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A study of Activity in the Water Vole *Arvicola terrestris*

A dissertation submitted by M. J. Duckett B.Sc. Hons. (Wales) to the University of Durham, as part of the requirements for the degree of Master of Science.

Department of Zoology
University Science Laboratories
South Road
Durham.

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INTRODUCTION

1. AIMS AND SCOPE OF STUDY

The impression had been gained from both literature and personal sources that the water vole *Arvicola terrestris* was more diurnal than many other species of small British rodents. The object of this study was to discover the major period of water vole activity and to examine its change over the seasons as far as possible, to compare the pattern found with that known for other small rodents, particularly close relatives, and to consider if any of the differences could be attributed to any ecological factor.

Barrett-Hamilton (1911) considers the water vole to be diurnal. Van Wijngaarden (1954) has analysed trapping results and found maximum activity at 21.00 rapidly dropping overnight and then steadily rising from 04.00 to 21.00. Worall reported by Southern (1964) believes maximum activity to be at dusk. Corbet (1966) records water voles as being diurnal or crepuscular. Ashby et al (1969) have observed water voles in the field over 24 hour periods and consider activity to be evenly distributed over the whole day. In this study, which was carried out close to Ashby's (1969) study area it has been shown that while considerable individual variation exists, the general tendency is for maximum activity to occur at night. The field data suggest that water voles may be almost completely nocturnal, while laboratory data indicate a substantial amount of diurnal activity with a series of maxima after dark. A reason for this difference is suggested.

This study covers the effects of day length on the activity of water voles in the laboratory, a consideration of a possible relationship between the amount of food eaten daily and the amount of activity shown daily, and the effect of the two sexes on the activity of each other. Information is also given on the possible effects of other factors, particularly light intensity, temperature and humidity; these have not been closely examined. The field study covers the general distribution of daily activity outside the burrow at two different areas for the months of June and July. These field data are only relevant to the summer months, and other times of the year still require investigation. It has not been possible to obtain a clear picture of the differences between the sexes as only two females were acquired. The differences found are recorded, but generally the activity of the females was within the range of variation shown by the males. Exhaustive trials of the apparatus were not possible and thus potential improvements have not been considered.

2. A REVIEW OF THE LITERATURE CONCERNING THE ECOLOGY AND BEHAVIOUR OF THE WATER VOLE

The water vole has never been of economic importance in Britain and there is little detailed published work in the English language. In Holland it is a pest, causing damage to dykes and fields of cultivated bulbs; Van Wijngaarden (1954) has extensively covered the biology and control of the animal in that country. The natural history of the animal in Britain has been described by Barrett-Hamilton (1911), Ryder (1962), Southern (1964) and Corbet (1966). Brief notes have been published by Dean (1947) on their above-ground habits and by Stoddart (1965) on overwintering. One important difference in the British and continental varieties appears to be the greater dependence on water of the former. However, Ashby & Crawley (1967) report having trapped two animals at some distance from water. On Reed's Island in the Humber, the voles are found to be almost entirely terrestrial (Southern & Crowcroft 1956). Most watercourses in Britain appear to be colonised by water voles but their preference is for steep banks and a constant water depth of over half a meter. Burrows are frequently constructed below trees, the roots of which conceal entrances at water level. Food appears to be almost entirely vegetable, but instances of animal food being taken have been recorded by Barrett-Hamilton (1911), Ryder (1962), Southern (1964) and Corbet (1966). The adaptation to an amphibious mode of life would appear to reduce predation (Barrett-Hamilton 1911), but the above authors have recorded water voles as being preyed upon by most of the usual small mammal predators, with the pike *Esox lucius* and the heron *Ardea cinerea* in addition. Possible competition is limited to the brown rat *Rattus norvegicus* and possibly the mole *Talpa europea*, but an overlap in habitats would appear to be minimal in both cases. This is interesting in that on Reed's Island, both the brown rat and the mole are absent (Southern & Crowcroft 1956). The home range of water voles has been studied by Worall (1964) who reports that dispersal appears to be very restricted. Perry (1943) has studied reproduction in the species. In Russia, study of water voles has been more extensive as they are a major source of the bacillus of tularaemia. Panteleev (1962) has described their changes in habitat throughout the year and Nikolaev & Chertova (1962) have related activity to certain aspects of weather.

3. ACTIVITY IN SMALL MAMMALS

The activity of small mammals has been studied extensively from behavioural, phynological and ecological standpoints, and these have been reviewed by Harker (1958) and Cloudsley-Thompson (1961). The nocturnal or diurnal preference of small mammals range from the very nocturnal, through those which have no preference, to the very diurnal, examples of which are the golden hamster *Mesocricetus auratus* (Cloudsley-Thompson 1961), the guinea pig *Cavia porcellus* (Nicholls 1922) and the ground squirrel *Citellus suslica* (Kalabukov 1940) respectively. Among mice and voles *Apodemus sylvaticus* (Elton et al 1931, Miller 1955, Brown 1956), *Rattus norvegicus* (Chitty & Shorten 1946) and various species of *Peromyscus* (Johnson 1926, and Hatfield 1940) show little diurnal activity. *Mus musculus* is less rigid in its behaviour according to Chitty & Southern (1954). Pearson (1962)and Miller (1955) showed 50 - 60% diurnal activity in *Clethrionomys glareolus*, but Saint-Girons (1960a,b) only attained comparable figures with females. Activity in the males did not exceed 30% in the daylight period. Pearson (1962) found females to be more diurnal than males in *Clethrionomys glareolus* but in *Clethrionomys rufocanus* this was reversed. *Microtus* is usually considered to be closely related to *Arvicola* (Barrett-Hamilton 1911, Corbet 1966). Its degree of nocturnal preference appears to vary more from season to season and from species to species than *Clethrionomys*. Davis (1933) and Brown (1956) found a slight nocturnal preference in *Microtus* agrestis as did Calhoun (1945) with Microtus ochogaster. Hatfield (1940) found Microtus californicus to show little activity during the daylight. Hamilton (1937), however, showed Microtus pennsylvanicus to have peaks of activity a few hours after dawn and a few hours before dusk. Erikinaro (1961) considers Microtus agrestis to show maximum activity at night in summer, and in the afternoon in winter.

A subsidiary rhythm of activity often associated with feeding, and recurring every two to three hours, is accepted as being typical of small mammals. This was first suggested by Elton et al (1931), and shown by Davis (1933) for Microtus. It has since been demonstrated for Peromyscus by Hatfield (1940), for Mus by Chitty & Southern (1954), for Apodemus by Miller (1955), for the varying lemming Dicrostonyx groenlandicus by Hansen (1957), Clethrionomys Saint-Girons (1960a,b) and Pearson (1962) and for the three British shrews by Crwocroft (1954). The rhythm appears to vary from three-quarters of an hour in Mus, to four hours in Rattus (Richter 1927).

A bimodal distribution of nocturnal activity is popularly referred to in relation to small rodents. Elton et al (1931) and Miller (1955) consider it to be the visible effect of a nocturnal habit on the "short term feeding rhythm". Erikinaro (1961) was only able to detect this in Clethrionomys in the spring and autumn months.

LABORATORY STUDY

1. METHODS

(1) Trapping and Maintenance

Voles were trapped on the west bank of the River Wear, Co. Durham, about 70-300 metres upstream from the junction with the Old Durham Beck where the study of Ashby et al (1969) was carried out; grid reference NZ 285420. In the week starting 3 March three male water voles (M1, M2, M3) and one female (F4) were caught using traps of a type designed by Lockie (1966) for weasles Mustela nivalis and baited with apple. During the last week in April, four more males (M6, M8, M9, M10) and two females F5, F7) were caught. One of these (F5) escaped shortly after and a male (M10) died after two days in captivity. The latter was never aggressive and appeared to be in a relatively poor condition when caught.

During the experimental period from 5 May till 18 July the animals were kept on Diet S.G.1 devised by Short & Gamage (1959) as an improvement on Diet 18. Worall (1963) has successfully used the latter for water voles. Water was supplied as required by the dropper method. Vegetable food was not given since it had been noticed early on that this was always removed to the nest within quarter of an hour of being given, and might have affected the results. This also allowed an estimate to be made of the amount of food being eaten by each animal under the different experimental conditions. The bedding was a mixture of cotton wool and wood wool. Between experimental periods the voles were housed in simple cages (21 x 26 x 40cu.cms). No attempt was made to tame the animals and no evidence of tameness was noted. No illness was noticed in the period of investigation and all animals were alive ten days afterwards.

(ii) Review of methods used in other work

A number of different methods are available for measuring activity in the laboratory. These have been reviewed by Kalabukov (1940). There are three types of method frequently used for rodents. Wheel cages recording the number of revolutions have been used by Shirley (1928a,b), Slonaker (1928), and Brownman (1943). Shirley (1928a) has shown the consistency of the method. Johnson (1926), Davis (1933) and Saint-Girons (1960a,b) used actographs which are recording devices sensitive to all movements of a suspended cage. These may be mechanical, electrical or pneumatic (Nicholls 1922 and Iverson et al 1967) in principle. A third type is to have a make-brake circuit controlled by a treddle or wire placed in a restricted place between feeding cage and nest box. Crowcroft (1954) found that for shrews such positioning of the 'switch' is unnecessary, and that results were similar wherever it was placed in the cage. Hatfield (1940), Miller (1955), Orr (1959), Erikinaro (1961) and Pearson (1962) have also used this method. Chitty & Southern (1954) had the 'switch' attached to a feeding station to study feeding activity in Mus.

An actograph, unless dampened, will record such activity as fidgeting and scratching as well as locomotory activity. One advantage of this type of apparatus is that it gives an absolute value for activity rather than a relative index. The wheel method is open to several criticisms. The most important being that it may encourage activity of a meaningless nature. Secondly it may not be expected to measure activity associated with feeding, since feeding boxes are usually attached to the axle of the cage. Thirdly as Kalabukov (1940) points out the measure of activity which is given by the number of turns of the wheel is not directly related to time since it will depend in part on the speed at which the animal moves. Calhoun (1945) used both actograph and wheel in the same apparatus. His results from the two sections of the apparatus were different for *Microtus ochogaster* but the same in *Sigmodon hispidus*. He considered he was examining feeding activity and spontaneous activity separately, but one might expect the actograph to record all types of activity including a spontaneous element. The 'switch' method will only give an index of activity and attempts to interpret in absolute terms should only be accepted when checked against an actograph. It might be expected that spontaneous activity will not be recorded. However, the fact that positioning is not important for reproducable results (Crowcroft 1954) suggests that a constant preportion of all activity is recorded.

The selection of method would depend on the type of study involved. For comparison with field results the wheel is unsatisfactory for reasons given above. Both actograph and 'switch' methods can be modified to measure nest and external activity separately. This is important since field methods are not usually concerned with nest or burrow activity. The accuracy of comparisons between this type of apparatus and field conditions have not yet been determined.

(iii) The apparatus and techniques used in this study

The apparatus used in this study which is shown in Fig.I and Plate I is of the 'switch' type. Each vole had two cages (16 x 22 x 37cu.cms) joined together by a steel run (5 x 8 x 124cu.cms), the latter was covered with ½cm square mesh. One cage was filled with nesting material, food and water were available in the other. Two units of four such systems were used. Neighbouring cages in each unit were separated by tinplate. The animals were thus unable to see each other, the tinplate also cut down auditory and olfactory communication. To further discourage any interaction, each unit was arranged so that nesting cages alternated with feeding cages. A wire 'switch' mechanism Fig.II was inserted in the centre of the run. In the case of the female voles a crush was also placed in the run at this point reducing its width by 1cm either side of the switch. This modification was considered essential from initial trials of the apparatus. The 'switches' were wired to "Rustrak" recorders.

Fig.I.

A UNIT OF APPARATUS FOR MEASURING ACTIVITY IN FOUR VOLES.

