THE UNIVERSITY OF MICHIGAN

COLLEGE OF LITERATURE, SCIENCE, AND THE ARTS
Department of Zoology

Final Report

SEASONAL EFFECTS OF LIGHT, TEMPERATURE, AND RADIATION ON ACTIVITY PATTERNS OF THE MEADOW VOLE (MICROTUS PENNSYLVANICUS)

Francis C. Evans

ORA Project 07306

under contract with:

U. S. ATOMIC ENERGY COMMISSION
CHICAGO OPERATIONS OFFICE
CONTRACT NO. AT(11-1)-1486
ARGONNE, ILLINOIS

administered through:

OFFICE OF RESEARCH ADMINISTRATION ANN ARBOR

January 1970

Engn
UMR
1375

TABLE OF CONTENTS

	Page
LIST OF ILLUSTRATIONS	iv
FRONTISPIECE. The meadow vole, Microtus pennsylvanicus Ord.	vi
INTRODUCTION	1
PROCEDURES	2
Field Studies	2
Laboratory Studies	2
Analysis of Data	2
RESULTS	5
Inherent Rhythm of Activity	5
Individuality of Activity Pattern	5
Distribution of Activity	5
Level of Activity	7
Synchrony in Activity Patterns	9
Activity as Measured by Distance Moved	10
Correlation of Activity with Environmental Factors	10
Effects of Confinement and Manipulation of Environmental Conditions on Activity	13
Effects of Additional Food on Activity	13
Effects of a Mate on Activity	13
DISCUSSION AND CONCLUSIONS	15
SUMMARY STATEMENT	17
REFERENCES	18
OTHER ACTIVITIES RELATED TO THIS PROJECT	19
PERSONNEL	20

LIST OF ILLUSTRATIONS

Table

Page

I. A Summary of the Conditions of Confinement and Environmental Regimes Under Which the Locomotory Activity of the Meadow Vole Was Observed, and the Numbers of Voles Tested in Each Category 3

II. Distribution of Activity at Different Times of Day and Year, for Voles Tested in Field Enclosures 7

III. The Level of Activity, as Measured by the Percent of Time Active at Different Times of Day and Year, for Voles Tested in Field Enclosures 9

IV. Minimum Distances Travelled in 24 Hours by Voles Tested in Field Enclosures 10

V. Effect of Extra Food on Distribution and Level of Activity of Voles Tested in Field Enclosures 14

VI. Effect of Mate on Distribution and Level of Activity of Voles Tested in Field Enclosures 14

Figure

1. Daily rhythm of activity in Microtus pennsylvanicus (Male No. 33) tested for five days in a 30-ft diameter field enclosure. 6

2. The percent of total activity concentrated in the daytime (sunrise to sunset) in Microtus pennsylvanicus in field enclosures, in relation to the duration of the natural photoperiod. 8

3. Minimum distances moved in each hour from noon to midnight by Microtus pennsylvanicus (Male No. 512) in a field enclosure, November 10, 1968. 11

4. Minimum distances moved in each hour from midnight to noon by Microtus pennsylvanicus (Male No. 512) in a field enclosure, November 11, 1968. 12



The meadow vole, Microtus pennsylvanicus Ord. Photo by W. J. Graham.

INTRODUCTION

Voles of the genus Microtus are widely distributed throughout North America and Eurasia and and are well-known even to the layman for their cyclic fluctuations in numbers and their frequency as pests in fields and orchards. Unlike many small mammals which are either clearly nocturnal or diurnal in their activity, voles move about in both day and night, but because they are usually concealed in runways through grass and litter the daily pattern of their activity is not at all obvious and has been deduced primarily from casual observation or the indirect evidence of trapping studies. The development of radioactive isotopes and of the means of detecting their presence and measuring their intensity under field conditions has provided a new basis for tracing the movements of such hidden animals and thus for investigating their activity patterns more accurately and extensively than was hitherto possible. The objectives of the project reported here were (1) to perfect a technique for examining the activity patterns of radioactively tagged meadow voles (Microtus pennsylvanicus) under field conditions, (2) to determine the temporal and seasonal features of activity in these animals, and (3) to investigate the effects of light, temperature, and radiation on their activity patterns. The project was intended to resolve the contradictions in published reports on the rhythm of activity in Microtus and to provide a better basis for evaluating the influence of radiation exposure on these and related small mammals.

This project was initiated on May 1, 1965, and terminated on June 30, 1969. Under the supervision of Mr. William J. Graham, field tests of vole activity were begun in June 1965, and continued through January 1967. Laboratory experiments on activity under controlled conditions were started in September 1965, and concluded in December 1966. The results of these studies have been presented in Progress Reports made to the U. S. Atomic Energy Commission in January 1966, February 1967, and April 1968. They formed the basis for Mr. Graham's doctoral dissertation, presented in 1968 to The University of Michigan under the title "Daily Activity Patterns in the Meadow Vole, Microtus Pennsylvanicus." On July 1, 1967, Graham was succeeded as Research Assistant by Mr. Moshe Katznelson, who continued in this capacity until June 1, 1969. Under Mr. Katznelson's supervision, the field testing program was extended and expanded. The present report gives the results of these later investigations and combines them with the earlier work, to reach a series of general conclusions for the study as a whole. However, the reader may find it helpful to refer to Dr. Graham's thesis and to the Progress Report for April 1968, both of which now constitute part of the published record, for description of methods and techniques and for other information which, in the interest of saving space, has not been repeated in this Final Report.

PROCEDURES

FIELD STUDIES

The field studies were carried on in a Kentucky bluegrass (Poa pratensis) meadow at the Matthaei Botanical Gardens of The University of Michigan. Three circular (30-ft diameter) enclosures were established and equipped with detection units to record the activity of individual voles tagged with ^{182}tantalum. The technique and apparatus have been described elsewhere (Graham and Ambrose, 1967) and will not be repeated here. Fifty-seven voles were continuously recorded in these enclosures for periods of five consecutive days each; records were secured at all seasons of the year (Table I).

