Some aspects of the daily activity of the water vole, arvicola terrestris linn, and the brown rot, rattus norvegicus linn

D.A. Knight

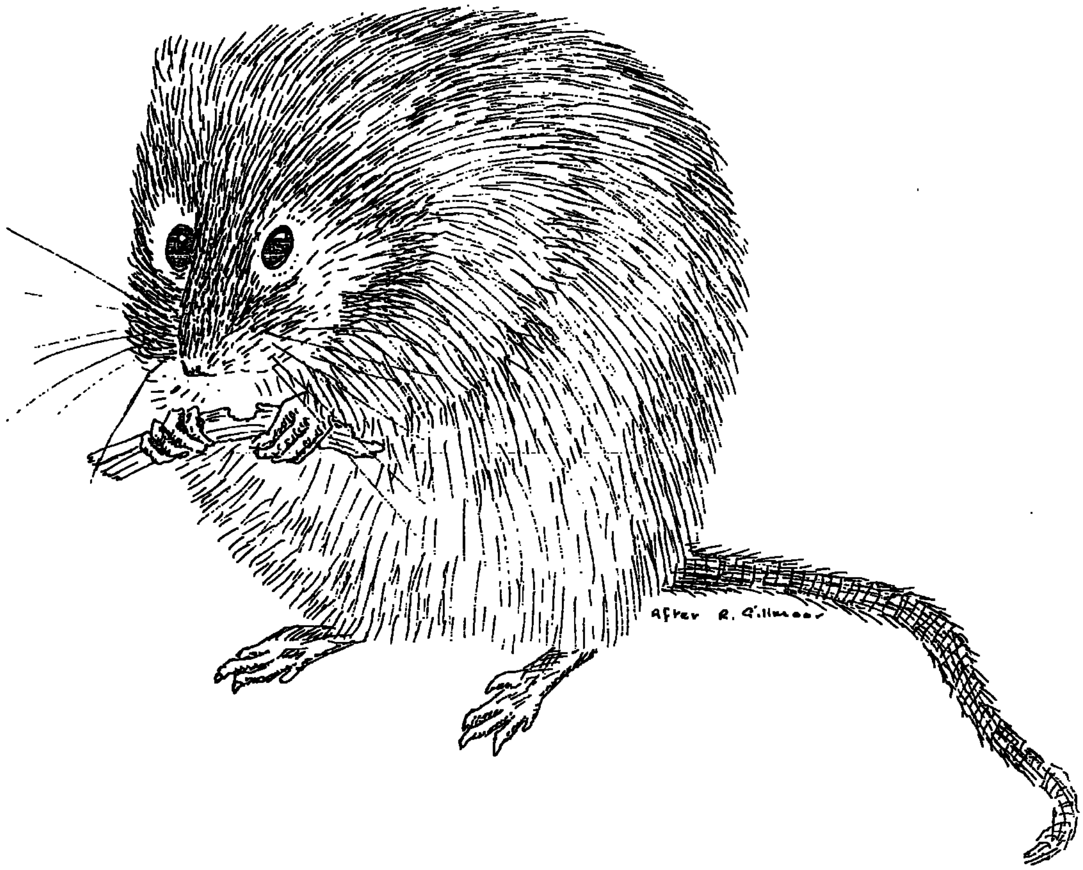
Knight, D.A. (1975) Some aspects of the daily activity of the water vole, arvicola terrestris linn, and the brown rot, rattus norvegicus linn. Masters thesis, Durham University.

Some Aspects of the Daily Activity of the Water Vole, *Arvicola terrestris* Linn. and the Brown Rat, *Rattus norvegicus* Linn.

A dissertation submitted by D.A. Knight 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.

September 1975.



... replied the Water Rat cheerfully ... "Why can't fellows be allowed to do what they like when they like and as they like, instead of other fellows sitting on the banks and watching them all the time ... "

Kenneth Graham
Wind in the Willows

TABLE OF CONTENTS

SECTION 3. METHODS

SECTION 4. RESULTS
4.1. Field Study

4.2. Laboratory Study

4.4. Comparison of the Results of the Present Study with those of Previous Studies

SECTION 5. DISCUSSION

TABLE OF CONTENTS (contd)

SECTION 5.