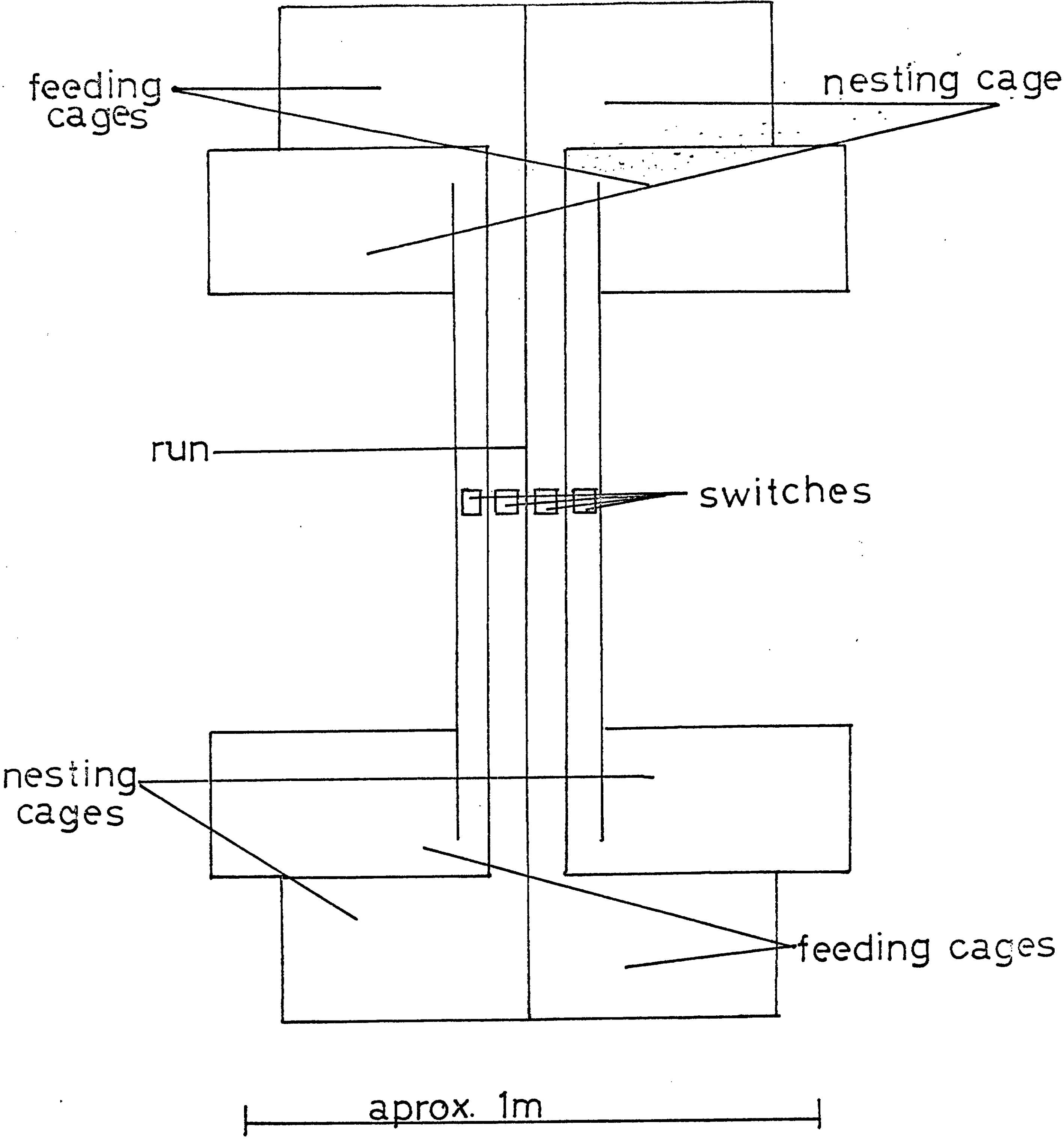


PLATE I

Apparatus used in the laboratory part of this study

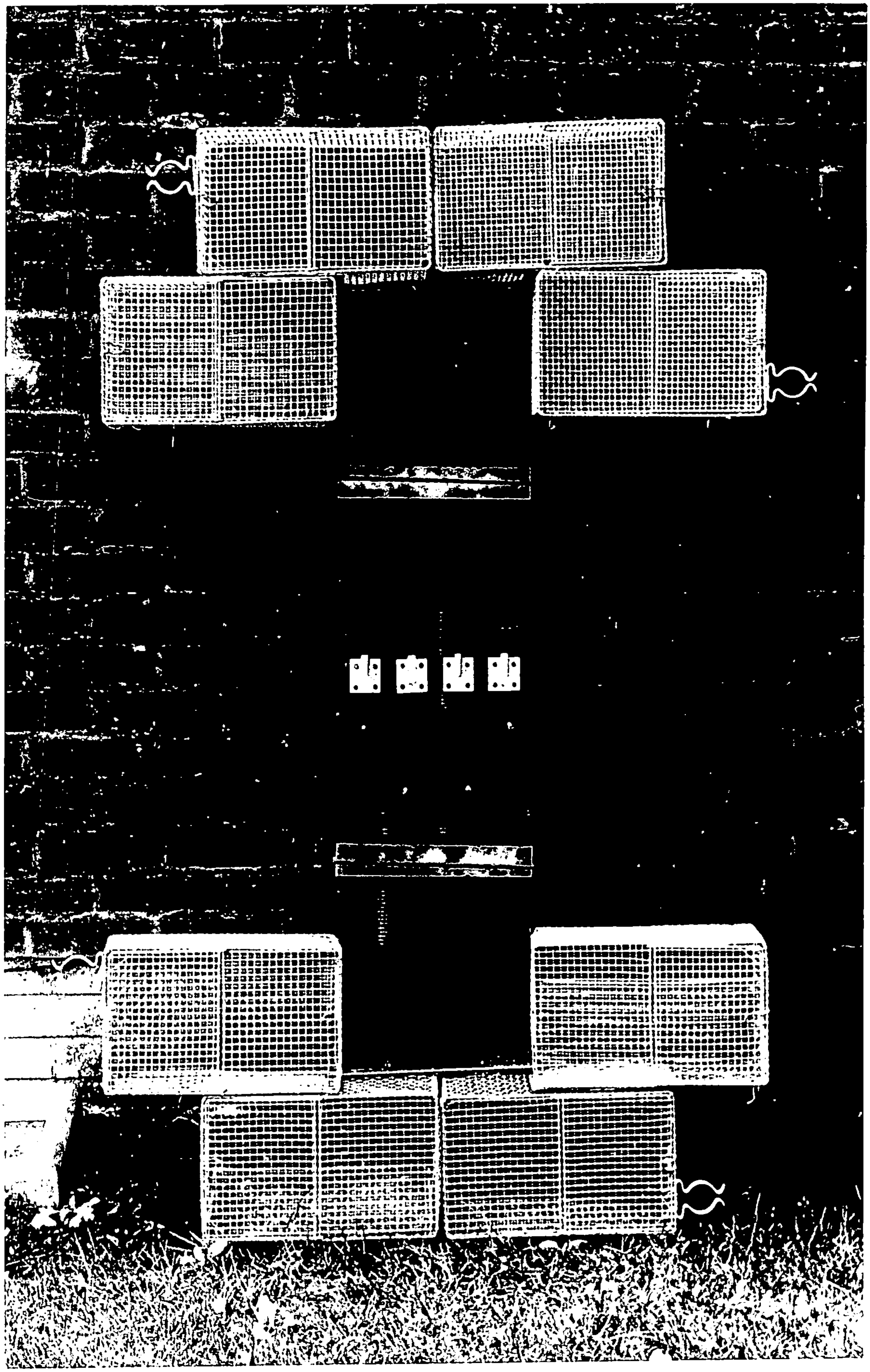
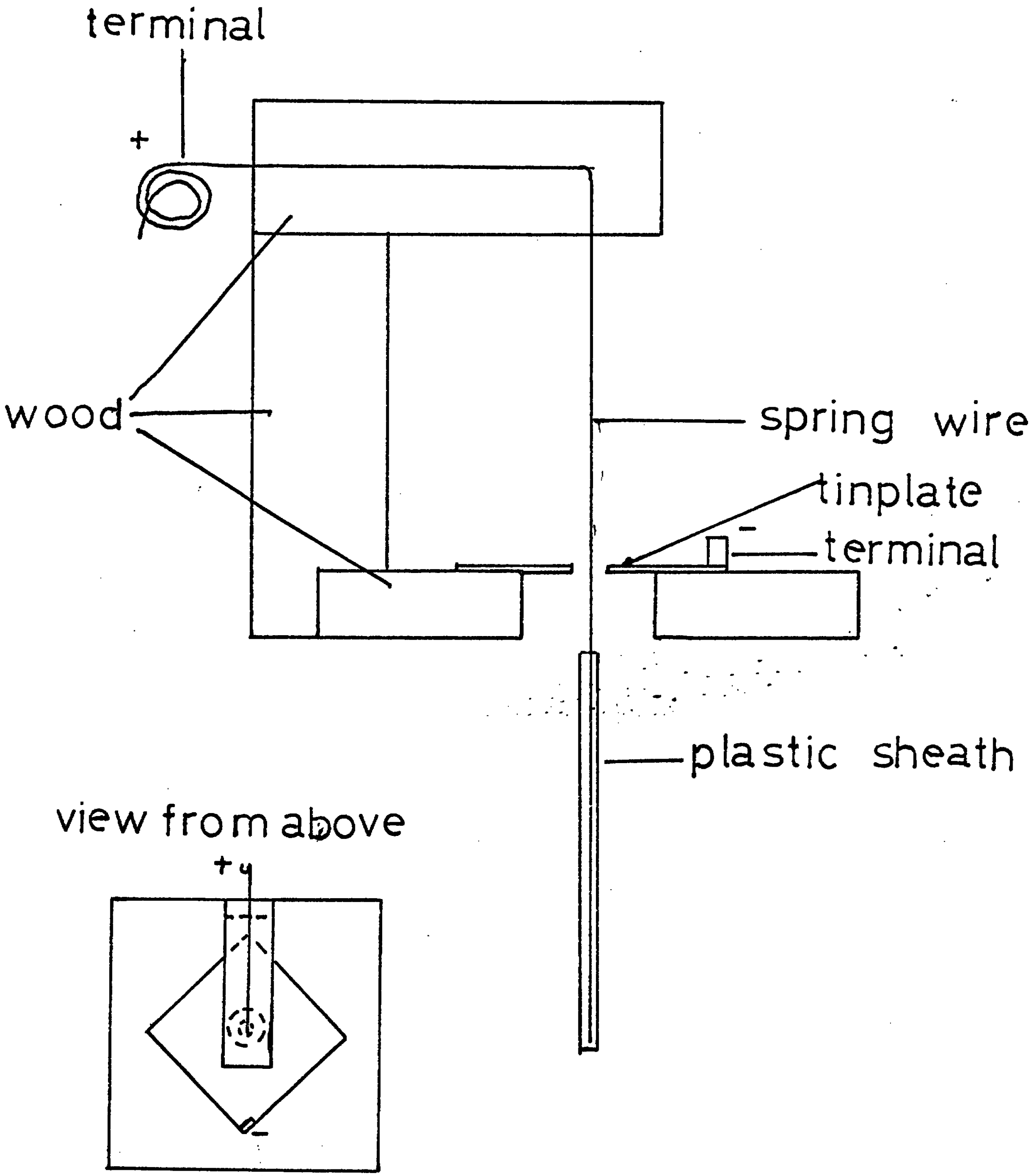


Fig.II.

SWITCH MECHANISM X2



view from above

Two recorders were used, each having four separate channels. Every time a 'switch' was brushed by a vole a single mark was made on a roll of waxed paper. This moved at 3 inches an hour in one recorder and 5 inches an hour in the other. The former was only changed at the end of a ten day period, the latter had to be changed after six days.

From 16.00 B.S.T. 17 March till 16.00 23 March four voles (M1, M2, M3, F4) were given a preliminary trial in the apparatus. The animals were maintained in a greenhouse without extra heating. The temperature over the seven days was 4° - 7°C, with a maximum at 14.00. The humidity was constant at 90% for the first five days but during the last two dropped and showed daily fluctuations. The maxima were 85% and 80% and the minima 65% and 60%, occurring at 16.00 and 02.00 respectively, on these days. Sunrise to sunset was 11 hours 51 minutes increasing to 12 hours 21 minutes (Whittaker's Almanack 1969). Visits to the voles for feeding were once a day at irregular times between 09.00 and 17.00. No record of the amount of food eaten was kept. Three days acclimatisation to the apparatus were allowed.

In all other experiments eight voles, six male and two female, were recorded for ten days in a controlled environment. The maximum and minimum temperatures were 25°C and 18°C respectively while the daily temperature fluctuation was not more than 3°C. These fluctuations closely followed the lighting regime with a maximum just before 'lights off'. The humidity approximately followed the reverse pattern, with the daily maximum before 'lights on'. but the pattern was not consistent, the absolute variation was between 52% and 82%. The room was lit by four 100 watt lights giving an intensity of 550 - 800 foot-Lamberts. The lights required three-quarters of an hour to turn on and off. Initially the voles were kept under a regime of 16 hours light, the lights starting to turn on at 05.00 and off at 21.00. Only three days were given for acclimatisation since the change in day-length from the greenhouse was less than half an hour. The voles were allowed one day to acclimatise to the apparatus itself. Visits for feeding were at 12.00 for the first six days and 16.00 for the last four. In two further experiments 12 hours and 8 hours light were provided, 'lights on' started at 07.00 and 09.00, 'lights off' started at 19.00 and 17.00 respectively. Ten days acclimatisation were allowed between each experiment, the last day being in the run. The voles were visited for feeding at 10.00. In all three experiments food and water were fed in excess, the food in 34 gram portions. At the end of each experimental series the residual food was collected, weighed, and the amount of food eaten per day calculated for each vole.