The enclosure studies were supplemented by records of activity of voles in small (10 in. x 15 in. x 7 in.) cages maintained at the field site and exposed to the natural regimes of light, temperature, and other meteorological variables. Details of cage construction and activity recording have been given by Graham (1968). Fifty-six voles were recorded in these cages for periods comparable with those of voles studied in the enclosures (Table I).

The field environment was monitored for temperature, humidity, light intensity, duration of photoperiod, and time and amount of precipitation. Details of the instruments used are given in Graham (1968).

LABORATORY STUDIES

The laboratory studies were carried out in a Hot Pak controlled environment chamber in The University of Michigan Museum of Zoology, in cages of the same types that were used in the field. Controlled regimes of photoperiod and temperature were established to simulate average seasonal conditions or to maintain one factor at a constant level while varying the other. Details of regimes and recording techniques are given in Graham (1968). Activity records were obtained for seventy-eight voles under these laboratory-controlled conditions (Table I).

ANALYSIS OF DATA

Indices of activity which were used in this study to characterize the pattern of meadow vole activity include:

(1) the distribution of activity over the 24-hr period, as measured by the percent of the total daily activity (total 6-min intervals) occurring at specified times of day and night;

TABLE I

A SUMMARY OF THE CONDITIONS OF CONFINEMENT AND ENVIRONMENTAL REGIMES UNDER WHICH THE LOCOMOTORY ACTIVITY OF THE MEADOW VOLE WAS OBSERVED, AND THE NUMBERS OF VOLES TESTED IN EACH CATEGORY

Confinement	Season	Photoperiod	Temperature	No. of Voles Tested
Field Enclosures	Winter	Natural	Natural	18
	Spring	Natural	Natural	11
	Summer	Natural	Natural	12
	Autumn	Natural	Natural	16
			Total	57
Field Cages	Winter	Natural	Natural	10
	Spring	Natural	Natural	13
	Summer	Natural	Natural	14
	Autumn	Natural	Natural	19
			Total	56
Laboratory Cages	Winter	10 L: 14 D	-4° to +5°	7
		10 L: 14 D	Constant (0°)	8
		Constant	Constant (0°)	9
	Spring	12 L: 12 D	+5° to +14°	9
		12 L: 12 D	Constant (9°)	7
	Summer	14 L: 10 D	+15° to +24°	7
		14 L: 10 D	Constant (19°)	9
		Constant	+15° to +24°	5
	Autumn	12 L: 12 D	+5° to +14°	7
		12 L: 12 D	Constant (9°)	5
		Constant	+5° to +14°	5
			Total	78
			Grand Total	191

(2) the level of activity over a specified period of time, as measured by the percent of that time spent in activity (the percent of total 6-min intervals which were considered active);

(3) the degree of synchrony, or the regularity with which an individual vole's activity periods occurred from day to day, as measured by a comparison of the observed distribution of activity with that expected under the assumption of random occurrence (Graham, 1968: 27); and

(4) the minimum distance moved over a specified time period.

For analysis of the correlation of activity with environmental factors, the records of vole activity and of measured meteorological conditions were compiled for each 6-min interval of the test period. These data were then punched on computer cards and a linear regression analysis was performed by the Regression Analysis Program, The University of Michigan Utility Program, on an IBM 7090 computer.

With the assistance of Dr. Frederick E. Smith a statistical test was designed for determining synchrony of activity (Graham, 1968: 27). This was applied to the activity records of all voles tested in field enclosures in 1966 and to those of five individuals kept in activity cages in each of the field and laboratory test periods.

The accuracy of the technique for locating voles in field enclosures permitted us to determine the position of a resting animal to within 1 ft (Graham and Ambrose, 1967). Positions at successive 6-min intervals throughout the test period were ascertained for selected individuals to determine the minimum distance moved within a specified period, thus providing us with a spatial measure of activity.

RESULTS

INHERENT RHYTHM OF ACTIVITY

Laboratory studies (Davis, 1933) had shown that locomotor activity in Microtus is concentrated in bursts of 1-3 hr duration alternating with intervals of inactivity of similar length. A strong rhythm of this sort was found not only in the voles tested in field enclosures, as illustrated in Fig. 1, but also in those kept in field and laboratory cages. Thus the 24-hr period is typically punctuated by six or seven evenly spaced bursts of activity. This rhythm appears to be physiologically based and so influential as to partially obscure the effects of daily and seasonal differences in photoperiod and other meteorological factors. This study demonstrates that the rhythm is not just an artifact of laboratory confinement, but is a natural and basic feature of the vole's activity pattern.

INDIVIDUALITY OF ACTIVITY PATTERN

There was considerable variation in the activity patterns of the individual voles tested in this study, even among those which were recorded at the same time of year under similar conditions (cf. Graham, 1968, Fig. 14). Despite the inherent rhythm discussed above, there was a wide range in the amount and distribution of activity shown by different individuals on a given day and by the same individual on successive days of a single test period. As a result, the variance about group mean values was high and frequently prevented us from making statistically significant comparisons. To overcome the influence of such individuality would have required larger samples than we were able to secure. Individuality of response is thus a factor of considerable importance in generalizing about activity patterns.

