the meadow vole was observed. There was a significant summer increase in percent of nocturnal activity compared

with spring nocturnal activity of voles in field enclosures and cages. The voles did not, however, become nocturnal in the summer and did not show extreme shifts in daily activity. No significant shifts were found in voles recorded in the laboratory. Other studies have suggested there is a seasonal shift in daily activity in Microtus (Calhoun, 1945; Pearson, 1947, 1960) and Erkinaro (1960) recorded a female Microtus agrestis which was clearly more nocturnal in summer and more diurnal in winter. These results were not supported by the present study.

METEOROLOGICAL EFFECTS ON ACTIVITY

RAINFALL

The linear regression analysis used in this study indicated that the activity of voles in activity cages in the field was affected by rain, while rainfall seemed to have little effect on activity of voles in enclosures. This discrepancy in results may not be a real difference. The irregular, heavy rain showers occurred in very few 6-minute intervals of the 1200 6-minute intervals in each test period; thus, there were few activity records (scored as active or inactive for each 6-minute interval) collected from each enclosure vole during the rain periods. These were insufficient to produce a high percentage of statistically significant interactions between lone voles and irregularly-occurring rainfall. When several voles were recorded simultaneously in activity cages in the field, a graded response was obtained and apparently more significant interactions were distinguished. Harrison Ambrose (pers. comm.) has found that isotope-tagged voles in field enclosures and free-ranging in a field nearly always returned to their nests during a heavy rain. It is probable that rainfall had a greater effect on the activity of voles in enclosures in the current study than was indicated

by the regression analysis.

BIOLOGICAL EFFECTS ON ACTIVITY

DIET

Changes in the activity level and the daily emphasis of activity during the year were also compared with probable changes in the quality of the diet from one season to another. Activity of voles in enclosures increased slightly in the day from winter to spring while the nocturnal activity decreased markedly, suggesting that the higher nutritive value of the spring diet did not require as much feeding activity as was needed in the winter. Indeed, the percent of time active was lowest in spring of the four seasons studied. The increase in nocturnal activity found in summer voles in enclosures may have resulted from a decrease in the nutritive value of the forage following the late spring growing season and the voles had to become more active during the night to satisfy their dietary requirements. Hardison, et al., (1954) found that the nutritive value of Kentucky bluegrass fed to steers in New York State decreased regularly from May 28 to July 28. A similar shift in the nutritive value of the bluegrass in the present study site could have accounted for the increase in summer activity seen in enclosure voles.

However, voles in activity cages in the field were fed on oats all year and they had a similar depression of nocturnal activity in the spring and a rise in summer activity. Of course, the entire emphasis of their activity was centered on the twilight periods and this strong crepuscular activity was probably produced by something other than diet. Seasonal changes in diet were not completely responsible for the changes seen in the daily emphasis of activity of voles in the field.

In the present study, activity levels of voles fed on natural vegetation were compared with caged individuals fed on rolled oats in the field. Voles in field cages showed a reduction in diurnal activity in comparison with voles in enclosures. This reduction could have resulted from differences between the two diets or from differences between the cage and the enclosure environment in general. Continual reduction of diurnal activity was found in the voles brought into the laboratory (Figure 16) and placed under different environmental conditions, though the diet remained the same in all activity cage experimental regimes. Under the conditions of this study, modifications of the environment seemed to have more effect on the daily distribution of activity in these voles than did the quality of the food.

Grodzinsky (1960) tested the effect of diet on activity level. He found an inverse relationship between the amount of activity of Microtus agrestis in the laboratory and the caloric value of their diet. Voles on a rich diet were less active and generally restricted their activity to darkness. Diets having less nutritional value produced greater total activity of the same test voles by increasing their daytime activity. The intensity of their activity during the night did not increase but the amount of time active during the 24-hour day did increase.