In the three experiments above the voles always had the same positions in the runs as in Table I(a). To investigate the effects of the females on the males, the voles were re-arranged as in Table I(b). To emphasise the effect, the tinplate partitions between the two neighbouring males and females were removed. All eight voles were recorded for ten days after ten days acclimatisation. Visits for feeding were at 10.000. The amount of food eaten was not recorded.

Table I(a)

Positions of voles in first three experiments under controlled conditions

Unit	1				2			
Position	1	2	3	4	1	2	3	4
Vole	M1	M2	M3	M6	F4	F7	M8	M9

Table I(b)

Positions of voles in fourth experiment under controlled conditions

Unit	1				2			
Position	1	2	3	4	1	2	3	4
Vole	M3	F4	F7	M1	M6	M2	M8	M9

It is not thought that the temperature and humidity fluctuations had an important effect in this series of experiments. Browman (1943) has shown temperature to be subsidiary to day length in affecting the activity of females white rats *Rattus norvegicus var.* Nikolaev & Chertova (1962) found no correlation between rainfall and water vole activity from trapping results. The general implications of these two factors are considered in the final discussion.

Brown (1956), working from field data, considered *Clethrionomys* to be most active at dusk. Previous investigators using artificial light such as Johnson (1926), Calhoun (1945), Miller (1955) and Pearson (1962) have ignored the possible importance of periods of reduced light intensity. Those investigators using daylight (Saint-Girons 1960a,b, Erikinaro 1961) have the problem of change in daylength to consider. While it is doubtful that this is significant in its effect on activity patterns over short periods of time, its effect over a month or more is unknown. For these reasons the time switch causing a period of reduced light intensity was incorporated into the apparatus in this study.

The analysis of results used here has been to take a minimum period of five minutes and record as either showing some activity or none. This yields greater detail than the studies of Davis (1933) who used six minute periods, Miller (1955) who used hour periods, and Pearson (1962) who used ten minute periods, but less than Crowcroft (1954) who used a period of three quarters of a minute. Five minutes was selected as the smallest unit which was easily identified. The fast speed of the recorders made a smaller unit potentially possible, but on odd occasions blocks of unseparated marks of up to three minutes duration could be found on the recording paper. These appeared to be due to voles snapping or scratching at the 'switch'. The treatment of these blocks of marks as more than a single unit would have heavily weighted the data for the period of the day in which they occurred.

2. RESULTS

Throughout this description of results the experiments will be referred to as follows; the preliminary greenhouse trial as PT, the three initial experiments under controlled conditions of 16 hours, 12 hours, and 8 hours light as L16, L12 and L8 respectively, and the experiment involving positional changes as S16. Activity is expressed as the number of unit five minute periods in which any activity was found, except where indicated elsewhere. The times refer to B.S.T. unless stated otherwise.

(i) The effect of interruptions for feeding

The results obtained from PT, where the voles were visited for feeding at sporadic times in the day, suggested that such visits were likely to increase activity at those times. Nicholls (1922) found this was so in the guinea-pig and discarded results obtained in the hour of feeding. Orr (1959) found the same with Peromyscus leucopus. Iverson et al (1967) found that a variety of hairless mouse was most active at 12.00. This was also the time when they were fed, but the authors do not comment on the fact. This result would be unusual if the animal was a variety of house mouse Mus musculus which Chitty & Southern (1954) have shown to be nocturnal.

To examine this problem in this study the interruptions for feeding were made at two different times of the day in L16. The values calculated below have been taken from seven voles (F4 is not included as its 'switch' broke down for four days in the experiment). Student's t test has been used to compare the results for the half hour after 12.00 for the first six days with results for the same time on the last four days, $t = 1.76$, $0.1 > P > 0.05$, 68 d.f. The half hour after 16.00 hours has been compared for the same two periods in the same way, $t = 2.88$, $P < 0.01$, 68 d.f. At both times the mean number of unit five minute periods active is greater in the half hour after interruption than not, but these results are not entirely conclusive in showing the difference. Comparison of the daily pattern of activity of all male voles together from this experiment, Fig. VI(a)with the equivalent pattern from S16 Fig. VI(b) shows an important difference. The former has a moderate period of activity at 12.00, the latter shows a distinct low at this time. (Neither the diurnal nor nocturnal parts of the pattern are randomly distributed in time). Since the voles were not visited at 12.00 in the latter experiment this also suggests that there is increased activity at interrupted times. Personal observations of the voles at feeding times in all experiments confirms this opinion, but also indicates that the response is not the same in each vole, nor from day to day in any one vole. The results over these interrupted periods have been included for the sake of completeness. Their possible bearing on other results is considered in the relevant section.

(ii) The daily variation in activity

The daily totals of activity of all voles together, and the daily totals of activity for each vole, are shown in Table II(a - e), together with the respective values of X^2 and P. Where $P < 0.05$, suggesting that the variation in daily activity is significantly greater than would be expected by chance, the individual values which are significant, $X^2 > 3.8$, 1 d.f., are marked $^+$ if greater than the mean and * if less than the mean. No significance was found in the daily variation of activity of all voles together for PT, L16 and L8. In L12 two days were significantly higher and two significantly lower than the mean activity value. In S16 two days were significantly higher and one significantly lower than the mean activity value. None of this variation was directly attributable to any extreme fluctuations of temperature or humidity by inspection. Another possible reason for the high daily variation in activity could be insufficient time being given to allow voles to settle to given conditions. To examine this, the total activity of all voles taken together, on the first five days of each experiment, has been compared with that on the last five days. (In PT the first three days have been compared with the last four days). The differences are only significant in L12 ($X^2 = 29.83$, $P < 0.001$, 1 d.f.) and S16 ($X^2 = 9.36$, $P < 0.01$, 1 d.f.) in both cases more activity was recorded in the first five days.

DAILY TOTALS OF ACTIVITY EXPRESSED AS UNIT 5 MINUTE PERIODS SHOWING ANY ACTIVITY

Table II(a)

Preliminary Greenhouse Trial (PT), about 12 hours light

	DAYS										
VOLES	1	2	3	4	5	6	7	MEAN	X^2	P<	d.f.
M1	16	20	17	16	21	22	21	18.9	1.68	0.90	6
M2	19	22	26	20	23	20	25	22.1	1.94	0.90	6
M3	36	32	33	27	30	23	17	28.3	9.03	0.20	6
F4	39	30	34	40	50	31	37	37.3	7.39	0.50	6
All voles	110	104	110	103	124	96	100	106.7	4.65	0.80	6

Footnote : Where $P < 0.05$, X^2 is underlined and individual values of daily activity which are significantly different ($X^2 > 3.8$) from the mean are marked :

* if less than the mean
\+ if greater than the mean

DAILY TOTALS OF ACTIVITY EXPRESSED AS UNIT 5 MINUTE PERIODS SHOWING ANY ACTIVITY

Table II(b)

16 hours light (L16)

VOLES	DAYS 1	2	3	4	5	6	7	8	9	10	MEAN	X^2	P<	d.f.
M1	52	42	54	45	60^{+}	40	44	28^{*}	28^{*}	30	42.3	26.48	0.01	9
M2	31	29	31	33	36	33	35	38	36	41	34.3	3.44	0.95	9
M3	65	71	64	73	78	76	68	53	53	57	65.8	11.33	0.50	9
M6	61	76	73	70	62	56	62	52	62	46	62.0	12.48	0.10	9
M8	98^{+}	73	74	46^{*}	73	90^{+}	68	58	47^{*}	61	68.8	36.88	0.001	9
M9	55	40^{*}	46^{*}	36^{*}	56	58	79	94^{+}	118^{+}	113^{+}	69.5	115.17	0.001	9
F4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
F7	64	62	56	44	55	49	52	72	69	63	58.6	12.23	0.50	9
All voles	426	393	398	347	420	402	408	395	416	411	401.6	10.91	0.50	9

Table II(c)

12 hours light (L12)

VOLES	1	2	3	4	5	6	7	8	9	10	MEAN	X^2	P<	d.f.
M1	37	26	28	48^{+}	36	23	20	31	22	25	29.6	22.51	0.01	9
M2	37	35	42	50	38	38	38	37	33	31	37.9	6.46	0.80	9
M3	43	49	35	57	46	49	33	36	36	41	42.5	12.72	0.20	9
M6	46	47	48	41	41	28	33	31	36	23^{*}	37.3	17.59	0.05	9
M8	78	101	92	99	85	75	69	64	81	81	82.5	15.96	0.10	9
M9	60	74	72	70	68	60	64	60	55	64	64.7	5.26	0.90	9
F4	53	60	55	52	45	47	52	41	40	43	48.8	8.02	0.80	9
F7	61	61	48	54	50	60	55	53	52	62	55.6	4.14	0.95	9
All voles	415	453^{+}	420	470^{+}	409	380	364	353^{*}	355^{*}	370	398.9	38.19	0.001	9

Footnote: Where $P < 0.05$, X^2 is underlined and individual values of daily activity which are significantly different ($X^2 > 3.8$) from the mean are marked :

* if less than the mean

\+ if greater than the mean

DAILY TOTALS OF ACTIVITY EXPRESSED AS UNIT 5 MINUTE PERIODS SHOWING ANY ACTIVITY

Table II(d)

8 hours light (L8)

VOLES	1	2	3	4	5	6	7	8	9	10	MEAN	X^2	P<	d.f.
M1	28	32	31	33	27	26	29	25	24	29	28.4	2.83	0.98	9
M2	42	47	47	38	38	39	45	39	38	45	41.8	3.20	0.98	9
M3	37	41	38	36	33	34	31	41	38	28	35.7	4.48	0.90	9
M6	48	51	39	40	39	29	33	29	35	29	37.2	14.67	0.20	9
M8	43	57	61	49	52	54	48	54	45	40	50.3	7.64	0.80	9
M9	78	61	56	61	63	68	59	62	91	65	66.4	15.3	0.10	9
F4	51	47	60	53	48	51	66^{+}	64	49	24*	51.3	24.1	0.01	9
F7	46	55	56	54	54	65	49	58	56	52	54.5	4.34	0.90	9
All voles	373	391	388	364	354	366	360	372	376	312	365.6	12.6	0.10	9

Table II(e)

16 hours light, positional changes (S16)

VOLES	1	2	3	4	5	6	7	8	9	10	MEAN	X^2	P<	d.f.
M1	65	41	46	69	58	69	55	53	50	48	55.4	15.42	0.10	9
M2	71	49*	66	58	67	64	76	120^{+}	60	48*	67.9	54.83	0.001	9
M3	52	50	46	52	55	38	45	40	45	41	46.4	6.34	0.80	9
M6	31	53	43	44	50	49	43	51	52	31	44.7	13.20	0.20	9
M8	162^{+}	131^{+}	113	106	106	99	82*	104	70*	78*	105.1	61.95	0.001	9
M9	68	62	61	69	77	82	94	90	68	72	74.3	15.37	0.10	9
F4	119^{+}	92^{+}	83	60	60	57	66	66	77	50*	72.9	52.52	0.001	9
F7	94^{+}	66	72	59	51	61	67	64	66	58	65.8	18.05	0.02	9
All voles	662^{+}	544	530	517	524	519	528	588^{+}	488	426*	532.6	63.54	0.001	9

Footnote : Where $P < 0.05$, X^2 is underlined and individual values of daily activity which are significantly different ($X^2 > 3.8$) from the mean are marked :

* if less than the mean
\+ if greater than the mean

This suggests that the significant variation shown above is due to an apparent trend to decreasing activity with time in these two experiments. However, the length of time the experiments ran is hardly sufficient to establish a direct relationship between this drop in activity and the length of time of acclimatisation. L8 in which the voles had a similar period of acclimatisation did not show this trend. Among individual voles showing significant variation in daily activity, inspection suggests only one with any notable trend. M9 in L16 shows a steady increase in activity from day 4 to day 9. The reason for this is not known, but it does emphasise that the above impression may not be regarded as conclusive since it cannot apply to this vole.

Slonaker (1928) found activity in female white rats increased every three to four days coincident with oestrus; this pattern was not found in the males. The water vole has a similar reproductive cycle (Perry 1943). Table III shows the standard deviations of the individual voles' daily totals. These values give no indication that the daily variation of activity is greater in the females than in the males. While it is not to be expected that ten days' results would produce conclusive evidence on this point, since a maximum of three cycles is all that could be shown by any female vole in the time, inspection of the results of the two females only suggests a three to four day cycle with F4 in L8. Even here the last of the two peaks is the only one significantly greater than the daily mean (for day 7 $X^2 = 4.2$, $P < 0.05$, 1 d.f.).