INDEX TO FIGURES

INDEX TO TABLES

INDEX TO TABLES (contd)

SECTION 1 INTRODUCTION

It has been shown that the activity and behaviour of many animal species tends to follow a definite pattern, giving rise to a periodic cycle within a certain time period. These rhythms of behavioural activity may have wavelengths of as much as a year, as in the hibernation of some mammals or the migration of many birds, or as little as a few hours, as in the feeding patterns of some Soricidae. Overwhelmingly however recent research on activity rhythms has concentrated on 24hr or circadian rhythms, with some emphasis in small mammal studies on short-term feeding rhythms. This synchrony of activity within a population may be considered as a temporal adaptation to environmental cycles (Enright 1970) and is as integral a part of the ecology of the population as adaptations to other environmental variables. In recent years much work has been carried out with the intention of defining circadian activity patterns for particular species and assessing the ecological significance of the patterns found. Notwithstanding this volume of work little is precisely known of the daily activity patterns of mammals, and detailed studies have been restricted largely to some of the smaller rodents (Ashby 1972). Most of these studies have taken place in the laboratory (eg Calhoun 1945, Crowcroft 1954, Miller 1955 and Kavanau 1966,1969) under highly unnatural conditions and it is consequently difficult to determine the relevence of results obtained in terms of the field situation. These circumstances have created a need for further field studies of mammalian activity patterns so that the advantages of temporal adaptations may be clearly defined in the natural situation and to complement the extensive laboratory studies already carried out. It is not intended to suggest that laboratory studies have little or no value. Sewell (1973) has shown how the imaginative manipulation of a laboratory environment may aid understanding of the ecological significance of the patterns of activity found, but in many cases the full import of laboratory studies cannot be realised until comparable field studies have been made.

In the present study the water vole, Arvicola terrestris amphibius was selected for study for several reasons; its size and habitat preferences make it more amenable to field observation than most other British rodents, several populations were known to exist in the Durham area and, most importantly, a number of previous field studies had yielded apparently contradictory results. Van Wijngaarden (1954), Worral (quoted in Southern, 1964) and Stoddart (1969) all used trapping techniques but whereas Van Wijngaarden found activity to be largely diurnal and crepuscular, Worral's results indicated that activity was predominantly nocturnal and crepuscular and Stoddart claimed a statistical daytime preference. Lund (1970) and Vincent (1974) both utilised outdoor enclosures, but whereas Lund demonstrated a daytime concentration of activity in winter Vincent's results showed little diel trend in winter. Again during the summer months Lund found no distinct 24hr cycle of activity whilst Vincent observed a nocturnal preference. Creasy and Duckett (unpublished) used the incidence of tracks on bankside mud as an index of activity and deduced a strong nocturnal peak in summer. Ashby, Harling and Whiles (1969) made observations throughout the diel period in early summer and found no marked rhythm of activity, although there was evidence of lulls at midday and in the early evening. Barret-Hamilton and Hinton (1910-1921), Corbet (1966) and Ryder (1962) all state that Arvicola is predominantly diurnal but do not cite any evidence to support this contention.

Under suitable conditions the most valid method of determining field activity is probably by direct observation; minimal equipment is required, activity may be timed precisely and the type and duration of different activities accurately assessed. In addition it is possible to note behavioural interactions and environmental factors that may modify the basic activity pattern. The value of such studies and the need for more accurate field observation has been stressed by Ashby (1972). However the secretive behaviour of most small mammals makes observation difficult and this, together with the fact that this technique is very time-consuming, has meant that most workers have used alternative methods of studying small mammal activity.

The use of radio-active tracers has been applied in several ways. Godfrey (1954, 1955) placed ^{60}Co in brass tubes soldered onto monel leg and tail rings to study the home-range of field voles (Microtus agrestis) and activity of the mole (Talpa europaeus) respectively. Labelled animals were tracked using a Geiger-Muller counter. Kaye (1960) implanted ^{198}Au wires under the abdominal skin of harvest mice (Micromys minutus). The use of radioactive tracers in small mammal ecology has been reviewed by Bailey, Linn and Walker (1973).