SHREW ACTIVITY - A COMPARISON

Crowcroft (1954) demonstrated that the daily activity patterns of British shrews (Sorex spp. and Neomys fodiens) consist of activity bursts and rest periods which are similar to those of Microtus; however, the activity unit, consisting of an activity burst and the subsequent rest period, is usually shorter than that found in voles. The length of the activity unit is positively related to body weight. The shrew activity

which Crowcroft measured in the laboratory appears to lack day-to-day synchrony. The only continuous record of shrew activity in the field (Graham, unpubl. data) is for 3 days immediately following the release of a radioactively tagged male Blarina brevicauda in one of the activity enclosures used in this study. This pattern was also not significantly synchronous. Its activity emphasis was at night rather than during the day as was found in Microtus. Osterberg (1962) also found Blarina to be more active at night than during the day. He also found a positive correlation between Blarina activity and precipitation and a negative correlation between activity and temperature during April and May in southern Michigan. The latter correlation might easily be explained if Blarina is largely nocturnal. And that might also explain the small effect which Blarina seems to have on Microtus activity.

SYNCHRONOUS ACTIVITY

With the development of a technique for getting automatic locations of small mammals in field enclosures, it is now possible to determine the beginning and end of their activity bursts in fairly natural habitat with some degree of certainty. From these data their nocturnal and diurnal patterns can be ascertained and calculations of synchrony can be made. Daily synchrony of activity is well known on the physiological as well as on the behavioral level (Halberg, 1960). The physiological mechanisms for regularly repeated locomotor activity in most mammals are closely tied to the daily light-dark cycle, with their activity being restricted to either day or night. The most reliable daily cues appear to be sunrise and sunset and these are used directly by the animal; long term periodicities such as breeding cycles and migratory flights of birds are probably cued by day length or photoperiod. The widespread existence

of daily activity patterns in all biological groups implies that there are biological advantages to being active at one time of the day and, equally as important, inactive at another.

Davis (1933) suggested that the 2-4 hour activity cycles of Microtus are basically feeding cycles; their food supply in their natural habitat is readily available and usually abundant and would allow them to maintain the synchronous activity patterns which we see they have developed. Animals with short-term feeding cycles might be expected to have a feeding pattern which repeats itself from day-to-day if its food supply was fairly dependable. The other small mammal with short-term feeding cycles, the shrew, is essentially carnivorous and does not have a food supply as temporally reliable as vegetation is; they may not have developed synchronous activity patterns. Their feeding habits may account for the apparent condition of being the only group of small mammals possessing a truly arhythmic activity pattern.

ACTIVITY AND PREDATION

Davis (1933) calculated that Microtus in England eat their own weight in natural vegetation each day. Shrews are also known to require large quantities of insect material to survive (Pearson, 1947). With such high daily feeding requirements, it is easy to see why these small mammals have short daily activity and feeding rhythms of 1-4 hours. However, it seems that it is necessary for them to restrict their activity to habitats which provide excellent cover so that they can escape the pressure of diurnal predators. Cloudsley-Thompson (1961:79) proposed that predation is the primary factor restricting the activity of small mammals to night-time; only those forms which feed mainly under dense cover and have large food requirements (which includes shrews and Microtus

spp.) have considerable daytime activity.

Predation is not the only important environmental factor which might determine daily activity patterns in mammals. By being active at one time of the day as opposed to another, the animal may reduce the effects of heat or cold stress; a particular activity pattern might result in an increased supply of food for a predator if it is keyed to the activity periods of its prey. In this study, the test voles in enclosures were reacting less to stress factors (temperature and humidity) than they were to the cueing factors (light intensity, twilight and light vs. dark). It seems reasonable to assume that the activity of these voles is determined more by their response to cover and to their natural diurnal activity pattern than it is by the effects of moderate temperatures and humidity.

SUMMARY

Daily activity patterns of the meadow vole, Microtus pennsylvanicus, were recorded throughout 1966 in 30-ft. diameter field enclosures, in activity cages in the field and in activity cages in the laboratory. Voles in enclosures were significantly diurnal, while the activity of voles in cages in the field was centered around sunrise and sunset and test voles in the laboratory were primarily nocturnal. Voles in enclosures were significantly more active than were test animals recorded in cages in the field. In the laboratory, the level of activity generally decreased as light and/or temperature were held constant. Under six different test conditions, females were always active longer than were males in the same test regime. The day-to-day phasing, or synchrony, of activity was more pronounced in voles in field enclosures, decreased in voles in cages in the field and was reduced as temperature and, particularly, light was held constant. Under extreme temperature conditions, the emphasis of activity of voles in cages shifted to the milder part of the day.