DISTRIBUTION OF ACTIVITY

The 1966 data were grouped as either Daytime (from sunrise to sunset) or Night (from sunset to sunrise) records, and a vole was considered diurnal if the percent of total activity concentrated in the daytime exceeded 50, or nocturnal if the reverse was the case. Voles maintained in field enclosures were predominantly diurnal at all seasons of the year, with an average 60% of activity concentrated during daytime hours (Evans, 1968: 15), and there was evidence of greater diurnality in spring and summer than at other times of the year. The data of subsequent years were further broken down to permit recognition of a Twilight period (2 hr centered around sunset and 2 hr centered around sunrise), and the percents of total activity attributable to daytime and night (exclusive of twilight) and to twilight are presented in this

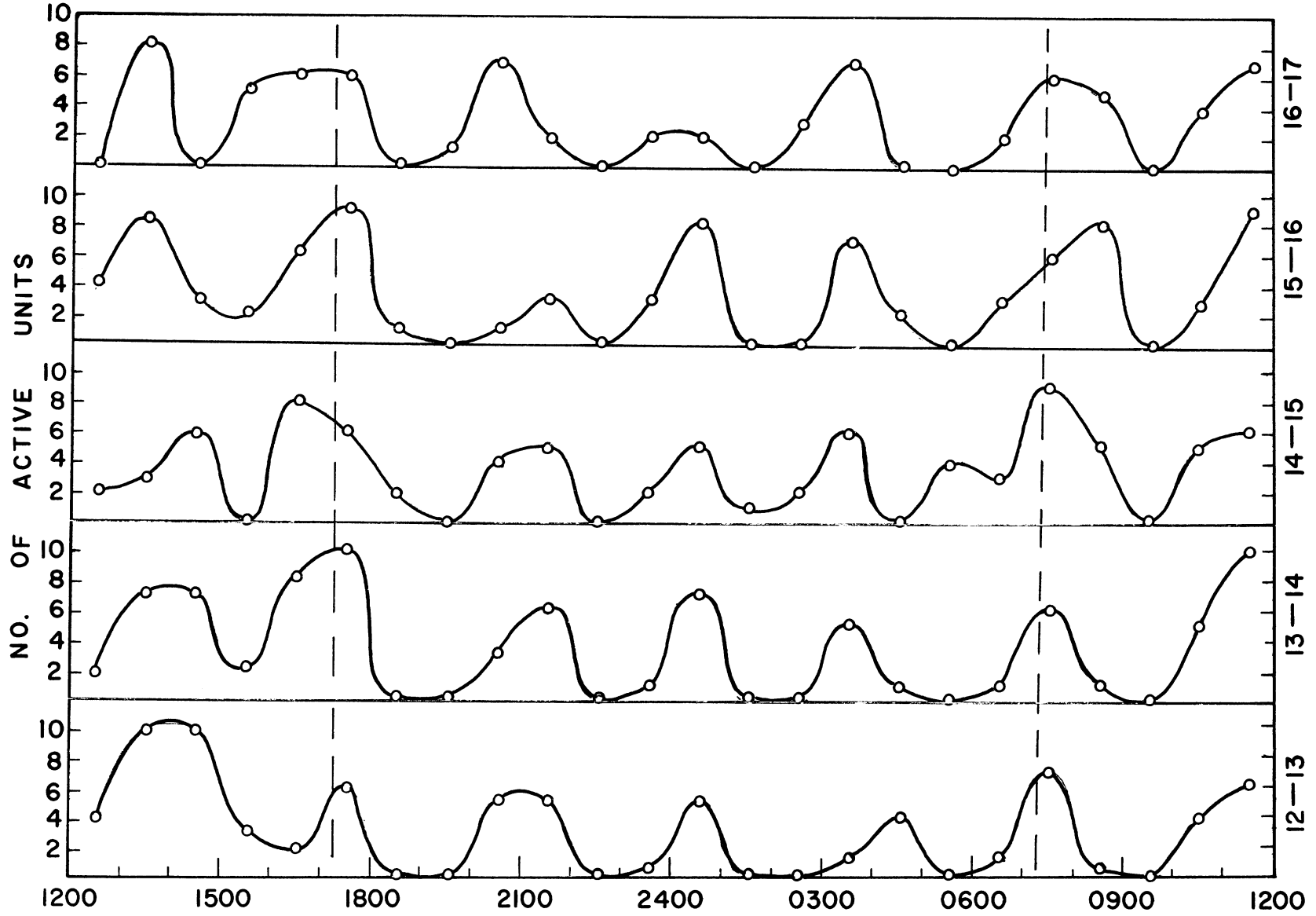


Fig. 1. Daily rhythm of activity in Microtus pennsylvanicus (Male No. 33) tested for five days in a 30-ft diameter field enclosure. The number of active 6-min time units is given for each hour of the day beginning at midnight. Dashed vertical lines indicate the time of sunrise and sunset.

report (Table II). The evidence confirms the earlier picture of predominantly diurnal activity and also suggests a strong crepuscular component in the overall pattern; as illustrated in Fig. 1, there is generally a burst of activity at dawn and another at dusk. Seasonal differences in the distribution of daytime and night activity are also indicated; they would of course be expected under the assumptions of an inherent activity rhythm coupled with a naturally occurring annual change in photoperiod (the relatively unvarying proportion of twilight activity can be attributed to the constant length of the twilight period as defined in this study). Figure 2 superimposes the percentage of total activity occurring in the daytime against the curve for the duration of the natural photoperiod; despite the variation in values, there is some indication that the distribution of activity is influenced by the length of the photoperiod.

TABLE II

DISTRIBUTION OF ACTIVITY AT DIFFERENT TIMES OF DAY AND YEAR, FOR VOLES TESTED IN FIELD ENCLOSURES

Season	No. of Voles Tested	Percent of Total Activity Occurring in		
		Daytime	Night	Twilight
Winter	12	37.2	39.9	22.9
Spring	7	50.3	27.8	21.9
Summer	8	56.0	24.6	19.4
Autumn	11	43.1	34.9	22.0
Entire Year	38	45.2	33.1	21.7

LEVEL OF ACTIVITY

For any given period of time, a vole's level of activity was measured in terms of the percent of the time available that could be classified as active, and levels were compared for different times of day and year and for different conditions of confinement (Graham, 1968: 21; Evans, 1968: 10; this report, Table III). For voles in field enclosures, daytime activity levels were consistently higher than those at night, and maximum activity values were reached at twilight, regardless of season. This consistency broke down under confinement in cages, where the overall level of activity was considerably lower (Graham, 1968: 23) and were night activity was often at a higher level than daytime activity.