Telemetry also makes possible measurements of actual activity and has been used by Cochran and Lord (1963). A transmitter implanted beneath the skin of the animal enables movement to be monitored from a receiving station.

Automatic photography has been utilised by Pearson (1959) in studying the activity of voles in their runways and this method has been refined by Dodge and Snyder (1960).

Among those techniques providing an index of activity live trapping has been used by many authors including Elton et al.(1931) studying Apodemus, Brown (1956), Kikkawa (1964) and Bergstedt (1965) studying Apodemus and Clethrionomys and Van Wijngaarden (1954), Worral (quoted in Southern, 1964) and Stoddart (1969) studying Arvicola.

Emlen et al.(1957) developed the use of dropping boards as a tool in the study of small mammal ecology and believed the technique could be applied to provide a measure of activity. Duckett (1969) attempted the use of this method in a study of water vole activity but failed to obtain any worthwhile results.

Signs of an animal's presence and activity have been detected in a variety of ways. The simplest method is probably the placing of a stick across a burrow entrance such that an animal entering or leaving the burrow displaces the object (Southern 1964). A modification of this method is to place a cylinder of smoked paper in the burrow entrance as Mayer (1957) did when studying ground squirrel activity. Hamilton (1937) compressed the tunnels of Brewer's

Mole (Parascalops breweri) and obtained an index of activity from the time of unblocking. Creasy and Duckett (unpublished) derived an index of activity from the percentage cover of tracks left by water voles on patches of mud adjacent to the water's edge. Brown (1969) used tracks left by toe-clipped Apodemus on metal foil overlaid with a fine talc suspension, in a study of home-range and movement. The technique might possibly be adapted to activity studies. Bait removal was used by Hamilton (1937) to provide a check on trapping results in a study of the activity of Microtus pennsylvanicus, and by Chitty and Shorten (1946) as a measure of activity in Rattus norvegicus. The latter authors were interested principally in the timing of feeding activity and did not attempt to interpret their data in more general terms.

None of the methods outlined above is entirely satisfactory and selection of techniques for any particular investigation will depend on the aims of the study and the resources available. If the activity pattern exhibited by the population as a whole is central to the aims of the study then one of those methods providing an index of activity may be satisfactory. If however a qualitative breakdown of activities is to be described then direct observation is almost essential, although automatic photography may provide some information.

In the present study it was necessary to use inexpensive and technically unsophisticated methods of measuring the activity of the population. It was felt that bait removal had a potential not reflected in the available literature notwithstanding the difficulties that might be expected using a technique based upon the provision of an attractive food source. The high surface/volume ratio of the water vole's body results in a relatively high heat loss which is compensated for by a correspondingly high metabolic rate; this in turn is maintained by the intake of large quantities of food at comparatively short intervals. Holišová (1970) has estimated that an individual water vole will consume 80% of its body weight in fresh food per day. In a herbivorous animal such as the water vole this is necessitated by the low digestibility of the diet which contains a high proportion of cellulose. As a result of this situation it was felt that active periods would include a very high feeding-activity component and consequently a measure of feeding activity would provide a valid index of total activity. Since the technique is comparatively novel its limitations and advantages are compared with those of other methods in the discussion. In addition it was decided to make concurrent observations of activity where possible and to position dropping boards in the area of study in the hope that water voles could be induced to use them and so provide an independent check on the activity pattern obtained.

Observations of activity in the field were combined with measurements of physical variables likely to be correlated with the timing and amount of activity. Since a particular pattern of activity is likely to be an adaptive response to environmental cycles, it may be assumed as a working hypothesis that if the pattern of activity obtained shows fluctuations in accordance with those of an environmental variable, the activity pattern exhibited might be largely responding to that variable. Selection of the variables measured was based on what factors previous studies suggested might be important and on ease of quantitative measurement. It was decided to take hourly measurements of light intensity, cloud cover, temperature, wind speed, rainfall and human disturbance.