In the field, factors associated with solar radiation (light vs. dark, twilight and light intensity) produced higher correlations with activity than did other meteorological conditions (temperature, humidity, change in temperature and change in humidity). Voles in activity cages in the field reacted to rainfall while voles in enclosures appeared to be little affected by rain. Physiological limitations to activity (activity occurs in short bursts followed by inactive periods) clearly have a dominant influence on the pattern of daily activity in Microtus pennsylvanicus, and the influence of environmental factors is relatively minor, at least under the conditions of the present study.

Appendix I. Daily activity of voles recorded in activity enclosures in the field, 1966.

Vole	Number of active 6-minute intervals in test period	Percent of time active	Number of active intervals Day Night		Percent of time active Day Night		Statistically significant synchrony	Nocturnal(-) or Diurnal(+)
Winter								
440♀	483	40.2	252	231	55.4	31.0		+
441♂	541	45.1	220	321	48.4	43.0	**	+
101♀	522	43.5	249	273	52.4	37.6	**	+
116♂	406	33.8	265	141	48.6	19.4	**	+
213♀	635	52.9	336	299	64.6	44.0	**	+
215♀	469	<u>39.1</u>	291	178	<u>56.0</u>	<u>26.2</u>		+
	$\bar{x} =$	42.4			54.2	33.5		
Spring								
223♂	500	41.7	364	136	65.0	21.2	**	+
400♀	462	38.5	319	143	56.4	22.4	**	+
232♂	499	41.6	367	132	60.2	22.4	**	+
243♂	372 ¹	<u>38.7</u>	231	141	<u>40.7</u>	<u>36.1</u>		+
	$\bar{x} =$	40.1			53.6	25.3		
Summer								
308♀	548 ¹	45.7	358	190	47.8	42.2		+
312♀	726	60.5	513	213	69.4	46.2		+
335♂	705	58.7	501	204	71.0	41.8		+
407♂	642	<u>53.5</u>	297	345	<u>44.6</u>	<u>64.4</u>	**	-
	$\bar{x} =$	54.6			58.2	48.6		
Autumn								
412♀	552	46.0	359	193	56.0	34.4		+
425♀	620	51.7	344	276	62.6	42.4	**	+
426♂	594	49.5	305	289	55.4	44.4		+
436♂	571	47.6	298	273	60.8	38.4		+
437♀	717	<u>59.7</u>	314	403	<u>64.4</u>	<u>56.8</u>	**	+
	$\bar{x} =$	50.9			59.8	43.3		

¹ = Four-day test period

** = significance at the $P < 0.01$ level

Appendix II. Daily activity of voles recorded in activity cages in the field, winter and spring, 1966.

Vole	Number of active 6-minute intervals in test period	Percent of time active	Number of active intervals Day Night		Percent of time active Day Night		Statistically significant synchrony	Nocturnal(-) or Diurnal(+)
Winter								
December 24-29								
448♂ ¹	155	16.1	44	111	12.1	18.6		-
456♀ ¹	274	28.5	79	195	21.7	32.7		-
452♀	390	32.5	161	229	35.4	30.7		+
454♂	344	28.7	140	204	30.8	27.4		+
257♂	344	<u>28.7</u>	156	188	<u>34.3</u>	<u>25.2</u>	**	+
	$\bar{x} =$	26.9			26.9	26.9		
February 10-14								
216♂	477	39.7	185	292	35.6	42.9	**	-
208♀	488	40.7	157	331	30.2	48.7	**	-
211♂	300	25.0	82	218	15.8	32.1		-
102♂	465	38.8	180	285	34.6	41.9		-
207♀	334	<u>28.7</u>	96	238	<u>18.5</u>	<u>35.0</u>		-
	$\bar{x} =$	34.6			27.0	40.1		
Spring								
March 26-30								
237♂	212	17.7	100	112	16.4	19.0		-
231♀	311	25.9	135	176	22.1	29.8	**	-
234♂	291	24.2	145	146	23.8	24.6		-
236♂	333	27.8	151	182	24.8	30.8	**	-
230♂	328	27.3	209	119	34.3	20.2		+
238♂	225	18.7	122	103	20.0	17.5		+
233♂	341	<u>28.4</u>	198	143	<u>32.5</u>	<u>24.2</u>	**	+
	$\bar{x} =$	24.3			24.8	23.7		
May 7-11								
248♂	403	33.6	257	146	35.5	30.1	**	+
256♀	477	39.7	306	171	42.8	35.3		+
244♀	408	34.0	215	193	30.1	39.8		-
246♀	421	35.1	240	181	33.6	37.3		-
247♂	253	21.1	128	125	17.9	25.8		-
253♂	461	<u>38.4</u>	292	169	<u>40.8</u>	<u>34.8</u>	**	+
	$\bar{x} =$	33.6			33.4	33.8		