Table III

Standard deviations of the daily activity totals for all voles in all experiments

VOLES	EXPERIMENTS				
	PT	L16	L12	L8	S16
M1	2.39	10.58	8.16	2.84	19.30
M2	2.10	3.44	4.95	3.66	7.68
M3	5.97	8.66	7.35	4.00	25.52
M6	-	8.80	8.10	7.39	10.69
M8	-	15.93	11.47	6.20	9.24
M9	-	28.29	5.83	9.98	5.43
F4	6.19	-	6.25	11.12	19.57
F7	-	8.46	4.80	4.86	10.90

The daily variation has also been examined to see if neighbouring voles were affecting each other's activity. The correlation coefficient r calculated from the daily activity totals of neighbouring voles is only significant $P < 0.05$, 9 d.f. in two pairs of voles in L12 (M1 and M2, $r = +0.71$) and (M8 and M9, $r = +0.76$) and one pair in S16 (F4 and F7, $r = +0.89$). This is three pairs of voles showing significant correlation out of a possible twenty three. These results might be expected to occur by chance, and there is no evidence to suppose interaction of any sort between neighbouring voles.

None of the high daily variation in activity above can be directly attributed to any one of the factors examined. It may be due to a complex interaction of the above factors, or it may be within the range of activity for the given conditions and significant only by chance. No evidence of the voles affecting each other's activity has been found.

(iii) The effect of one sex on another

Richter (1927) records that female white rats will decrease their activity for the first few days when placed with male rats, Calhoun (1945) has found the same with *Sigmodon hispidus*. Slonaker (1928) has found that male white rats in cages near the females tended to follow the four day cycle of the latter. In this study in L16, L12 and L8, M8 and M9 were consistently the most active male voles and also those in the same apparatus unit as the females. Thus it was considered possible that the females might be stimulating these males to greater activity. To investigate this possibility the voles had their positions changed as outlined on page 13.

Table IV summarises the totalled activity over ten days for each vole in S16 compared with L16, in which day length was the same. All other factors except the times of feeding were similar. The significance of interruptions has been discussed, its effect in this context is thought to be negligible since the number and length of interruptions were the same in both cases. The mean total activity in S16 was 15% greater than in L16 in the male voles, and 25% greater in the females. This has been subtracted from the actual percentage change in each vole according to sex to enable comparison between the voles. In Table IV the voles are arranged in pairs which received similar treatments, M8 and M9 do not compare exactly since the latter vole, though near to the females in L16, was not next to them. Since the individuals of each pair of voles show the opposite changes in all cases, it would seem most unlikely that any effects of sexual stimulation have been shown.

It has already been indicated in the section on daily activity that the adjacent couples in S16 show no significant correlation in their daily activity. (The two females are an exception but this result could have arisen by chance). The correlation coefficient for the two couples in S16, not quoted in that section, were $r = +0.10$ for M1 and F4, and $r = +0.14$ for M3 and F7, $P > 0.1$ and 19 d.f. in both cases.

Table IV

Comparison of activity, totalled over ten days for each vole, in L16 and S16

(Activity in units of 5 minute periods showing any activity)

		Total activity			
TREATMENT	VOLE	L16	S16	% increase or decrease	Corrected % Increase or decrease
No contact with females in either experiment	M2	343	679	98%	83%
	M6	620	447	-29%	-44%
No contact with females in L16, next to females in S16	M1	423	554	31%	16%
	M3	658	464	-28%	-43%
Next to females in L16 not in S16	M8	688	1051	53%	38%
Near to females in L16 not in S16	M9	695	743	7%	-8%
Contact with males improved	F4	522	730	40%	15%
	F7	586	658	12%	-13%

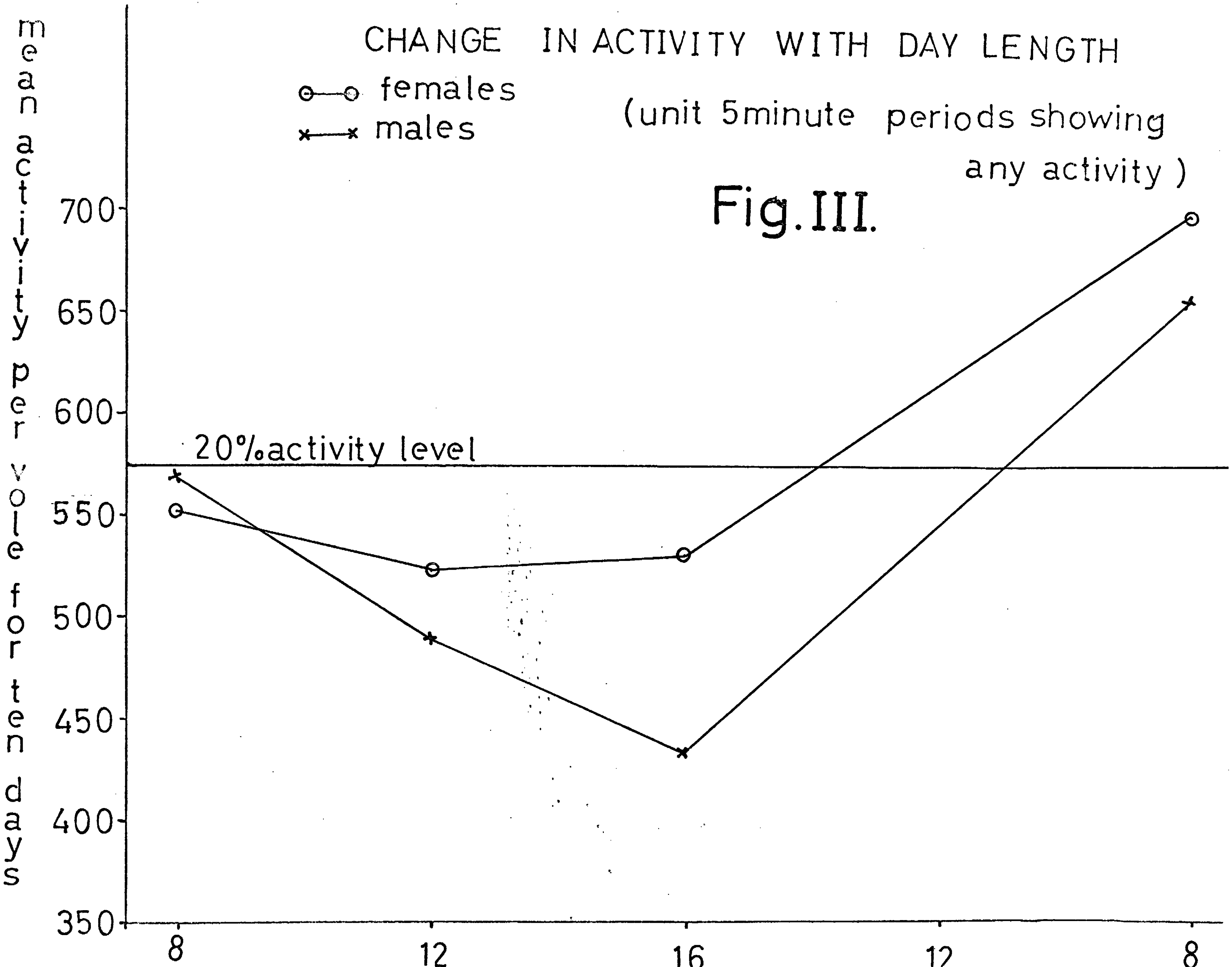
No evidence of stimulation of either sex, by the other, to increase or decrease their level of activity has been found. In all further consideration of results from L16 and S16, the effects of positional changes will be regarded as negligible.

(iv) Total activity

The changes in mean activity per vole over ten days, following the changes in length of hours of light, for the four controlled experiments are shown in Fig.III. The overall decrease in activity from L16 to L8 is 13% in the males, 5% in the females. Analysis of variance of the individual results for the males in L16, L12, and L8 gives $F = 1.14$, $P < 0.2$, 17 and 15 d.f., showing individual variation to be more significant than the drop in activity. It was thought possible that the time between experiments might be insufficient for the voles to exhibit a significant change in total activity. Student's t test has been used to compare the total activity of the male voles in L16 with those in L8, $t = 1.84$, $P < 0.1$, 10 d.f. No statistical tests have been applied to the females but their changes in activity are clearly not significant. Treatment of the data for all eight voles together, as the data of the males has been treated above, gives $F = 1.48$, $P < 0.02$, 23 and 21 d.f., and $t = 1.98$, $P < 0.1$, 14 d.f. These results in themselves cannot be regarded as conclusive in showing decreasing activity with decreasing amounts of light, but they do not negate the possibility. After L8 the voles were returned to a regime of 16 hours light for S16. Comparison of L16 and S16 using student's t test gives t = 1.19, 10 d.f., if the males only are considered, and t = 1.17, 14 d.f., if both sexes are considered, $P > 0.4$ in both cases. Thus there is no significant difference between the data for L16 and S16. If we compare L8 with S16 for the males alone, t = 2.28, $P < 0.05$, 10 d.f., and for all eight animals together t = 2.85, $P < 0.02$, 14 d.f. This clearly shows a significant increase in activity from L8 to S16. This increase is 52% in the males and 31% in females. The difference in activity between males and females is only significant ($P < 0.05$) in L8, but even here M9 was more active than both females. The comparison is shown in Table V. The response of the males to all changes in lighting conditions is greater than that of the females; this is shown by the slope of the graph in Fig.III.

Fig. III.

The 20% activity level has been included for comparison with other work. Its validity depends on a vole being active for the whole of any five minute period in which activity was recorded, and not being active when no activity was found. This has not been demonstrated in this study.



CHANGE IN ACTIVITY WITH DAY LENGTH

(unit 5minute periods showing any activity)

Fig.III.

Table V

Difference in number of unit 5 minute periods, recorded over 10 days, between males and females

	Activity			
	Observed	Expected	X^2	p
		L16		
Males	3427	3401	0.20	
Females	1108	1134	0.59	
Total	4535	4535	0.79	< 0.5
		L12		
Males	2945	2992	0.74	
Females	1044	997	2.21	
Total	3989	3989	2.95	< 0.1
		L8		
Males	2598	2742	7.56	
Females	1058	914	22.69	
Total	3656	3656	30.15	< 0.001
		S16		
Males	3938	3995	0.80	
Females	1388	1331	2.40	< 0.1
Total	5326	5326	3.20	

It may be concluded that the intensity of activity in the male voles decreases with decreasing day length and increases with increasing day length. Under the conditions of this study the response to the former is less than the response to the latter. The female voles appear to respond in the same way as the males but only the increase in activity is significant.

(v) The relationship between amounts of food eaten and amounts of activity shown

The weight of food eaten by each vole in L16, L12 and L8 was recorded to see if a direct relationship between food intake and activity could be shown. The correlation coefficient between mean daily activity and mean daily food intake is not significant, $r = +0.33$, $P > 0.1$, 23 d.f. The differences in the amounts of food eaten between L16 and L8 are not significant, $t = 0.97$, $P \; 0.1$, 14 d.f. The actual amounts eaten per day by each vole are shown in Table VI. The only evidence of storage of food by voles was given by M3 in PT.

Table VI

Weights of food eaten per day for each vole (g)

	Vole								
Experiment	M1	M2	M3	M6	M8	M9	F4	F7	Mean
L16	23.5	22.7	20.5	23.8	20.5	28.4	18.8	20.5	22.3
L12	21.7	19.8	19.1	18.3	19.1	28.2	17.4	21.1	20.6
L8	18.9	21.6	15.6	18.0	21.2	22.0	13.5	19.3	18.7

(vi) Nocturnal and diurnal activity

The relationships between nocturnal and diurnal activity in experiments L16, L12, L8 and S16 are shown in Fig. IV. In all experiments the light and dark periods have been regarded as starting half an hour after the lights started to turn on and off respectively. Table VII shows that both male and female voles are significantly more active in the dark than in the light in all regimes. Only F4 in L16 and L12 and M2 in L8 show a greater

Fig.IV. CHANGE IN % OF DIURNAL AND NOCTURNAL ACTIVITY.