Although the interpretation of results obtained in the laboratory must always be made with great care, especially when attempts are made to extrapolate them into the field situation, such studies may be very useful. They may help in understanding the influence of modifying effects on the 24hr rhythm and in establishing the existence of any short-term rhythm at the individual level. The degree of control that can be exerted over events in the laboratory make such studies especially amenable to automation, freeing the worker for other activities; this is reflected in the techniques selected by most workers. However both Crowcroft (1959) and Sewell (1973) advocate direct observation of captive animals, in the belief that much valuable qualitative information is lost by automatic recording. Where time is available this method is to be preferred.

Wheel cages in which the revolutions of the wheel provide a measure of activity have been used by Browman (1943) and Shirley (1928). The method is open to criticism since the number of revolutions of the wheel will depend to some extent on the speed at which the animal is running, and the apparatus may encourage spontaneous activity. However Kavanau (1966,1969) believes the method gives a reliable index of total activity.

A number of laboratory techniques rely on the triggering of a suitable switch mechanism by the animal. Variations of this method have been applied by Miller (1955), Erkinaro (1961) and Duckett (1969). Crowcroft (1954) showed that the activity pattern obtained was unaffected by the positioning of the switch.

Actographs have been used by Johnson (1926), Richter(1927), Davis (1933) and St. Girons (1960)(1961). The cage containing the animal is supported in such a way that movements are transmitted from the animal to the cage and hence to a recording device. Complex arrangements of such cages can be utilised to obtain seperate recordings of different types of activity (Richter 1927). The method has the added advantage that all activity is recorded, making it suitable for comparative studies. It was for this latter reason that the method was selected in the present study.

The aims of the present study were to:

i) Investigate the relationship of field activity in the water vole to that exhibited in the laboratory.

ii) Attempt to explain some of the apparent contradictions in the reported patterns of activity exhibited by water voles.

In addition it was desirable to develop an inexpensive convenient method of assessing field activity. This method was validated as far as possible in the present study. The presence of Rattus norvegicus at the study site enabled an expansion of the study to incorporate a related species and consider the effects the species were having on each other.

SECTION 2 SITE OF FIELD STUDY

The field study was carried out along a 750m stretch of the River Wear, 1km south-east of Durham, between Maiden Castle Bridge (map ref. NZ 417285) and Shincliffe Bridge (map ref. NZ 411286)(Fig 1). The width of the river at this site varies between 17m and 50m, but along most of the length is between 25m and 30m. The Wear is a 'flash' river, and depth and flow of the water are consequently very variable. During the period of the study rainfall was very low and the river was only 2-3m deep at most points, flowing at a rate of approximately 10m per minute. The bottom is of gravel and larger stones, overlain with silt where the current is slack. The banks are predominantly a fine sand with some admixture of clay and very steep, varying in height between 3m and 10m. They are covered in vegetation that reaches a maximum height of 1•5m but in most places is between 0•5m and 1m tall. In many places the vegetation overhangs the water's edge and trails in the water, thus screening this from view.

During the summer the dominant plants are Butterbur (<u>Petasites hybridus</u>), Himalayan Balsam (<u>Impatiens glandulifera</u>), Creeping Thistle (<u>Cirsium arvense</u>), Rosebay Willowherb (<u>Epilobium angustifolium</u>) and Stinging Nettle (<u>Urtica dioica</u>). The predominant grasses are Sweet Vernal Grass (<u>Anthoxanthum odoratum</u>), Cocksfoot (<u>Dactylis glomerata</u>), False Oat (<u>Arrhenatherum elatius</u>) and Perrenial Rye Grass (<u>Lolium perenne</u>). Willow (<u>Salix</u> sp.), Sycamore (<u>Acer pseudoplanatus</u>) and Ash (<u>Fraxinus excelsior</u>) occur at intervals along both banks.

The nine feeding stations used during the study are described in Section 4.1.4., where their characteristics are related to bait removal by <u>Arvicola</u>.