¹ = Four-day test period

** = significance at the $P < 0.01$ level

Appendix III. Daily activity of voles recorded in activity cages in the field, summer and autumn, 1966.

Vole	Number of active 6-minute intervals in test period	Percent of time active	Number of active intervals		Percent of time active		Statistically significant synchrony	Nocturnal (-) or Diurnal (+)
			Day	Night	Day	Night		
Summer								
June 7-11								
305q	596	49.7	437	159	58.2	35.3	+	
303q	518	43.2	278	240	37.1	53.3	-	
300q	657	54.7	487	170	64.9	37.7	+	
313s	520	43.3	360	160	48.0	35.6	+	
302q	532	<u>44.5</u>	281	251	<u>37.5</u>	<u>55.8</u>	-	
	$\bar{x} =$	47.1			49.1	43.5		
August 5-9								
351s	360	30.0	186	174	26.4	35.2	-	
333s	558	46.5	258	300	36.6	60.6	**	
346q	460	38.3	289	171	41.0	34.5	+	
322q	615	51.2	253	362	35.9	73.1	**	
343q	448	37.3	228	220	32.3	44.4	-	
342s	446	37.2	229	217	32.5	43.8	**	
312q	513	42.7	266	247	37.7	49.9	-	
354s	428	35.7	232	196	32.9	39.6	**	
50s	254	<u>26.4</u>	157	97	<u>27.8</u>	<u>24.5</u>	+	
	$\bar{x} =$	38.4			33.6	45.1		
Autumn								
September 10-14								
401q	406	33.8	217	189	38.7	29.5	+	
402q	553	46.1	283	270	44.2	48.2	-	
405q	480	40.0	206	274	32.2	48.9	**	
406s	326	27.2	148	178	23.1	31.8	-	
340s	395	32.9	203	192	31.7	34.3	**	
403s	463	38.6	249	214	38.9	38.2	+	
358q	498	<u>41.5</u>	301	197	<u>47.0</u>	<u>35.2</u>	+	
	$\bar{x} =$	37.2			36.5	38.0		
October 19-24								
356q	243	20.2	124	119	22.5	14.6	+	
414q	375	31.3	160	215	29.1	33.1	**	
350s	379	31.6	190	189	34.5	29.1	**	
337s	340	28.3	158	182	28.7	28.0	**	
336s	211	17.6	72	139	13.1	21.4	**	
410q	477	39.7	248	229	45.0	35.2	+	
348s	351	<u>29.2</u>	197	154	<u>35.8</u>	<u>23.6</u>	+	
	$\bar{x} =$	28.3			29.8	26.4		
November 15-19								
424q	219	18.2	83	136	16.9	19.1	-	
438s	366	30.5	134	232	27.3	32.7	-	
433q	302	25.2	104	198	21.1	27.9	**	
432q	271	22.6	118	153	24.1	21.5	**	
435s	149	<u>12.4</u>	66	83	<u>13.5</u>	<u>11.7</u>	+	
	$\bar{x} =$	21.8			20.6	22.6		

Appendix IV. Daily activity of voles recorded in activity cages in the laboratory, seasonal photoperiod and temperature

Vole	Number of active 6-minute intervals in test period	Percent of time active	Number of active intervals		Percent of time active		Statistically significant synchrony	Nocturnal (-) or Diurnal (+)
			Day	Night	Day	Night		