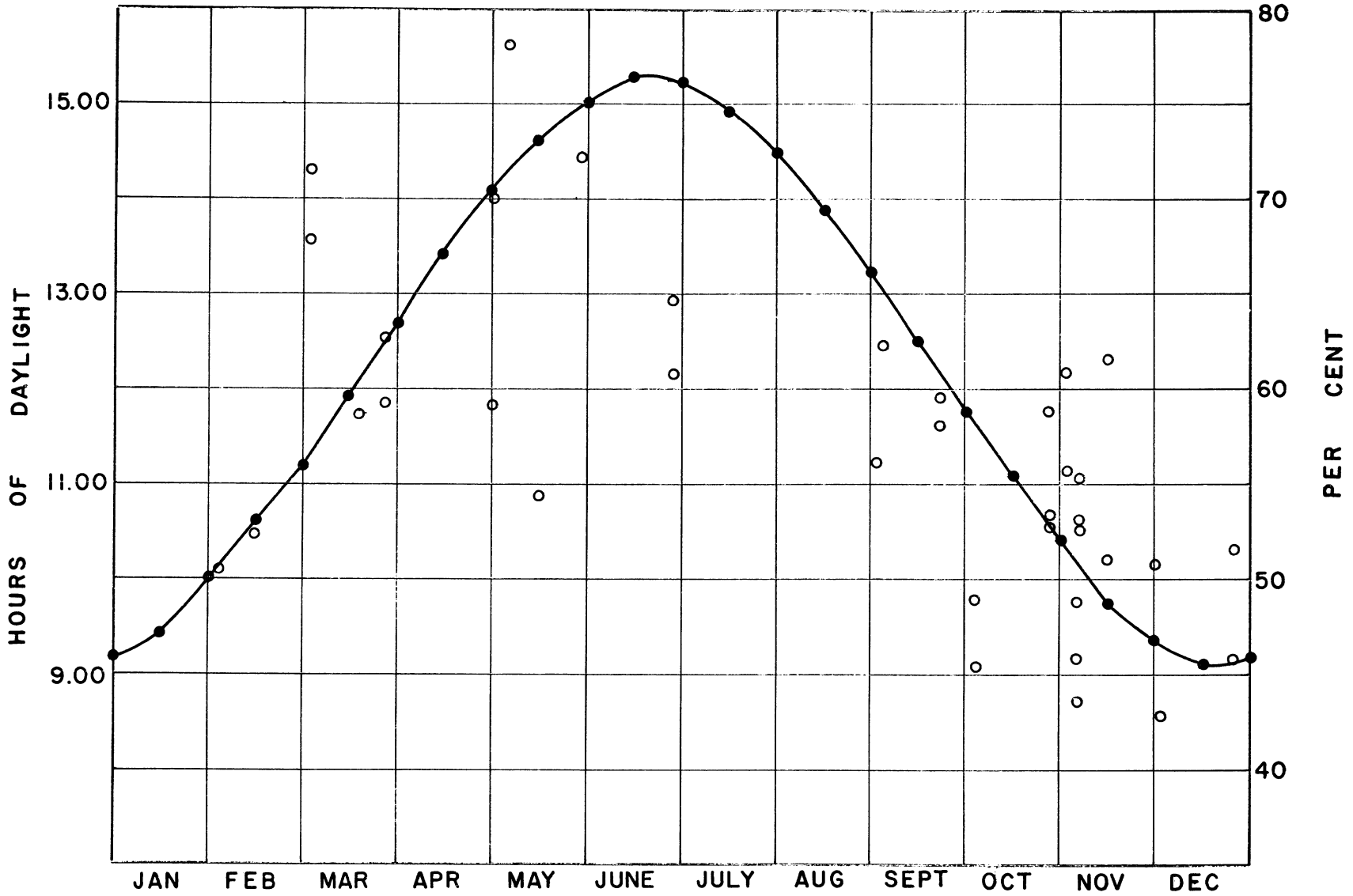


Fig. 2. The percent of total activity concentrated in the daytime (sunrise to sunset) in Microtus pennsylvanicus in field enclosures, in relation to the duration of the natural photoperiod. Hours of daylight can be read on the left-hand side; percent of total activity can be read on the right-hand side. Open circles represent mean values for a five-day test period. Solid circles represent bi-weekly means of the natural photoperiod.

TABLE III

THE LEVEL OF ACTIVITY, AS MEASURED BY THE PERCENT OF TIME ACTIVE AT DIFFERENT TIMES OF DAY AND YEAR, FOR VOLES TESTED IN FIELD ENCLOSURES

Season	No. of Voles Tested	Mean Level of Activity			
		24 hr	Daytime	Night	Twilight
Winter	12	36.7	42.3	28.7	50.5
Spring	7	37.5	47.6	23.9	49.1
Summer	8	36.5	38.8	29.5	42.0
Autumn	11	39.8	43.8	31.5	52.0
Entire Year	38	37.7	42.9	28.7	49.0

Seasonal differences in level of activity for voles in field enclosures (this report, Table III) were not statistically significant, either in the daytime or at night, but for twilight the summer level of activity was significantly lower than that at other seasons.

There was some evidence of a sex difference in the level of activity (Graham, 1968: 46). Females consistently exhibited a higher level of activity than did males in the same test situation.