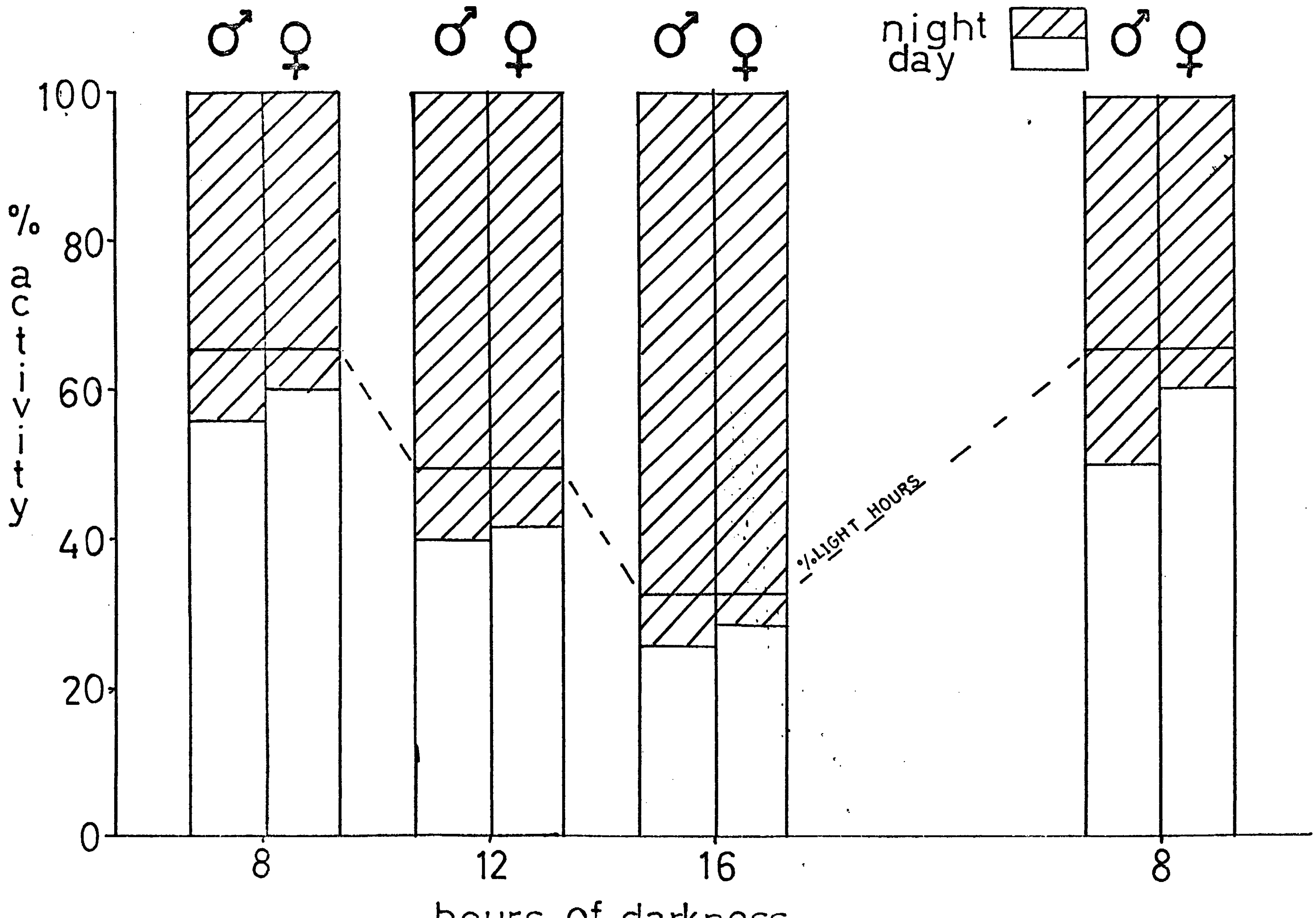


Table VII

Ten day totals of activity for the day and night periods

(Activity in units of 5 minute periods showing any activity, totals from six male voles and two female voles)

	L16		L12		L8		S16	
	Males	Females	Males	Females	Males	Females	Males	Females
Diurnal activity	1929	666	1189	437	685	308	1989	852
Nocturnal activity	1498	442	1748	604	1913	749	1949	536
X^2	166.47	21.46	106.39	26.79	56.75	8.35	462.16	17.27
p (1 d.f.)	0.001	0.001	0.001	0.001	0.001	0.01	0.001	0.001

intensity of activity in the light than in the dark. On decreasing daylight from 16 hours to 8 hours diurnal activity drops 30% in the male voles and 31% in the females. Increasing daylight again from 8 hours to 16 hours in S16 caused diurnal activity to increase 25% in the males and 32% in the females. If there were no change in the diurnal to nocturnal ratio of intensity of activity, changes of 30% would be expected. The mean ratios of diurnal to nocturnal activity are given in Table VIII. The maximum was given by M1 in S16 (1:2.96), the minimum by M2 in L8 (1:0.85). Student's t test has been used to compare this ratio for the male voles only, in pairs of experiments. A significant difference was only found between L8 and S16, $t = 2.86$, $P < 0.05$, 10 d.f. The males are more nocturnal than the females under all lighting regimes, but the difference is only significant in the two regimes providing 16 hours light (for L16 $X^2 = 4.99$, $P < 0.05$, 1 d.f. and for S16 $X^2 = 48.77$, $P < 0.001$, 1 d.f.).

Water voles show a nocturnal preference which may be stronger in long hours of daylight, but this latter point is not conclusive. The differences in the sexes may not be taken as valid for all water voles since only two females were examined. There is some overlap, between the sexes, in the diurnal to nocturnal activity ratio except in S16. Diurnal values given in Table VII may be regarded as maximal, since all interruptions for feeding occurred in the period regarded as day, thus increasing the amount and percentage of diurnal activity.

(vii) The preliminary trial

In PT the light period has been taken as 07.30-19.30. However, this experiment was carried out on the spring equinox, in the seven days covered sunrise changed from 07.20-07.03. The total activity recorded over these seven days was 486 unit five minute periods for M1, M2 and M3 and 261 for F4. The female was significantly more active $X^2 = 3.97$, $P < 0.05$, 1 d.f. The males showed 43% of all activity in the light, the female 57%; this difference was also significant, $X^2 = 14.3$, $P \leqslant 0.001$, 1 d.f. Since the ratio of length of day to length of night is 1:1, the above percentages also reflect the ratio of activity in each period of the day. In Table IX the activity of the four voles concerned is compared in PT and L12, where the light period was of similar length. Both males and female increased their mean activity per day when indoors, the males by 58%, the female by 31%. Calculation of X^2 from a 2 x 2 contingency table shows that the proportion of diurnal activity is similar in the two

Table IX

Comparison of activity in PT and L12

(Activity in unit 5 minute periods showing any activity)

	Males		Females	
	PT	L12	PT	L12
Mean activity/day/vole	27.1	36.7	37.3	48.8
% in day	43%	42%	57%	51%
% at night	57%	58%	43%	49%

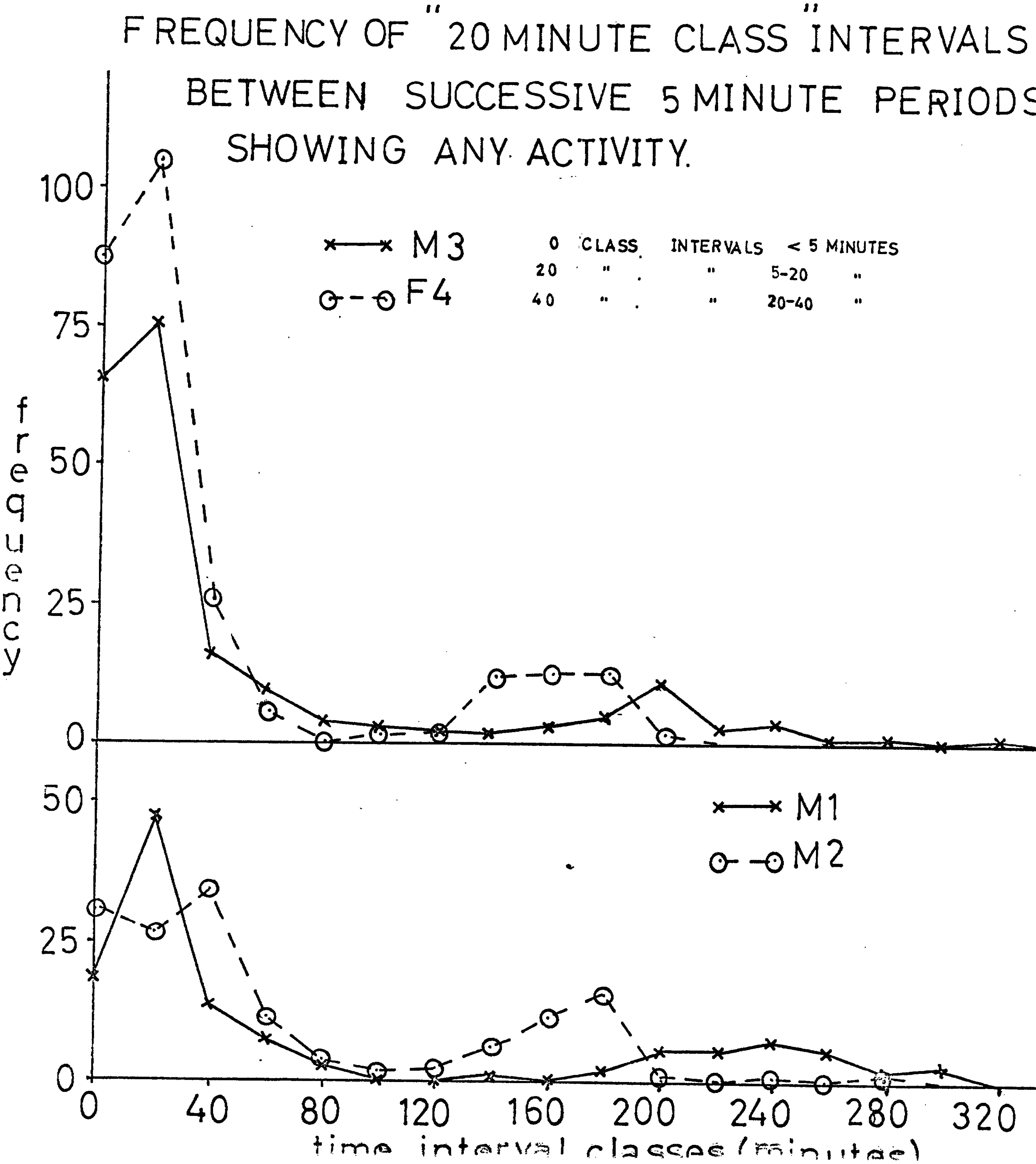
regimes for the males, but significantly smaller in L12 for the female ($X^2 = 19.7$, $P < 0.001$, 1 d.f.).

The most important facet of activity in PT is that the mean daily activity is much less than in L12. Other differences do not merit further comment because of the low numbers of voles involved.

(viii) The subsidiary activity phase

The distribution of unit five minute periods during any activity, over the seven days of PT suggested a rhythm of activity subsidiary to the diurnal nocturnal rhythm. Fig. V shows a frequency diagram of intervals of time between two successive five minute periods showing any activity. These intervals have been arranged in 20 minute classes to show the pattern clearly. The data from each vole in PT are plotted separately. These frequency curves appear to have two separate elements. Periods of inactivity of less than 80 minutes occur on a random basis. Periods of longer

Fig.V.


FREQUENCY OF "20 MINUTE CLASS" INTERVALS BETWEEN SUCCESSIVE 5 MINUTE PERIODS SHOWING ANY ACTIVITY.

than this are more normally distributed around a time of 160-210 minutes. The exact time of the latter varies from vole to vole. The overall picture is thus of groupings of activity periods separated by periods of inactivity of a relatively well defined length. Fig. V has been used to calculate the mean number of peaks of activity per day, and the mean length of interval between each peak, for each vole. This is shown in Table X. The number of periods of activity can be more approximately identified by counting the number of periods of inactivity of greater than half an hour between any half hour periods showing activity. These inactive periods separate the activity peaks giving the values in brackets in Table X.

Table X

Mean number of peaks of activity per day in PT for each vole

M1	M2	M3	F4
4.9	6.0	5.0	6.4
(4.9)	(6.6)	(5.3)	(6.0)

Mean length of time between each peak

	M1	M2	M3	F4
Nearest 20 minutes	3H.50min	2~~4~~H.40min	3H.15min	2H.35min
Nearest 30 minutes	(3H.15min)	(2H.5min)	(2H.50min)	(2H.5min)

For other experiments, M6 and M8 were selected from S16 for brief examination. These two were selected since they showed relatively low and high activity under conditions very different from PT. Neither of the two voles showed the bimodal pattern demonstrated in Fig.V, using a half hourly class grouping. The frequency of such half hour class groups is shown in Table XI. No subsidiary rhythm is indicated.