Winter photoperiod - winter temperature

143♂	402	33.5	155	247	31.0	35.2		-
138♂	305	25.4	144	161	28.8	23.0		+
132♀	402	33.5	136	266	27.2	38.0	**	-
135♀	374	31.2	177	197	35.4	28.1	**	+
136♂	291	24.2	160	131	32.0	18.7	**	+
134♀	400	30.0	177	223	35.4	31.8	**	+
141♂	439	<u>36.6</u>	201	238	<u>40.2</u>	<u>34.0</u>		+
		$\bar{x} = 30.6$			<u>32.9</u>	<u>29.8</u>		

Spring photoperiod - spring temperature

230♂	373	31.1	170	203	28.3	33.8	**	-
235♂	214	17.8	90	124	15.0	20.7		-
141♂	203	16.9	84	119	14.0	19.8		-
231♀	381	31.8	134	247	22.3	41.2	**	-
238♂	339	28.2	170	169	28.3	28.2		+
233♂	292	24.3	113	179	18.8	29.8		-
236♂	258	21.5	87	171	14.5	28.4		-
237♂	202	16.8	109	93	18.2	15.4		+
228♂	283	<u>23.6</u>	105	178	<u>17.4</u>	<u>29.6</u>	**	-
		$\bar{x} = 23.6$			<u>19.7</u>	<u>27.4</u>		

Summer photoperiod - summer temperature

326♀	415	34.6	287	128	41.0	25.6	**	+
303♀	166	13.8	50	116	7.1	23.2		-
302♂	226	18.8	83	143	11.9	28.6		-
327♀	638	53.2	452	186	64.6	37.2	**	+
305♂	239	19.9	111	128	15.9	25.6		-
300♀	218	18.2	111	107	15.8	21.4		-
313♂	355	<u>29.6</u>	174	181	<u>24.8</u>	<u>36.2</u>		-
		$\bar{x} = 26.7$			<u>25.9</u>	<u>28.2</u>		

Autumn photoperiod - autumn temperature

410♀	447	37.2	194	253	32.3	42.2		-
414♀	336	28.0	148	188	24.5	31.2		-
348♂	390	32.5	192	198	32.0	33.0		-
337♂	308	25.7	141	167	23.5	27.8	**	-
356♀	207	17.3	84	123	14.0	20.5		-
350♂	445	37.1	228	217	38.0	36.2		+
341♀	274	<u>22.8</u>	100	174	<u>16.7</u>	<u>29.0</u>		-
		$\bar{x} = 29.4$			<u>25.8</u>	<u>31.4</u>		

Appendix V. Daily activity of voles recorded under the seasonal photoperiod - constant temperature regimes.

Vole	Number of active 6 minute intervals in test period	Percent of time active	Number of active intervals Day Night	Percent of time active Day Night	Statistically significant synchrony	Nocturnal(-) or Diurnal(+)
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Winter photoperiod - constant temperature

204♂	470	39.2	172 298	34.4 42.6		-
44♀	202	16.8	54 148	10.8 21.1		-
202♂	302	25.2	140 162	28.0 23.1		+
130♀	173	14.4	52 121	10.4 17.3		-
128♂	240	20.0	79 161	15.8 23.0		-
203♂	338	28.2	150 188	30.0 26.8		+
112♂	224	18.7	70 154	14.0 22.0	**	-
214♀	175	<u>14.6</u>	72 103	<u>14.4</u> <u>14.8</u>		-
		$\bar{x} = 22.1$		19.7 24.5		

Spring photoperiod - constant temperature

247♂	143	11.9	58 85	9.7 14.2		-
256♀	260	21.7	132 128	22.0 21.3		+
253♂	249	20.8	117 132	19.5 22.0		-
244♀	183	15.2	72 111	12.0 18.5		-
f ₁ ?	409	34.1	205 204	34.2 34.0		+
248♂	159	13.2	71 88	11.8 14.6		-
246♀	263	21.9	65 198	10.8 33.0		-
245♀	363	<u>30.2</u>	169 194	<u>28.2</u> <u>32.4</u>		-
		$\bar{x} = 21.1$		18.5 23.7		