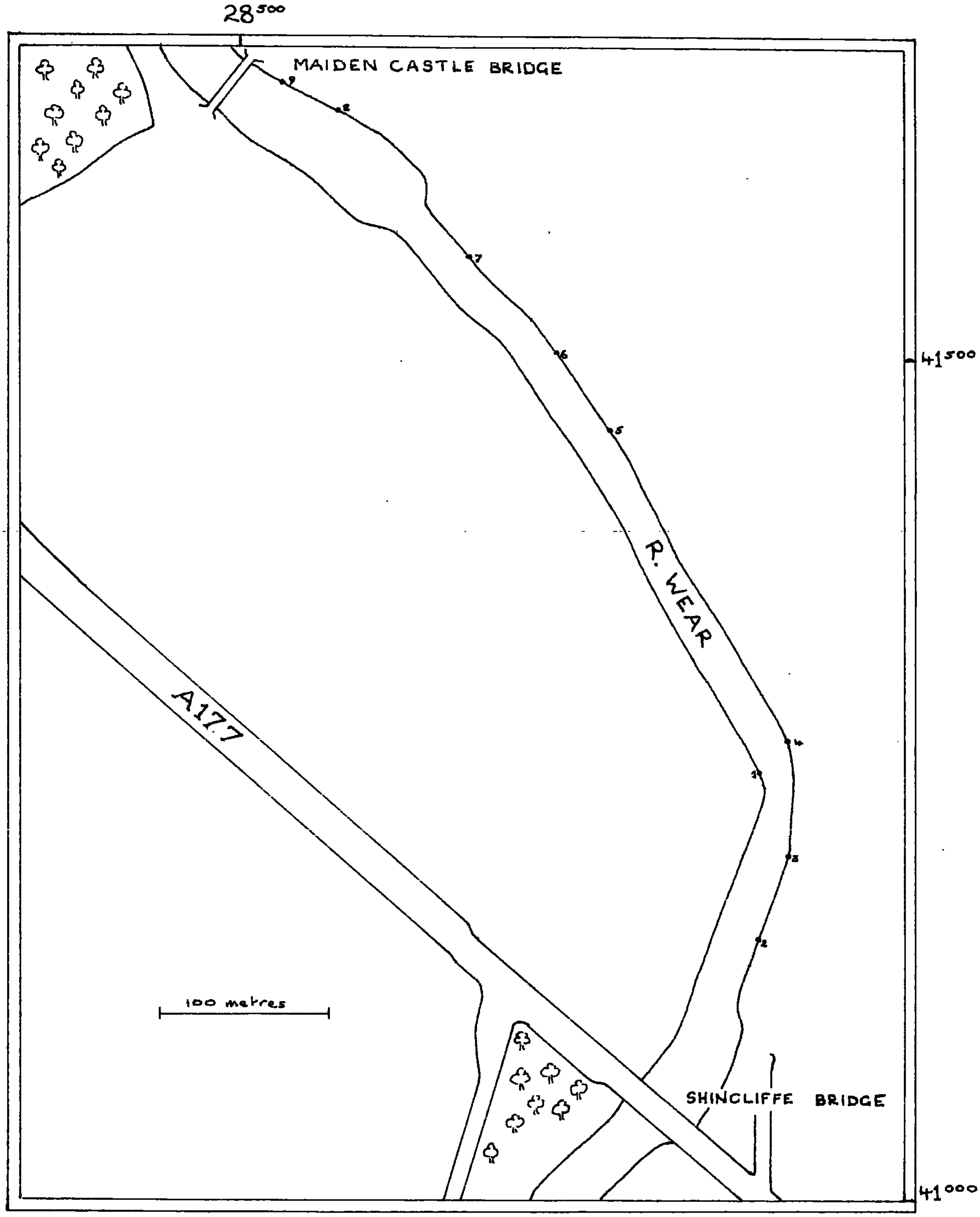


Fig 1. The site of the field study, showing the position of the final baiting stations. (From O.S. map NZ 24 SE).

SECTION 3 METHODS

3.1. Field Study

Seventeen trial feeding stations were selected along both banks of the river in early June and baited with carrot. The carrot was cut into pieces of approximately the same volume (2-3cc) and ten pieces placed close to the water's edge at each station. In selecting the stations, accessibility by the observer was taken into account as well as the presence of signs of vole activity such as chewed grass, faeces and footprints. Dropping boards, consisting of 15cm squares of hardboard, were placed at a further fifteen sites, where the presence of faeces of varying age denoted a latrine and at feeding sites. The bait stations and dropping boards were visited two days later. The bait had been completely removed at eleven stations and partially at four, and six of the dropping boards had been used, all on established latrines.