Table XI

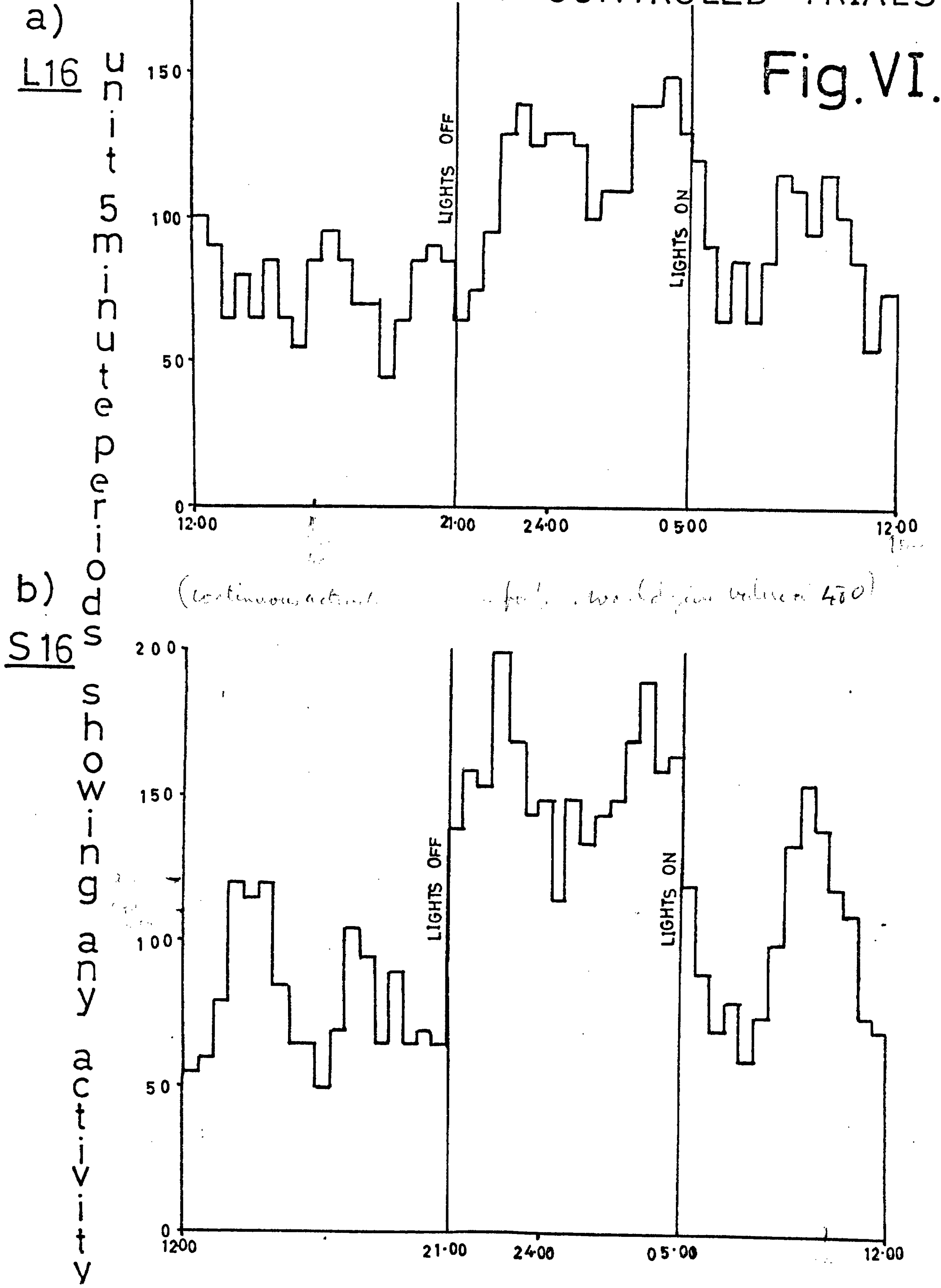
Frequency of half hour class groups of inactivity for two voles in S16

No. of half hours in group		1	2	3	4	5	6	7
Frequency in each vole	(M6	57	17	15	14	2	2	1
	(M8	33	18	4	2	1	-	-

To test if any significant aggregation of half hourly periods showing inactivity was recurring with these two voles, a 2 x 2 contingency table was constructed. The values tested against each other were the number of active half hourly periods followed by active half hour periods, the number followed by inactive half hour periods and vice-versa. This was done separately for the two voles for light and dark periods of the day in S16. The calculated values of X^2 and P for 1 d.f. are shown in Table XII. This analysis fails to reveal any significant aggregation of active or inactive half-hour periods for either vole during the dark part of the day.
For the light part of the day M6 shows no significant aggregation, but M8 shows significantly greater aggregation than would be expected by chance. This indicates that activity does not occur at random for this vole for this part of the day, suggesting a rhythm may be present.

THE DIEL DISTRIBUTION OF ACTIVITY OF ALL VOLES IN THE FOUR CONTROLED TRIALS.

Fig.VI.



(continuous activity [illegible] for [illegible] would give value of 480)

Fig VI.

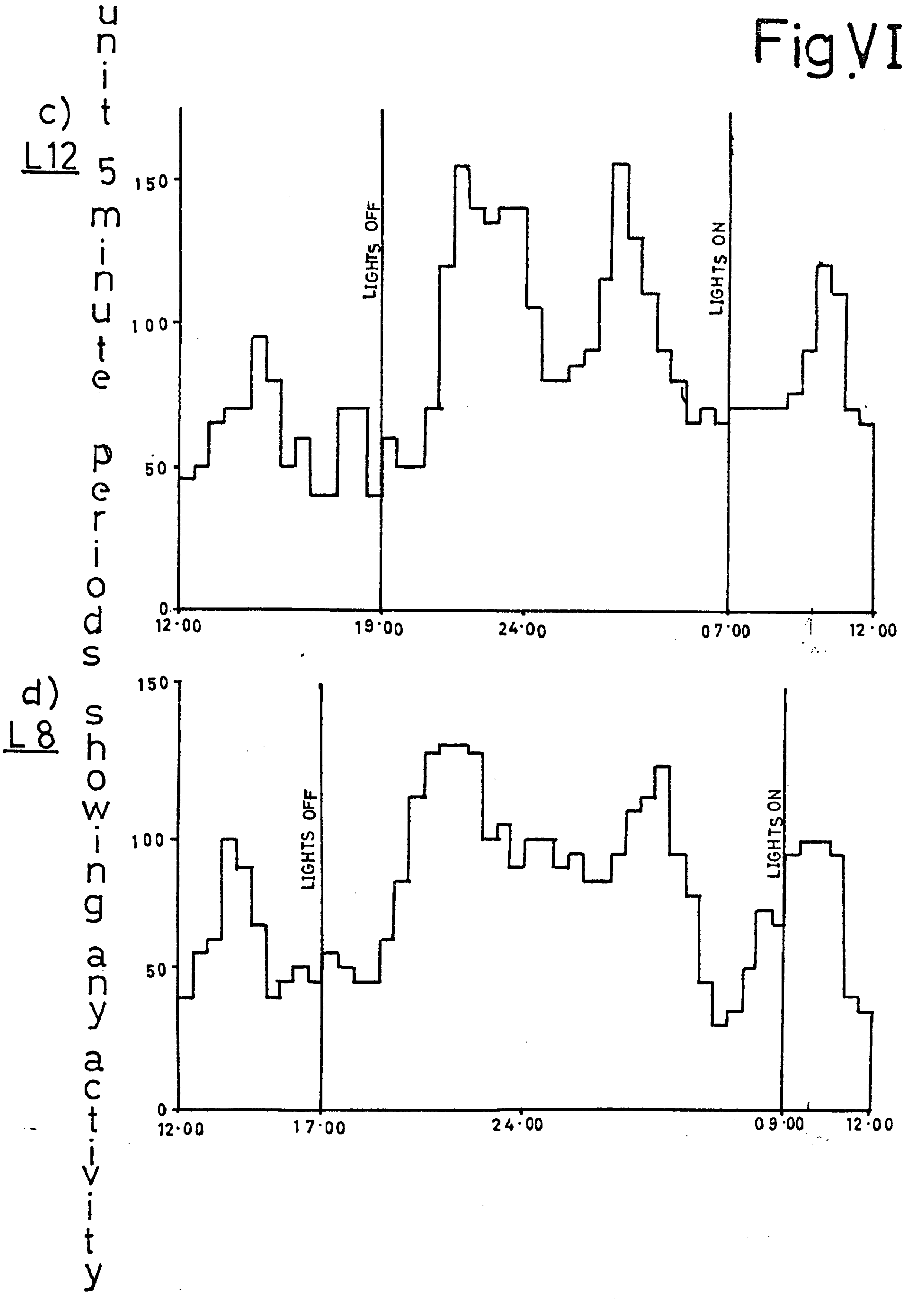

c)
L12
unit 5 minute periods showing any activity
150
100
50
0
LIGHTS OFF
LIGHTS ON
12·00
19·00
24·00
07·00
12·00
d)
L8
150
100
50
0
LIGHTS OFF
LIGHTS ON
12·00
17·00
24·00
09·00
12·00

Table XII

		Light period	Dark period
Voles	(M6	$X^2 = 1.7 \quad P > 0.2$	$X^2 = 2.24 > P \quad 0.2$
	(M8	$X^2 = 10.4 \quad P < 0.01$	$X^2 = 1.90 > P \quad 0.2$

The subsidiary rhythm shown in PT has not been found in either of two voles in S16. The analysis of the data for the latter has not established whether the rhythm is no longer present or has merely lost the form shown in PT.

ix) The overall patterns of activity

The overall patterns of diel activity for all experiments except PT are shown in Fig. VI. The distributions of activity are not random, X^2 tests when applied to the half hourly values of activity give highly significant results (Table XIII) for both parts of the day in all experiments. The data from the males and females have been combined, since the difference in pattern between the two females is greater than between individual males and females. The following features are found under all regimes; a period of relatively little activity at or before lights off is followed by an increase in activity which reaches a maximum several hours after lights off. This was shown by all voles at all times except M6 in L16, the reason for this apparent aberrance in unknown. The length of time between the start of "lights off" and the first maximum of activity increases with the decreasing number of light hours; this is shown in Fig. VII. A second maximum of nocturnal

Fig.VII.

CHANGE IN TIME BETWEEN START OF LIGHTS OFF AND THE FIRST MAXIMUM OF ACTIVITY.

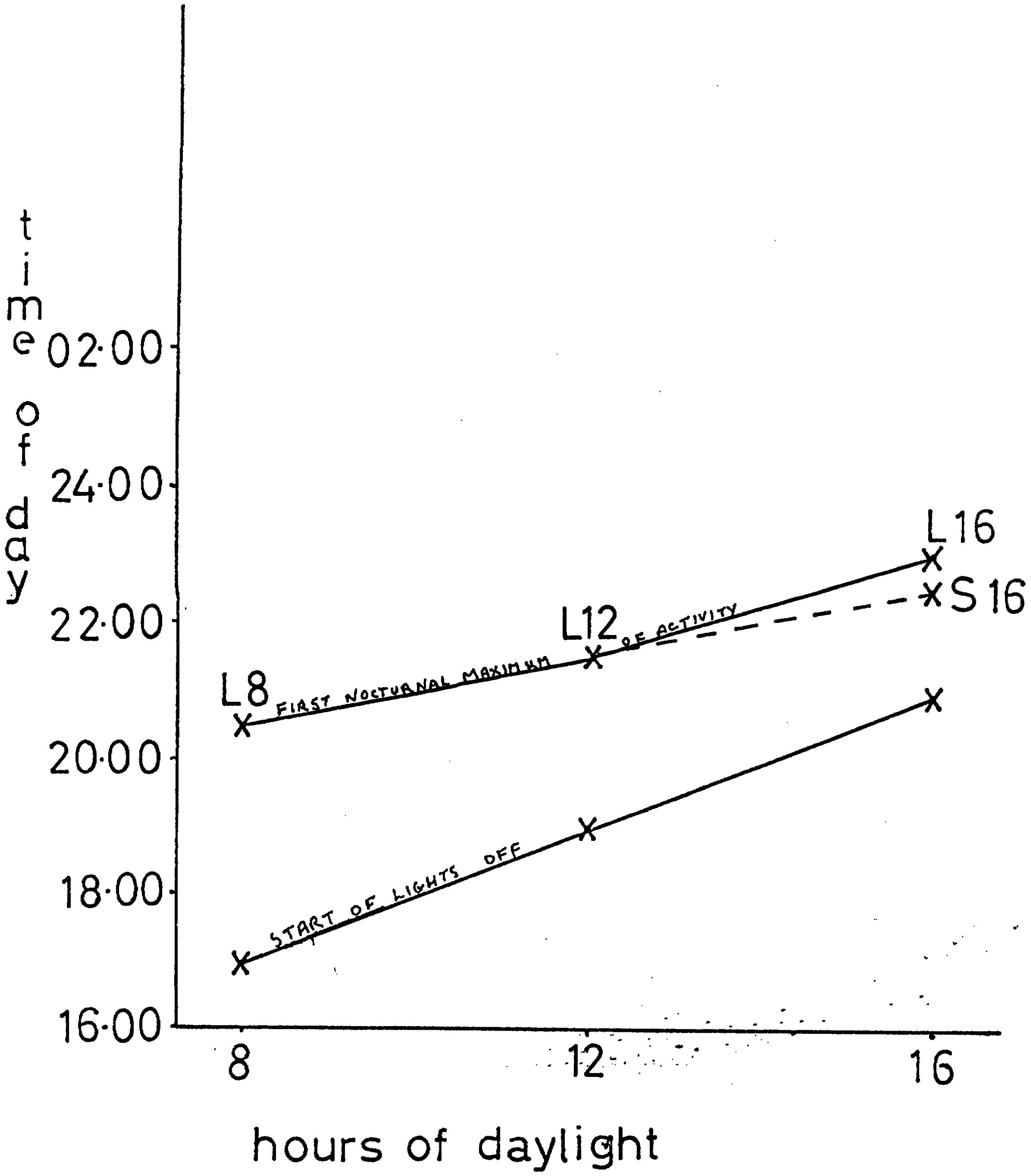


Table XIII

Values of X^2 calculated for the diel activity patterns shown in Fig. VI, from the half hourly data for the light and dark periods of the day taken separately