Differences in the level of activity were consistent with those in the proportions of total activity attributed to different times of day. Voles whose activity was concentrated in the daytime generally had higher levels of activity in the day than at night, thus reinforcing the impression of diurnality. The importance of a twilight period of activity was confirmed by exceptionally high levels of activity observed at that time of day (Table III).

SYNCHRONY IN ACTIVITY PATTERNS

Despite much individuality in activity patterns, voles in field enclosures often exhibited a remarkable degree of day-to-day regularity, with periods of activity and inactivity occurring at approximately the same times of day, as illustrated in Fig. 1. A statistical test to evaluate such synchrony (Graham, 1968: 31) showed a significant tendency to regularity in more than 50% of the voles tested in field enclosures. Day to day regularity is consistent with the finding of a strong inherent physiological rhythm, but it may also be subject to the influence of environmental cues. Although the degree of synchrony achieved under field conditions did not appear to be significantly greater at one season of the year than at another, the laboratory experiments suggest that change in the length of the photoperiod may have some effect in the vole's ability to maintain synchrony (Graham, 1968: 33).

ACTIVITY AS MEASURED BY DISTANCE MOVED

Meadow voles typically have small home ranges and do not travel as extensively as many other small mammals. In the present study, voles permitted to move about freely within 30-ft diameter enclosures were found to travel from 334 to 1220 ft in the course of 24 hr (Table IV). The movements of one animal in each hour of one day and one night are shown in Figs. 3 and 4, in which the nest sight is indicated by a small circle surrounding a dot. Movement was generally in a clockwise direction, with frequent returns to the nest, where the animal rested from time to time for periods of 1-2 hr. The minimum distances travelled allow for numerous (10-40) crossings and recrossings of the animal's home range and thus permit a rather thorough coverage of the entire area.

TABLE IV

MINIMUM DISTANCES TRAVELLED IN 24 HOURS BY VOLES TESTED IN FIELD ENCLOSURES

Vole No. and Sex	Test Period	Minimum Distance (ft) Travelled in 24 Hours	
		Range	Mean
511 ♀	November 10 - 15	529 - 746	662.0
512 ♂	November 10 - 15	634 - 1220	976.5
503 ♂	February 16 - 21	334 - 1023	563.6
5010 ♂	April 27 - May 2	668 - 1007	840.0
12 ♂	September 19 - 24	770 - 924	832.0

CORRELATION OF ACTIVITY WITH ENVIRONMENTAL FACTORS

Correlation of vole activity was sought with respect to associated measurements of light, temperature, precipitation and humidity, and to changes in the magnitude or intensity of these factors. For voles in enclosures, the strongest positive correlations of activity were with light and temperature (Graham, 1968: 65), and there was a generally negative correlation with humidity. A high positive correlation of activity with twilight was shown by field-caged animals, and light factors in general produced more real effect on the activity of voles than did temperature and/or humidity. The effect of environmental factors on vole activity varied through the year, but at no time did they account for more than 30% of the variation in daily activity (Graham, 1968: 68), and it appears that the strong physiologically-based rhythm referred to above tended to obscure the influence of meteorological conditions on the activity pattern.