The eleven baiting stations where all the bait had been eaten or removed were rebaited as before and these and the dropping boards visited at one hour intervals, baits being replaced and dropping boards cleared as necessary. It took just under half an hour to visit all the stations, which were visited between quarter to and quarter past each hour. The study was carried out between June 12 and August 1, 1974. As far as possible observations were carried out for 12hr periods, one commencing 24hr after the previous one ended, two such periods constituting a diel cycle. Due to transport difficulties it was not always possible to adhere to this arrangement and consequently some of the diel cycles are composites of several smaller periods of observation. The breakdown of diel cycles into periods of study is given in Appendix A. Readings for a total of six diel cycles were obtained during the study. In diel periods I and II most of the observations were carried out in early June but a total of 5hr is included from observations made in mid-July. As the daylight length is approximately the same at both times it was felt that the inclusion of these results was permissible

Between visiting the feeding stations time was spent during the first

was all the bait eaten [illegible]

few weeks of the study watching station seven in the hope of making a partial assessment of the relationship between total activity and bait removal. Observation was made from the opposite bank of the river using a pair of 10 x 50 binoculars. During the latter part of the study observations were made at each of the other feeding stations to determine the distance of the nearest vole burrow and to further check the identity of the animals using the station.

Environmental variables were measured at hourly intervals throughout the periods of observation. Rainfall was measured as the number of five minute periods during which rain fell in each hour. Cloud cover was assessed by dividing the sky into tenths and noting whether each tenth was cloudy or clear. Although subjective, the method is accurate and accords with standard meteorological practice. Light intensity was measured using an Aico CA-411 exposure meter which gave readings on a nought to ten scale. A Griffin thermometer placed 5cm above the ground in a sheltered position was used to obtain temperature readings. Wind speed was measured on the Beaufort Scale by eye with reference to a descriptive sheet. Finally disturbance was measured as the number of boats, or groups of boats, passing through the study area each hour.

Measurements were taken of a number of physical parameters at each feeding station. These are listed in Section 4.1.4. Measurements of length and depth were made to the nearest centimetre with a 1m ruler. The percentage vegetative cover of each station was assessed by visualising a cube around the station, with the ground as base, and assessing the the extent of cover on each of the other faces of the cube. This gives a maximum reading of 80% since stations were selected to facilitate observation from the opposite bank and thus the face of each cube nearest the river was always free of vegetation. Strength of current was assessed by measuring the time taken for a matchstick to travel 10m, commencing 5m above the feeding station approximately 0·5m from the bank. Flow is expressed in metres per minute.

Of the eleven feeding stations originally used, two had to be abandoned, one because of flooding and one because of heavy use by anglers. The dropping boards were abandoned early in the study as they were used only sporadically during the first period of observation and not at all during the second period of observation.