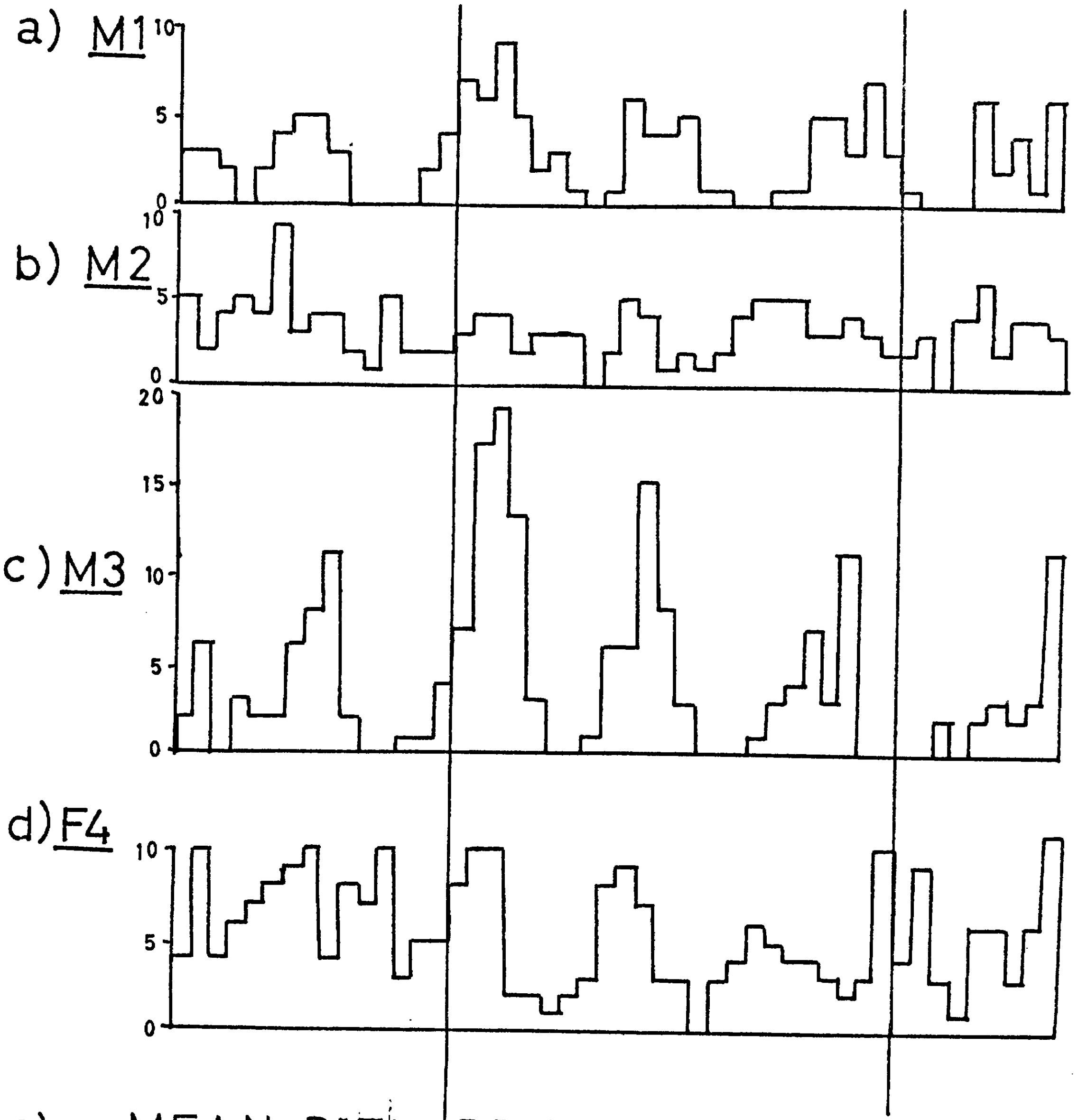
	Light	Dark
L16		
X^2	110.81	47.58
P	<0.001	<0.001
d.f.	31	15
L12		
X^2	141.93	247.29
P	<0.001	<0.001
d.f.	23	23
L8		
X^2	127.97	284.03
P	<0.001	<0.001
d.f.	15	31
S16		
X^2	289.36	47.46
P	<0.001	<0.001
d.f.	31	15

activity is found in all experiments. In L8 the two peaks are less clearly separated than in L16, L12 and S16. This appears to be because the individual variation in the number of nocturnal peaks of activity is greater in the former experiments. There appears to be a tendency for more peaks of nocturnal activity to occur in the longest dark period. A diurnal peak of activity is consistently found in mid-morning. This might have been associated with the morning feeding time, but the pattern from L16 also shows this peak. As feeding was not carried out at 10.00 in this experiment, the peak of activity does not appear to be induced. However, it seems probable that interruptions have tended to increase the size of this peak of activity. A smaller peak of diurnal activity is found in the early afternoon of all experiments except L16; since this experiment was interrupted for feeding at both 12.00 and 16.00 it seems likely that these interruptions have altered the exact time of activity in the afternoon in this experiment.

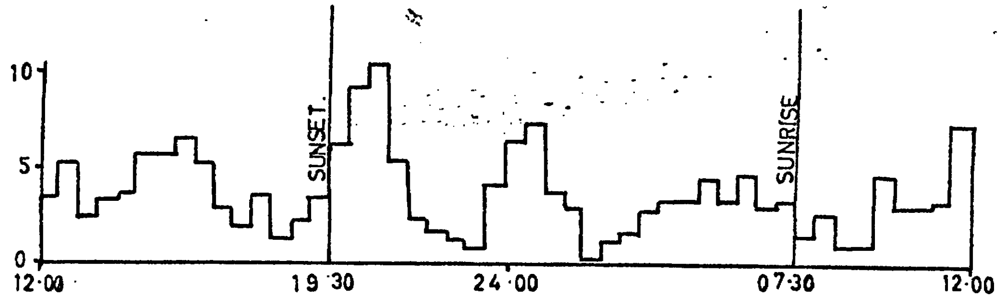
The subsidiary rhythm of activity has been demonstrated as occurring in PT. Two forms were found, one in M1 and M3 has the peaks of activity occurring at the same time of day every day causing an overall phased pattern Fig. VIII(a) and (c), in the other as in M2 the peaks of activity do not occur at the same time each day and no phased pattern is shown Fig. VIII(b). F4 was intermediate in that the pattern became fixed only in the last three days, the result is Fig. VIII(d) which is phased at night but not during the day. The overall pattern Fig. VIII(e) is phased with three nocturnal peaks of activity, the first occurring a few hours after dusk.

The overall patterns of activity have been shown to be phased, this phasing alters to some extent with the time at which feeding occurs. The time between the start of decreasing light and the increase in activity after dark increased with decreasing day length.

THE DIEL DISTRIBUTION OF ACTIVITY Fig.VI
OF FOUR VOLES OVER 7 DAYS IN MARCH
(unit 5 minute periods showing any activity)



e) MEAN DIEL DISTRIBUTION OF ACTIVITIY OF THE ABOVE VOLES.



FIELD STUDY

1. METHODS

(1) Review of methods used in other work

Field methods of measuring activity are diverse, but can be classified into two basic types. One is the continuous recording of activity, the other is spot observations at regular time intervals to yield an index of activity. In the first category Canivance & Lachaud (1957) have emplanted radio transmitters under the skin of badgers and followed their activity from a receiving station. Ashby et al (1969) have carried out twenty four hour watches on water voles. Meese & Cheesman (1969) have labelled moles with radioactive tail rings and followed them using a Geiger-counter. This latter technique was first used by Godfrey (1954) for studying home-range in *Microtus agrestis*. In the second category Hamilton (1937) and Chitty & Shorten (1946) used the amount of bait removed from a bait-station to provide an index of activity. Van Wijngaarden (1954), Brown (1956), Gentry & Odum (1957) and Nikolaev & Chertova (1962) have obtained activity indices from trapping results. Hamilton (1939) compressed the tunnels of Brewer's mole *Parascalops breweri* and used the time of unblocking as an index. Recently photographic techniques have been tried. Pearson (1959) has used a camera, which was set off by a treddle placed in a vole run, to study the activity of small vertebrates.

Continuous methods, while giving the most detailed picture of activity, are handicapped by the operator's time involved.

This can be overcome in the case of radiotelemetric and radioactive techniques by using expensive recording devices. Radioactive techniques have an advantage in that they can be used to record nest and burrow activity. Results obtained in this way should be more comparable with the laboratory actograph than other field techniques. A major drawback of this technique is that only one animal can be studied in one area at a time. Field index methods like those in the laboratory require a check before absolute values of activity can be obtained. Both bait stations and traps may encourage activity in the animals to be studied. The use of tunnel compressing is restricted to burrowing animals and even then results are only relevant to activity in surface burrows. Photographic techniques appear to be promising but they do not yet appear to have been applied to small mammals in a quantitative manner. Time lapse photography (pictures taken at short regular intervals) has been used to study behaviour in sheep and cattle (Rutter 1968). This technique could be used to study activity; it has an advantage in that the time interval between pictures is so short that any index obtained is likely to come very close to the real activity values.

Effective and efficient field techniques for studying activity are expensive. A number of simple index techniques are available but none are suitable for refinement to obtain accurate measurements of activity in the field. All these simple techniques require round the clock attendance by the observers involved.

(ii) The technique used in this study

Initially observation had been chosen to study water vole activity in the field. Ashby et al (1969) found it a suitable technique in summer, while Dean (1947) and Ryder (1962) both indicated that water voles can be watched with comparative ease. However, it became apparent in this study that this method would not yield results in any quantity. In 30 hours observation from November 1968 to April 1969, in periods of between two and five hours each, only three voles were sighted.

Dropping boards were also tried. In an initial trial twenty five 100cm square boards were covered with tinfoil and smeared with water vole faeces. These boards were placed at recently used latrines along 125 yards of the east bank of the River Wear at Maiden Castle Durham City. They were left for five days without examination. At the end of this period only twenty boards were left, of which only one had been used.

In the section of work following, the part done at Maiden Castle was carried out with the help of Mr. M.J. Creasy. The author would like to thank him for permission to use these joint observations. The field work was carried out on a shared basis; the analysis of results is the author's own work.

Water voles leave clear tracks in the mud alongside watercourses (Barrett-Hamilton 1911, Ryder 1962). These tracks were utilised in the study of water vole activity at two places.

Firstly, about 500 metres of the west bank of the River Wear at Maiden Castle; grid reference NZ 288411 - NZ 285416 (Plate III). Secondly, about 200 metres of a small beck alongside the A1 road, north of Pity Me, Co. Durham; grid reference NZ 265460 - NZ 265463 (Plate II). Patches of mud of varying size and distribution were selected for ease of identification and access. These were cleaned of all footprints, marked, and examined at regular intervals afterwards. The size of the site was estimated to the nearest 0.1 M^2, or 0.05 M^2 in the case of patches less than 0.1 M^2. At each examination of a patch of mud, the percentage cover of footprints was recorded to the nearest 5%, the intensity of marking was recorded on a 1 to five scale, and the site was again cleaned. An interpretation of the intensity scale is given in Table XIV. Plates IV and V are examples, the former showing an intensity of five, the latter showing an intensity of four. Fifty sites were examined every four hours for four days in June at Maiden Castle. Twenty six sites were examined every six hours for six days in early July at Pity Me.