Summer photoperiod - constant temperature

312♀	383	31.9	160 223	22.9 44.6		-
f ₁ ?	247	20.6	157 90	22.4 18.0		+
345♂	291	24.3	144 147	20.6 29.4		-
342♂	216	18.0	118 98	16.9 19.6	**	-
322♀	440	36.7	245 195	35.0 39.0	**	-
334♀	320	26.7	162 158	23.2 31.6		-
f ₁ ?	225	18.8	122 103	17.4 20.6	**	-
f ₁ ?	258	21.5	161 97	23.0 19.4	**	+
353♂	265	<u>22.1</u>	119 146	<u>17.0</u> <u>29.2</u>		-
		$\bar{x} = 24.5$		22.1 27.9		

Autumn photoperiod - constant temperature

432♀	264	22.0	113 151	18.8 25.2	**	-
435♂	122	10.2	43 79	7.2 13.2		-
427♀	301	25.1	100 201	16.7 33.5	**	-
438♂	384	32.0	213 171	35.5 28.5	**	+
433♀	232	<u>19.3</u>	110 122	<u>18.3</u> <u>20.3</u>	**	-
		$\bar{x} = 21.7$		19.3 24.1		

Appendix VI. Daily activity of voles recorded under constant light regimes.

Vole	Number of active 6-minute intervals in test period	Percent of time active	Number of active <u>intervals</u>		Percent of time active		Statistically significant synchrony	Nocturnal (-) or Diurnal (+)
			High temp.	Low temp.	High temp.	Low temp.		

Constant light - summer temperature

344♀	381	31.7	134	247	28.8	33.6		-
401♀	339	28.3	133	206	28.6	28.0		+
406♂	168	14.0	75	93	16.1	12.7		+
407♂	476	39.7	241	235	51.8	32.0	**	+
405♀	215	<u>22.4</u>	80	135	<u>21.5</u>	<u>23.0</u>	**	-
		$\bar{x} = 27.2$			29.4	25.9		

Constant light - autumn temperature

456♀	325	27.1	87	238	20.5	30.7		-
454♂	213	17.8	80	133	18.8	17.2		+
455♀	320	26.7	150	170	35.3	21.9		+
453♂	177	14.8	64	113	15.1	14.6		+
443♂	257	<u>21.4</u>	122	135	<u>28.7</u>	<u>17.5</u>		+
		$\bar{x} = 21.6$			23.7	20.4		

Constant light - constant temperature

208♀	253	21.1						
227♀	245	20.4						
206♂	132	11.0						
225♀	156	13.0						
213♀	448	37.3						
226♂	239	19.9						
210♀	214	17.8						
211♂	207	17.2						
224♀	262	<u>21.8</u>						
		$\bar{x} = 19.9$						

Appendix VIII. Synchrony of daily activity in the laboratory and the field.

Season	Month of test	Number of voles	Number with significant synchrony	Level of significance	
				0.05	0.01
Field - Activity Enclosure					
Winter	December, January, February	6	4	-	4
Spring	March, May	4	3	-	3
Summer	June, July, August	4	1	-	1
Autumn	September, October, November	$\frac{5}{19}$	$\frac{2}{10}$	-	$\frac{2}{10}$
Field - Activity Cages					
Winter	December, February	10	3	1	2
Spring	March, May	14	5	2	3
Summer	June, August	14	4	1	3
Autumn	September, October, November	$\frac{19}{57}$	$\frac{8}{20}$	$\frac{2}{6}$	$\frac{6}{14}$
Laboratory - Activity Cage Experimental Condition					
Winter	W. Photo/ W. Temp.	7	4	-	4
	W. Photo/ C. Temp.	8	1	-	1
	C. Light/ C. Temp.	9	-	-	-
Spring	Sp. Photo/ Sp. Temp.	9	3	1	2
	Sp. Photo/ C. Temp.	7	-	-	-
	C. Light/ C. Temp.	-	-	-	-
Summer	Su. Photo/ Su. Temp.	7	2	1	1
	Su. Photo/ C. Temp.	9	3	-	3
	C. Light/ Su. Temp.	5	2	1	1
Autumn	A. Photo/ A. Temp.	7	1	-	1
	A. Photo/ C. Temp.	5	4	3	1
	C. Light/ A. Temp.	$\frac{5}{78}$	$\frac{-}{20}$	$\frac{-}{6}$	$\frac{-}{14}$
Total number of voles tested		154			

Appendix IX. Length of acclimation period and levels of activity and significant synchrony.