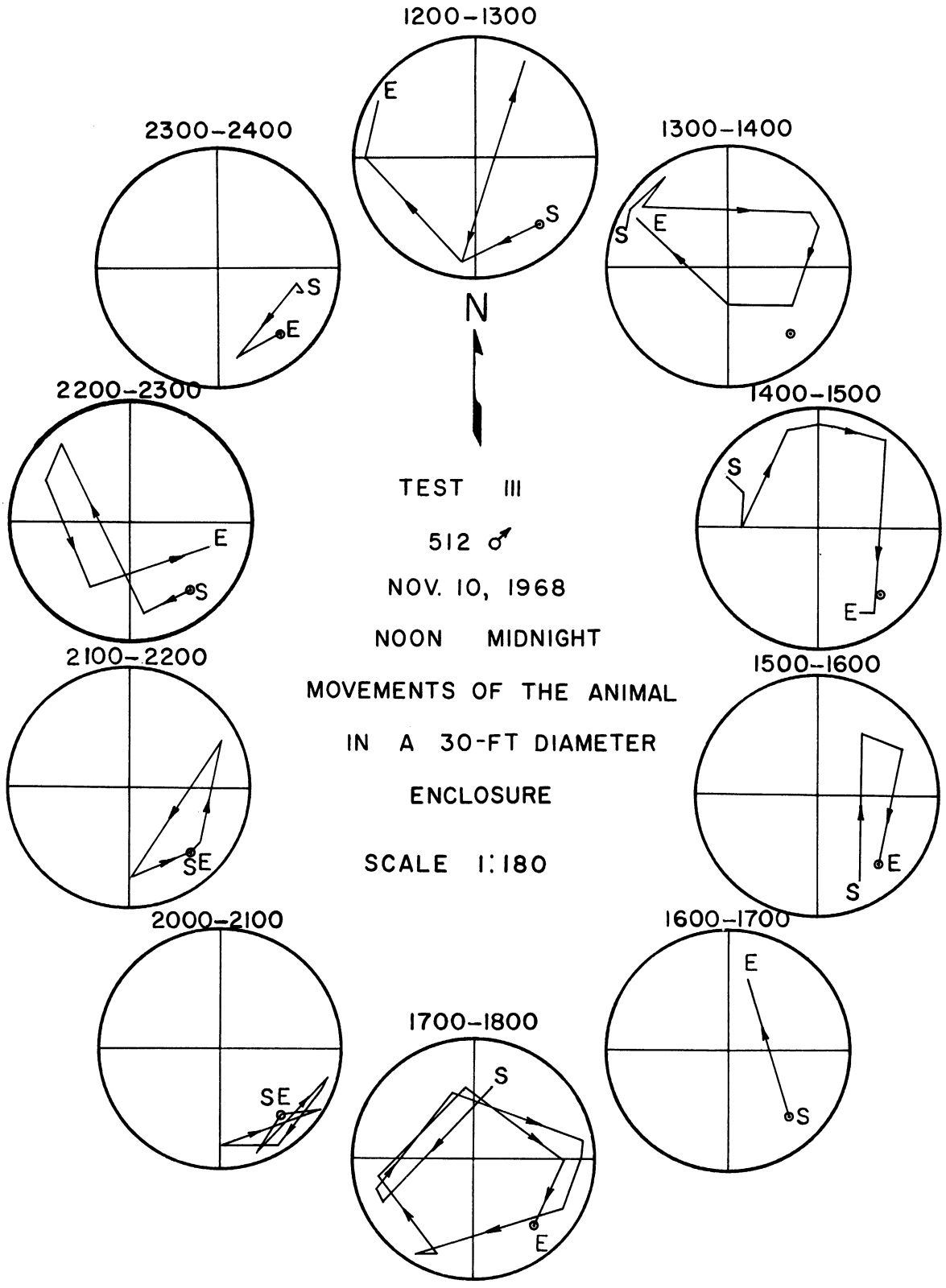


Fig. 3. Minimum distances moved in each hour from noon to midnight by Microtus pennsylvanicus (Male No. 512) in a field enclosure, November 10, 1968. The circled dot indicates the location of the nest. Position at the start of the hour is indicated by S, that at the end of the hour by E. Arrows indicate the direction of movement.

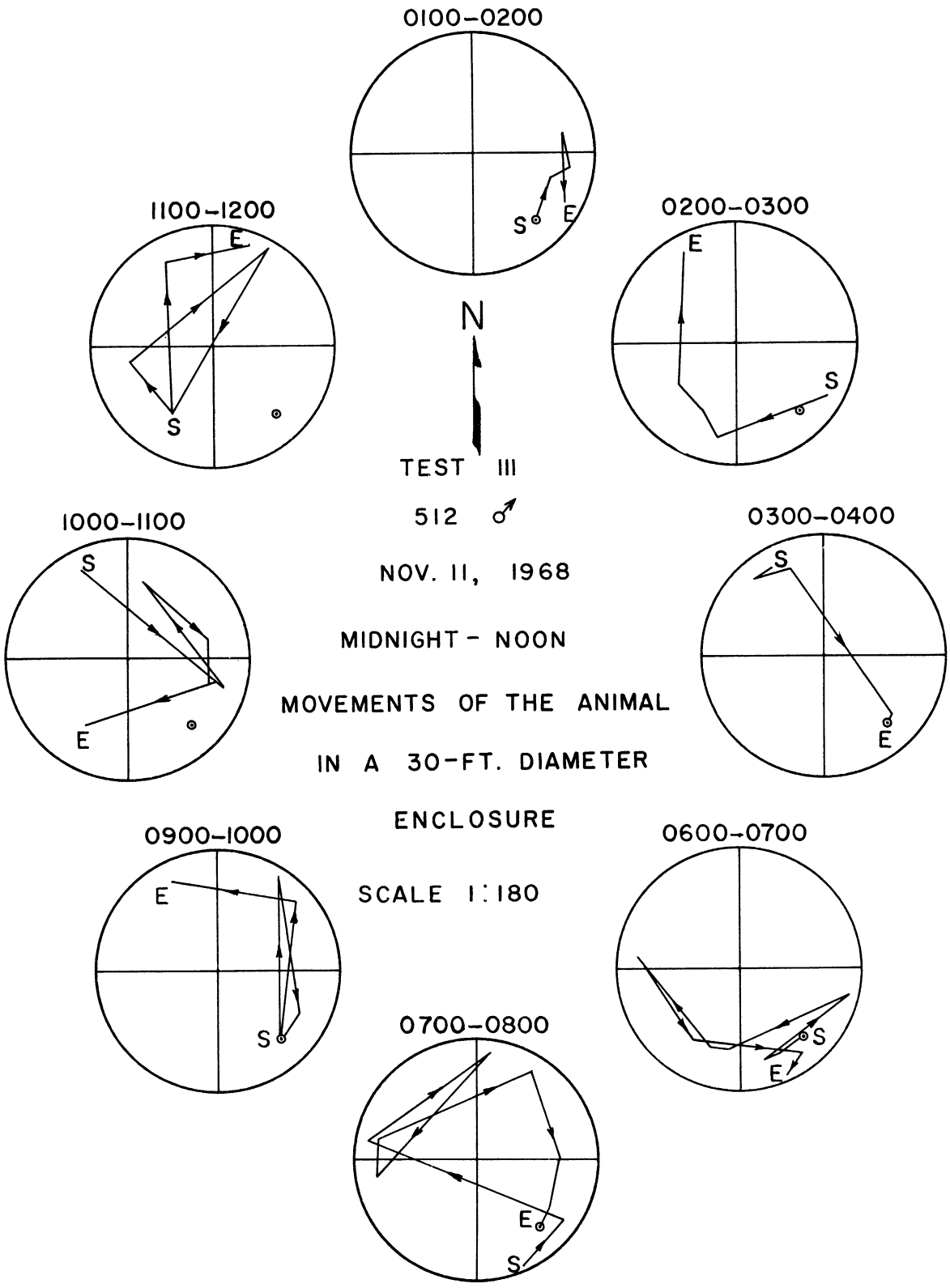


Fig. 4. Minimum distances moved in each hour from midnight to noon by Microtus pennsylvanicus (Male No. 512) in a field enclosure, November 11, 1968. The circled dot indicated the location of the nest. Position at the start of the hour is indicated by S, that at the end of the hour by E. Arrows indicate the direction of movement.