Observer interference in the above method is restricted to actual disturbance of the voles and the scent of man left in clearing muddy patches. These are regarded as negligible since only one vole was known to be disturbed in the entire field study and no evidence of reluctance to use recently cleaned sites was noted in the results. The question of some of the footprints being made by the brown rat Rattus norvegicus arises. This is felt unlikely on a number of points. Firstly, no rats were seen or trapped on that part of

PLATES IV and V

Mud patches showing footprints made by water voles

Table XIV

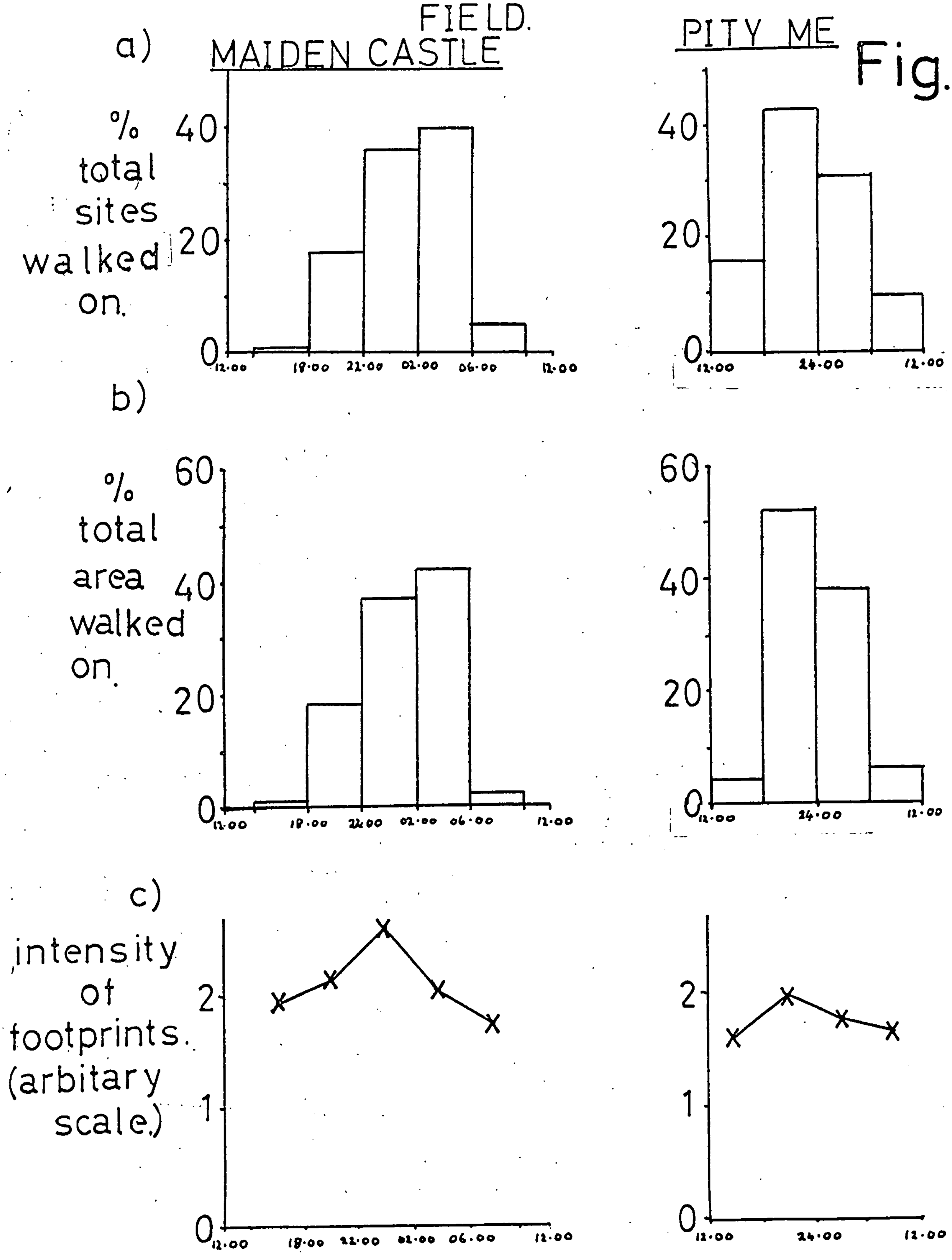
Scale of intensity of footprints on muddy patches

Intensity	Definition
1	Single footprints
2	Single sets of tracks
3	Single sets of tracks with some side tracks
4	Extensive cross tracks
5	Extensive puddling of the mud

the river. Secondly, though there is some overlap in the size and type of tracks made by the two species, those tracks found showed greater resemblance to those of the water vole (Barnett-Hamilton 1911). Thirdly, rats are sensitive to habitat disturbance (Chitty & Shorten 1946), and this might be expected to show in the results, which it did not. The method is restricted in flash rivers such as the Wear by sudden rises in water level occurring a few hours after the beginning of heavy rain. This occurred on one day when records were taken, a number of sites were under water for two four-hour periods at Maiden Castle. The results for this time have not been corrected for the smaller number of sites available, since those sites which were available should be proportionately more used. Heavy rain also limits the method in that footprints are washed away. On none of the days of observation was there more than a slight drizzle.

TIME OF ACTIVITY OF WATER VOLES IN THE FIELD.

Fig.IX.



(see text.)

2. RESULTS

The field results are shown in Fig. IX. The results are shown in three ways. a) is the distribution of activity over the day, shown as the percentage of used sites at a given time out of all used sites. Similarly b) is the percentage of area covered at a given time out of the total area covered. c) shows the change in mean intensity at used sites. The latter has only been included as a check on the former two, since it is possible for activity to increase at one point without increasing the number of sites or the area covered. The results from section c) viewed in this light emphasise the results of the other two sections. The results from Maiden Castle are the same for both ways in which the data is expressed; 75% of all activity occurring between 22.00 and 06.00, and 90% of all activity between 18.00 and 06.00. The area cover method (b) from Pity Me is in close agreement, but the site method (a) would suggest a lower percentage of activity from 18.00 till 06.00 of 75%. This slight discrepancy between the results of the two areas suggests that diurnal activity is likely to be limited to sorties close to the holes. These sorties would be less likely to show in the larger areas. It may also be due to the number of voles involved in each case. The number at Maiden Castle was not estimated but was certainly greater than at Pity Me where evidence suggested there were no more than two pairs.

DISCUSSION

The importance of activity rhythms in animal ecology has been stressed by Miller (1955). There are two major theoretical reasons for this approach to activity. The first is the possible importance of time in the avoidance of interspecific competition. Miller (1955) and Brown (1956) compared the activity of *Apodemus sylvaticus* with *Clethrionomys glareolus*, which have many similar ecological requirements, in an attempt to clarify their relationship. Both authors showed differences between the two species, but failed to show these were important ecologically. The most important demonstration of this principle has been by Schaller (1967). He has shown that competition in some species of large Indian herbivores is avoided by feeding at different times of the day. The major suspected competitor of the water vole is the brown rat, but the pattern of activity of the former as found in this study is similar to that found in the latter (Chitty and Shorten 1946). Further the laboratory data found here shows a similar pattern to that found in the laboratory for *Clethrionomys glareolus* by Miller (1955), Saint-Girons (1960a,b) and Pearson (1962) and for *Microtus agrestis* by Davis (1933). All this suggests that the nocturnal patterns of activity which are found in many small rodents may be more important for other reasons. This leads to the second point which is that many small mammals may avoid heavy predation by being nocturnal.

Many small-mammal predators are apparently most active when their prey are and this would negate any advantage gained by the latter. However, there is no detailed analysis to confirm this generally held opinion, most animals simply being considered as diurnal, nocturnal or crepuscular. In the case of the water vole the importance of predation is unknown. The type of habitat occupied suggests a measure of protection from the usual small-mammal predators but then others already mentioned have to be considered. Much more work needs to be done on predation in water voles before the importance of a nocturnal habitat can be evaluated in this respect.

Activity has an equally important bearing on more central ecological problems in an indirect way. This is the question of interpretation of results of studies on animal numbers and distribution. The chances of making any type of observation on an animal depend not only on how many there are but also on how active they are. This problem can be eliminated by marking animals, but where this is not possible, allowances may be made if the activity pattern is well understood. The possible effects of such factors as food, weather and day length on activity are important in this respect. The problems of trying to estimate the changes in numbers of an animal with a greatly reduced winter activity are considerable.

No effect of one sex on the other was found under the conditions of this study. However, this factor has been found in other rodents. The possible result should be considered in any field study of activity, particularly in spring. In considering the effect of day length on activity, one important fact must be borne in mind. At the start of the experiments under controlled conditions the voles were coming into breeding condition. Both the females were perforate and while the fecundity of the males was not confirmed owing to difficulties of handling without anaesthetics, a rise in agression on being handled was noticed in the three males which had been in captivity a month. Baker and Ranson (1932) kept *Microtus agrestis* in two groups, one with 15 hours light, the other with 9 hours light. The capacity to breed in the latter regime was restricted in both sexes. Relationships between breeding condition and activity have been established in white rats, including the relationship of both these factors to age (Shirley 1928b). Thus some activity in rodents would appear to be related to day length via the reproductive condition of the animal. The period of decreasing day length from the end of L16 to the start of L8 was only 30 days, at the end of L8, the females and at least three males were still fecund. The decreasing day length had not obviously affected the reproductive conditions of the voles. Thus decreasing the day length decreases activity in spite of the reproductive condition and the result is not significant in itself. On increasing the day length, both this factor and the breeding condition act together to increase activity. If this effect is real, then the reverse might be expected from a similar set of experiments carried out in autumn; this remains to be examined. Little comment has been found concerning the effects of decreasing daylength on total activity in other rodents. Hansen (1957) has shown an increase in activity with decreasing daylength in the varying lemming; this he considers to be an adaption to life in the arctic. Saint-Girons (1960a,b) found maximum activity in winter in *Clethrionomys glareolus* and minimum in the autumn; the females (1960b) also showed a spring maximum. Miller (1955) showed decreasing activity with decreasing daylight in both *Apodemus sylvaticus* and *Clethrionomys glareolus* but did not consider the latter result significant. The results found here for the water vole are consistent with its known biology. Barret-Hamilton (1911) has suggested they hibernate and while this is not regarded as true, Ryder (1962) indicates extensive periods spent in their burrows in winter. Evidence of water vole activity in winter was not collected in a quantitative manner in this study, but a fortnight's trapping in February failed to collect any water voles, and other evidence of their presence was also relatively scarce. Food storage by water voles has been recorded by Barrett-Hamilton (1911). It was also found in an isolated instance in this study. No food storage occurred on reduction of day length as Miller (1955) found in *Apodemus sylvaticus* and *Clethrionomys glareolus*, but since it has been recorded, it seems likely that either the length of time of the experiments was insufficient to elicit this type of response, or that other stimulae than day length are involved. If much of the summer activity of water voles is associated with feeding, then we might expect this portion of activity to be reduced in winter when less food is available above ground.

The fact that no direct relationship between amounts of activity and amounts of food eaten was found may be attributed either to lack of information or to the fact that the relationship is not direct. Hatfield (1940) was also unable to establish this type of simple relationship in Microtus pennsylvanicus. Hitchcock (1928) has found that white rats show a considerable increase in activity on protein free and starvation diets. Further study in this direction, especially under field conditions, would be valuable in its bearing on studies of small mammal populations, particularly at times of peak numbers.

This study has shown the water vole to have a nocturnal preference for activity. The laboratory data gives 57% of all diel activity between 18.00 and 16.00 for L16 and 59% for S16. The field data, however, gives values of over 90% for the same time. This discrepancy could be accounted for by activity in the nest and burrow which would not be recorded in the field by the method used. The information from other sources indicates a higher level of activity above ground in the daytime. This may be real, and the populations examined in this study may be unusually nocturnal, but in all cases except Van Wijngaarden (1954) the information appears to be based on general impressions. The above author used a trapping technique to examine activity in water voles, and her results differ from those in this study mainly in that she found little activity after 24.00. This could be due to the fact that all voles were caught at earlier times (Worall 1964 has shown them to be highly trappable), the disturbance of capture being sufficient to prevent recapture the same night.

The period of decreasing light appears to act as a stimulus to the higher level of activity found at night. This was also found by Saint-Girons (1960a,b) in *Clethrionomys glareolus*, but she found the length of time between dusk and peak activity was maximal in summer when the day was longest. This study found the reverse effect with the above period of time greatest in the experiment with the longest dark period. In an animal which is preferentially nocturnal, as water voles have been found in this study, it might be expected that the fewer the hours of darkness the more fully they would be used. The results are thus to be expected.

Two important differences were found between PT and L12. The first is the low level of activity found in the former. This could be due to differences in breeding condition of the voles in the two experiments but this has already been discussed. Three other factors were also different between the two experiments. The humidity was about 30% higher in the former, the temperature 15°C lower. The light intensity was much lower in L12 and the light meter used gave a comparable reading in early evening in daylight. The effect of this last factor cannot be assessed; little work has been found on the topic. It is thought possible that it may have contributed to the high level of activity in the controlled experiments. Maximov in Nikolaev and Chertova (1962) which can be gained in the laboratory, their composition depending on all the factors mentioned so far. The possibility remains that this phasing would not be seen in a larger number of voles taken over a long period of time and this would explain much of the controversy over general patterns found in the literature. The alternative is that the phasing of general patterns has some greater significance in which case their demonstration in the field would be valuable.

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8. A subsidiary rhythm of activity of about 2½ hours periodicity was found under natural light in March, the temperature was 5°C the humidity 90%. This rhythm could not be detected by a similar simple analysis in the experiments under artificial lighting of a lower intensity, where the temperature was 20°C and the humidity 65%. The overall data suggests such a rhythm may still be present.
9. The activity patterns of water voles do not differ in any important respect from other small rodents. This suggests that the ecological importance of activity rhythms in this group of animals is associated with common factors in their lives, such as predation and acquisition of food, rather than differences in habitat between them.

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