Vole	Enclo- sure	Release Date	Test Period	Number of days of acclimation	Level of activity (in per cent)	Level of significant synchrony
101q	1	Jan. 11	Jan. 11-16	1	49.9	*
101q	1	Jan. 11	Jan. 23-28	13	43.5	**
116q	2	Jan. 19	Jan. 23-28	5	33.8	**
213q	1	Feb. 4	Feb. 8-14	4	52.9	**
215q	2	Feb. 6	Feb. 8-14	2	39.1	
223q	2	Feb. 16	Mar. 1-5	13	41.7	**
400q	1	Feb. 16	Mar. 2-6	14	38.5	**
232q	2	Mar. 6	Mar. 26-30	21	41.6	**
243q	1	Apr. 15	May 7-10	21	38.7	
308q	2	June 3	June 7-10	4	45.7	
312q	2	July 14	July 20-26	6	60.5	
335q	2	Aug. 1	Aug. 5-9	4	58.7	
407q	3	Aug. 19	Aug. 27-31	8	53.5	**
412q	2	Aug. 22	Sept. 9-13	18	46.0	
425q	2	Sept. 26	Oct. 17-26	21	51.7	**
426q	3	Oct. 5	Oct. 17-26	12	49.5	
436q	3	Oct. 27	Nov. 14-19	18	47.6	
437q	2	Oct. 27	Nov. 14-19	18	59.7	**
440q	2	Dec. 10	Dec. 24-29	13	40.2	
441q	3	Dec. 12	Dec. 24-29	11	45.1	**

* = significance at the $P < 0.05$ level

** = significance at the $P < 0.01$ level

Appendix X. Correlation coefficients between measured environmental variables and activity of individual voles in field enclosures

1966 Date	Vole	Tempera- ture	Change in Temp.	Humidity	Change in Humid.	Light Intensity	Light vs. Dark	Twilight	Rain- fall	Multiple Correlation Coefficient
Jan. 12-16	101♀	.124	.074	.067	.079	.092	.108	.040	-	.170
Jan. 23-28	101♀	.066	.085	.105	.046	.121	.161	-.030	-	.197
	116♂	.003	-.072	-.152	-.049	.074	.185	.154	-	.310
Feb. 8-14	213♀	.164	.038	.110	-.067	.214	.269	.180	.046	.325
	215♀	.080	.150	-.077	-.032	.185	.234	.083	-.057	.314
Mar. 1-6	223♂	.248	.193	-.013	-.383	.483	.465	.009	-	.524
	400♀	.262	.142	-.105	-.217	.280	.350	.103	-	.395
Mar. 26-30	232♂	.333	.157	.033	-.232	.370	.454	.192	.095	.509
May 7-10	243♂	-.027	-.046	-.056	-.026	.090	.085	.126	-	.220
June 7-10	308♀	.042	.155	.089	.194	-.012	.071	.057	-.096	.248
July 20-26	312♀	.119	.090	.141	-.019	.096	.225	.050	-	.265
Aug. 5-9	335♂	.139	.075	.036	.031	.126	.301	-.021	-.043	.325
Aug. 20-25	407♂	-.189	.021	.003	.141	-.123	-.201	.016	-	.274
Sept. 9-13	412♀	.163	.114	.083	.092	.150	.218	-.023	-	.265
Oct. 17-26	425♀	.184	.025	.102	-.015	.093	.215	.152	.102	.296
	426♂	.155	.121	.047	-.084	.185	.130	.084	.051	.217
Nov. 14-19	436♂	.117	.217	.080	-.072	.356	.251	-.129	-	.386
	437♀	.164	-.010	.042	-.107	.166	.210	.085	-	.228
Dec. 24-29	440♀	.067	-.042	.134	-.0004	.176	.267	.037	-	.306
	441♂	.039	.037	.050	-.001	.091	.051	.086	-	.134

- = No rainfall during test period

Appendix XI. Correlation coefficients between measured environmental variables and activity of voles in field activity cages