EFFECTS OF CONFINEMENT AND MANIPULATION OF ENVIRONMENTAL CONDITIONS ON ACTIVITY

Voles confined to cages in the field were less clearly diurnal than those permitted to move about in enclosures (Evans, 1968: 15). Field-caged voles concentrated more of their activity in the daytime than at night in spring and summer, but less in autumn and winter. Their activity levels were also generally lower than those of animals kept in enclosures, and they showed less pronounced synchrony in their day-to-day patterns. These effects were even more striking in the laboratory-caged voles. The latter were generally predominantly nocturnal and displayed the lowest levels of activity observed; in the laboratory, the level of activity tended to decrease as light and/or temperature were held constant. Synchrony under laboratory conditions was also reduced, and none of the voles subjected to continuous light and constant temperature was able to maintain a regular activity pattern (Graham, 1968: 34).

EFFECTS OF ADDITIONAL FOOD ON ACTIVITY

Four reciprocal tests were carried out on voles in enclosures, in which animals were first provided with additional food rations (rolled oats) throughout the experimental period and were then subsequently tested for the same length of time without extra food. Table V presents the results of these comparisons. The presence of additional food did not significantly alter the diurnal distribution of activity, but it did result in slightly but consistently lower levels of activity. With less need to search for food, voles tended to reduce the amount of their activity.

EFFECTS OF A MATE ON ACTIVITY

Six radioactively-tagged voles were tested in enclosures in the presence of untagged mates to determine the influence of the latter on the activity pattern. Table VI compares the results of these tests with those of six similar individuals tested without mates. Animals provided with a mate throughout the test period showed consistently higher levels of activity than those maintained singly. The difference in levels was most pronounced during the daytime. However, when a mate was present, less of the total activity was concentrated in the daytime, i.e., the vole was not so clearly diurnal. Thus the presence of a mate appeared not only to increase the level of activity but also to modify its timing, causing a reduction in diurnality.

TABLE V

EFFECT OF EXTRA FOOD ON DISTRIBUTION AND LEVEL OF ACTIVITY
OF VOLES TESTED IN FIELD ENCLOSURES

Vole No. and Sex	Date of Test	Mean Level of Activity (Percent of Time Active)			Percent of Activity Concentrated in Daytime
		24 hr	Daytime	Night	
		Animals Provided with Extra Food			
511 ♀	8/30- 9/6	31.0	36.5	24.4	62.1
512 ♂	10/30-11/6	24.6	31.2	19.5	55.8
511 ♀	11/10-11/16	25.8	39.7	15.8	64.2
503 ♂	2/5 - 2/11	25.2	29.5	21.9	50.6
MEANS		26.6	34.2	20.4	58.2
		Animals Not Provided with Extra Food			
512 ♂	8/31- 9/7	33.9	36.0	31.5	56.7
511 ♀	10/30-11/6	32.6	45.3	22.5	61.0
512 ♂	11/10-11/16	29.1	35.5	24.5	51.1
503 ♂	2/16- 2/22	28.0	33.6	23.6	52.7
MEANS		30.9	37.6	25.5	55.4

TABLE VI

EFFECT OF MATE ON DISTRIBUTION AND LEVEL OF ACTIVITY
OF VOLES TESTED IN FIELD ENCLOSURES

Vole No. and Sex	Date of Test	Mean Level of Activity (Percent of Time Active)			Percent of Activity Concentrated in Daytime
		24 hr	Daytime	Night	
		Animal Accompanied by Mate			
503 ♂	3/5 - 3/12	49.1	69.6	30.4	67.9
30 ♂	10/22-10/27	40.0	48.4	33.5	52.8
35 ♂	11/5 -11/9	38.7	40.5	37.5	43.6
35 ♂	11/12-11/17	42.9	54.0	35.0	52.5
40 ♂	11/29-12/5	37.5	48.8	30.3	50.7
45 ♂	12/22-12/27	37.4	51.1	29.2	51.7
MEANS		41.0	52.1	32.7	53.2
		Animal Unaccompanied by Mate			
512 ♂	8/31- 9/7	33.9	36.0	31.5	56.7
511 ♀	10/30-11/6	32.6	45.3	22.5	61.0
512 ♂	11/10-11/16	29.1	35.5	24.5	51.1
503 ♂	2/16- 3/11	28.0	33.6	23.6	52.7
10 ♀	3/5 - 3/11	37.7	55.9	21.0	71.5
5010 ♂	4/27- 5/2	32.6	33.1	31.8	59.1
MEANS		32.3	39.9	25.8	58.7

DISCUSSION AND CONCLUSIONS

These studies confirm the existence of a strong rhythm in the activity pattern of the meadow vole, punctuated by bursts of activity of 1-3 hr each alternating with rest periods of similar length, and demonstrate that the regularity occurs not only under laboratory conditions but also in the relatively unconfined situation of a 30-ft diameter enclosure in the field. Such a rhythm might well be expected in a grazing herbivorous animal which does not cache its food and which, because of its small size, can ingest only a limited amount at any one time. When excess food was added experimentally, the vole's level of activity was lowered but the pattern of activity was not otherwise affected. This apparently physiologically based rhythm persisted under both natural and induced variations in meteorological conditions, and tended to obscure the effects of light, temperature, humidity, and other factors on the activity pattern.

Most previous studies of activity in meadow voles and related rodents have been limited to observations of small numbers of individuals. Although the present project employed larger samples, even these frequently proved insufficient to handle the effect of variability in activity that was found from individual to individual and from day to day in the same vole, so that group comparisons at desirable statistical levels were not always possible. The large individual differences demonstrated by this study may explain some of the divergence in published opinions about the activity patterns of small mammals and suggest the exercise of caution in generalizing from limited observations. Nevertheless, we believe our investigations warrant the following conclusions.