1966 Date	No. of Voles	Tempera- ture	Change in Temp.	Humidity	Change in Humid.	Light Intensity	Light vs. Dark	Twilight	Rain- fall	Multiple Correlation Coefficient
Feb. 10-14	5	-.029	.008	-.209	-.044	.003	.105	.125	-.104	.257
Mar. 26-30	7	.110	-.085	.070	.020	.085	.038	.232	.225	.327
May 7-11	6	.127	-.054	-.046	.016	.047	.099	.185	-	.259
June 7-11	5	-.056	.023	-.071	-.005	-.048	.088	.135	-.115	.250
Aug. 5-9	9	-.108	-.051	-.011	.186	-.187	.150	.258	-.145	.351
Sept. 10-14	7	.037	-.196	-.034	-.096	-.027	-.019	.448	-	.471
Oct. 19-24	7	.053	-.148	.013	.089	-.107	.118	.314	.099	.403
Nov. 15-19	5	.139	-.110	.063	-.043	-.020	.047	.330	-	.354
Dec. 24-29	5	.055	-.009	.034	.170	-.005	.038	.188	-	.247

- = No rainfall during test period

Appendix XII. Order of influence of measured environmental factors having a statistically significant effect on the activity of voles in enclosures. (Statistical level= $P < 0.01$)

1966 Date	Vole	Tempera- ture	Change in Temp.	Humidity	Change in Humid.	Light Intensity	Light vs. Dark	Twilight	Rain- fall	Coefficient of Determination
Jan. 12-16+	101q	1	-	-	2	3	-	-	0	2.9
Jan. 23-28	101q	-	-	2	-	-	-	-	0	3.9
	116d	-	4	3	-	-	2	2	0	9.6
Feb. 8-14	213q	3	-	-	-	-	2	2	-	10.5
	215q	-	4	2	-	-	1	3	-	9.9
Mar. 1-6	223d	-	-	-	3	1	2	-	0	27.5
	400q	2	-	-	4	-	1	3	0	15.6
Mar. 26-30	232d	3	-	4	-	-	1	2	-	25.9
May 7-10	243d	4	3	-	-	2	-	1	0	4.8
June 7-10	308q	-	-	-	1	-	2	-	3	6.1
July 20-26	312q	-	-	2	-	-	1	-	-	7.0
Aug. 5-9	335d	2	-	-	-	-	1	-	3	10.5
Aug. 20-25	407d	-	-	2	3	-	1	-	0	7.5
Sept. 9-13	412q	3	-	-	2	-	1	-	0	7.0
Oct. 17-26	425q	3	-	-	-	4	1	2	-	8.8
	426d	-	-	-	-	1	-	2	-	4.7
Nov. 14-19	436d	-	-	-	2	1	-	3	0	14.9
	437q	-	2	-	-	-	1	-	0	5.2
Dec. 24-29+	440q	-	-	-	-	1	-	2	0	9.3
	441d	2	4	3	-	-	1	-	0	1.8

+ = snow cover during test period
 - = no significant effect on activity
 0 = no rainfall during test period

Appendix XIII. Order of influence of measured environmental factors having a statistically significant effect on the activity of voles in field activity cages. (Statistical level = $p < 0.01$)

1966 Date	No. of Voles	Temper- ture	Change in Temp.	Humidity Change in Humid.	Light Intensity vs. Dark	Light vs. Dark	Twilight	Rain- fall	Coefficient of Determination
Feb. 10-14	5	-	-	1	-	-	2	3	6.6
Mar. 26-30	7	3	-	-	-	-	1	2	10.7
May 7-11	6	2	-	3	-	-	1	0	6.7
June 7-11	5	-	-	-	4	3	1	2	6.3
Aug. 5-9	9	-	-	2	-	4	1	3	12.3
Sept. 10-14	7	-	2	-	-	3	1	0	22.2
Oct. 19-24	7	4	-	-	2	3	1	-	16.2
Nov. 15-19	5	2	-	-	-	-	1	0	12.5
Dec. 24-29	5	-	-	2	-	-	1	0	6.1

- = no significant effect on activity
0 = no rainfall during test period

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