1. Under field conditions, the meadow vole has a fundamental, rhythmic pattern of daily activity marked by alternating periods of rest and action. Six or seven periods of activity occur in each 24-hr cycle, and there is generally a burst of activity at dawn and another at dusk. The vole has, on the average, a higher level of activity in the daytime than at night, and more of its total activity is concentrated in the daylight hours, so that it may be said to have a definite tendency towards diurnality, though its daily pattern also has a strong crepuscular component.

2. Seasonal differences in activity were observed but were not as striking as had been anticipated. In summer, voles spent more of the available time in moving about and less in resting, and the greater proportion of their activity occurred during the daytime. In winter, their level of activity was reduced and movement was more evenly distributed between day and night. These seasonal differences were most pronounced in voles maintained in field enclosures, where they were most fully exposed to natural seasonal changes. On the whole, though, the daily activity pattern remained remarkably constant from season to

season and did not respond substantially to changes in either climate or vegetational cover or food supply.

3. In field enclosures, vole activity generally showed a positive correlation with length of photoperiod, with light intensity, and with temperature up to 85°F, and a negative correlation with humidity, especially in the spring. These correlations were not strong, however, and at no time did the variability in climatic factors account for more than 30% of the variability in activity. Correlation of activity with changes in environment may have been more or less hidden by the voles' underlying short-term rhythm, but in any case meteorological factors did not appear to be the primary influence in determining the nature of the activity pattern.

4. Confinement to small spaces and subjection to artificial environmental conditions were shown to have significant effects on the pattern of activity. Restriction of movement to cages results in an overall reduction in the amount of activity, in less activity being concentrated in the daytime, and in less synchrony in the timing of activity bursts. The activity pattern can be further broken down under the stresses of continuous light and constant temperature, resulting in a very low level of activity and virtually complete loss of synchrony. These results suggest that the study of activity in laboratory cages does not provide an adequate basis for evaluating natural activity patterns.

SUMMARY STATEMENT

Use of a continuously rotated scintillation probe to detect the position of radioactively tagged meadow voles (Microtus pennsylvanicus) has been shown to be a feasible and accurate method of recording small mammal activity in field enclosures. The technique has permitted the observation of individual animals at all times of year and has yielded a better characterization of vole activity than had previously been available.

The meadow vole has been shown to possess a strong rhythm in its activity, with about six or seven 1-3-hr periods in the course of the 24-hr cycle, so adjusted that one period usually occurs at dawn and one at dusk. It is on the whole a diurnal animal, with generally higher levels of activity in the daytime than at night and with more of its total activity concentrated between sunrise and sunset. Seasonal adjustments occur, with a reduction in activity level and a more even day-and-night distribution of activity in winter. Correlation of activity with length of photoperiod, light intensity, and temperature was weak, however, and in general meteorological factors did not seem to have major effects in modifying the pattern of activity. Confinement to cages results in a marked reduction in activity, in more nocturnal behavior, and in less synchrony in the timing of activity bursts. When caged under conditions of continuous light and constant temperature, a vole may show a very low level of activity and complete loss of synchrony.

REFERENCES

Davis, D.H.S. 1933. Rhythmic activity in the short-tailed vole (Microtus). J. Anim. Ecol. 2: 232-238.

Evans, Francis C. 1968. Seasonal effects of light, temperature and radiation on activity patterns of the meadow vole (Microtus pennsylvanicus). Progress Report, May 1, 1967 - April 30, 1968. Office of Research Administration, The University of Michigan, Ann Arbor, Project 07306.

Evans, F. C. and M. Katznelson. 1969. Activity patterns in the meadow vole, Microtus pennsylvanicus Ord, under field conditions. Bull. Ecol. Soc. Am. 50(2): 106. (Abstract)

Graham, W. J. 1968. Daily activity patterns in the meadow vole, Microtus pennyslvanicus. Ph.D. dissertation, The University of Michigan. University Microfilms, Ann Arbor, No. 68-13-315. 98 pp.

_____ and H. W. Ambrose. 1967. A technique for continuously locating small mammals in field enclosures. J. Mammalogy, 48: 639-642.

OTHER ACTIVITIES RELATED TO THIS PROJECT

On June 20-24, 1965, W. J. Graham attended the Annual Meeting of the American Society of Mammalogists in Winnipeg, Manitoba and presented a preliminary report on the project and its objectives. In November 1965, the project was discussed with Dr. L. L. Getz at the University of Connecticut and with Dr. D. Q. Thompson and Mr. H. W. Ambrose at Cornell University.

On June 12-16, 1966, W. J. Graham attended the Mammalogists Society meeting at Long Beach, California, and gave a paper on the technique for locating small mammals in field enclosures.

Visits to the site of the project were arranged in connection with the Second National Symposium on Radioecology, held at Ann Arbor, Michigan, May 15-17, 1967. The Principal Investigator served as Co-chairman of the Committee to organize the Symposium and was Editor, with D. J. Nelson, of its Proceedings, which were published in March 1969.

On August 17-22, 1969, the Principal Investigator attended the Annual Meeting of the Ecological Society of America held at Burlington, Vermont, and presented a report on the field and laboratory data available at that time.

PERSONNEL

The following persons have assisted with the work of this project:

William J. Graham, Research Assistant, full-time, July 1, 1965 to August 31, 1967.

Moshe Katznelson, Research Assistant, full-time, July 1, 1967 to May 31, 1969.

Assistance in transcribing data and punching cards for computer analysis was given by Carol J. Bershad, Margaret Cockrell, Bertie C. Lawlor, James McCammon, Roderick T. Roscoe, and Shirley A. Stevens.

Grateful acknowledgment is also made to the Matthaei Botanical Gardens of The University of Michigan for permission to carry out the field studies and to The University of Michigan Museum of Zoology for the use of a controlled-environment chamber.

UNIVERSITY OF MICHIGAN
3 9015 02827 3079