3.2. Laboratory Study

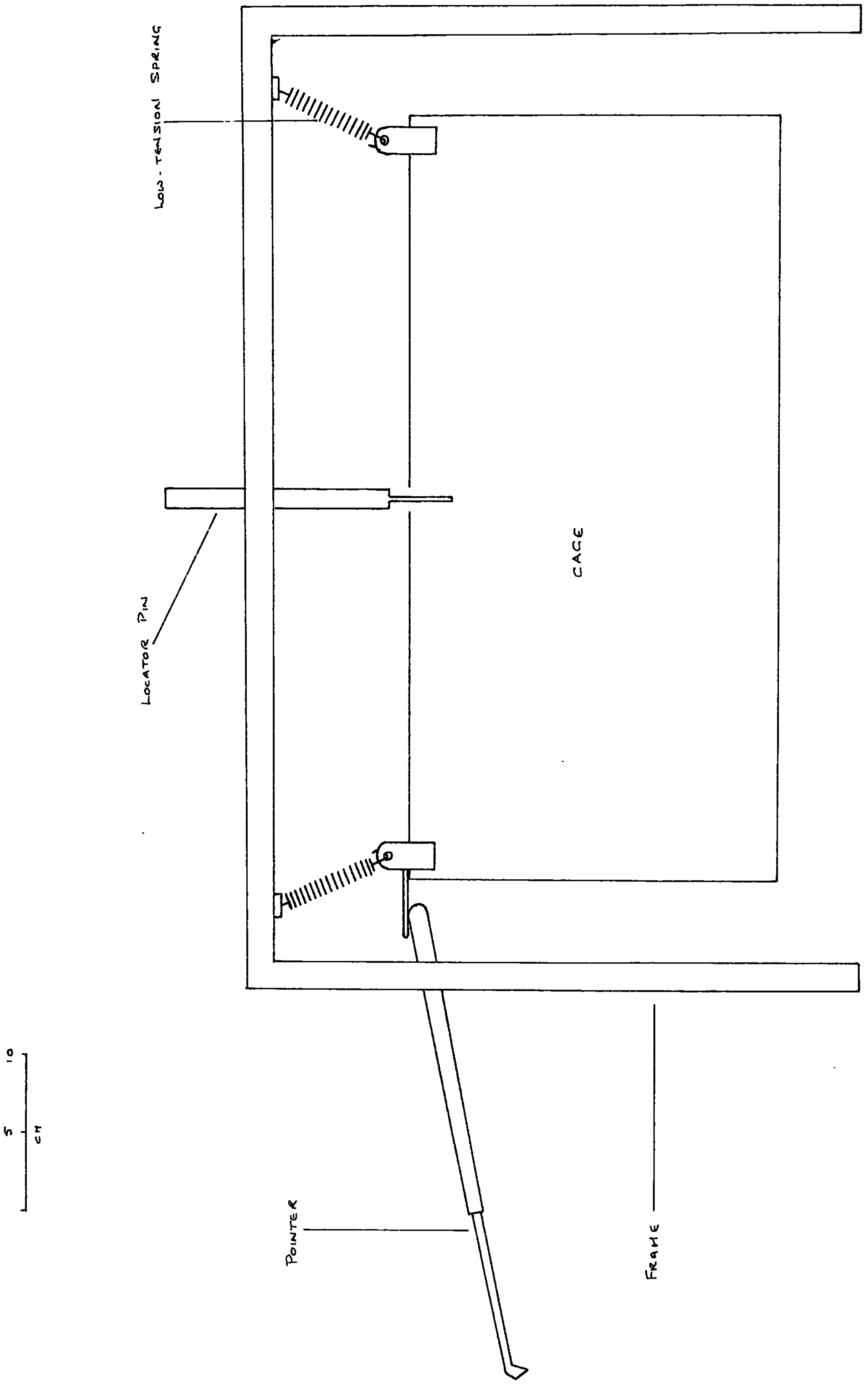
The actograph used in this study consisted of a steel frame in which a cage was suspended by four low-tension springs. The frame measured 45cm x 30cm x 30cm and the cage 36cm x 19cm x 17cm (Figs 2 and 3). A locating pin ran from the frame, through the top of the cage, which helped to direct movements of the cage vertically. A metal plate projecting beyond the lip of the cage transmitted movements to a lever mounted on the frame and a pointer at the end of the lever made a mark on smoked paper attached to a clockwork drum which revolved once every twenty five hours. The pattern obtained on the smoked paper was preserved by applying a coat of dilute shellac.

3.3. Capture and Maintenance of Experimental Animals

Trapping was carried out at the beginning of June and the beginning of August at three sites. The traps used were a modification of the design used by Lockie (1966) for catching weasels , _Mustela nivalis_ and stoats, _Mustela erminea_, and were baited with carrot.

Five traps were set for a week in early June at South Burn, Chester-le-Street (map ref. NZ496277) and visited at 09:00 and 21:00 each day. During this time two male water voles were caught, one of which subsequently died. A week later fifteen traps were set on a pond and a stream at Croxdale Hall, Sunderland Bridge (map ref. NZ 3827). When these traps were visited the following morning six had been stolen and seven otherwise vandalised. The remainder were taken up. Fifteen more traps were set on the River Wear between Shincliffe Village and Old Durham Beck (map ref NZ 415286) prior to the field study and visited twice daily for three days. During this time two female

Fig 2. Actograph apparatus - side view.



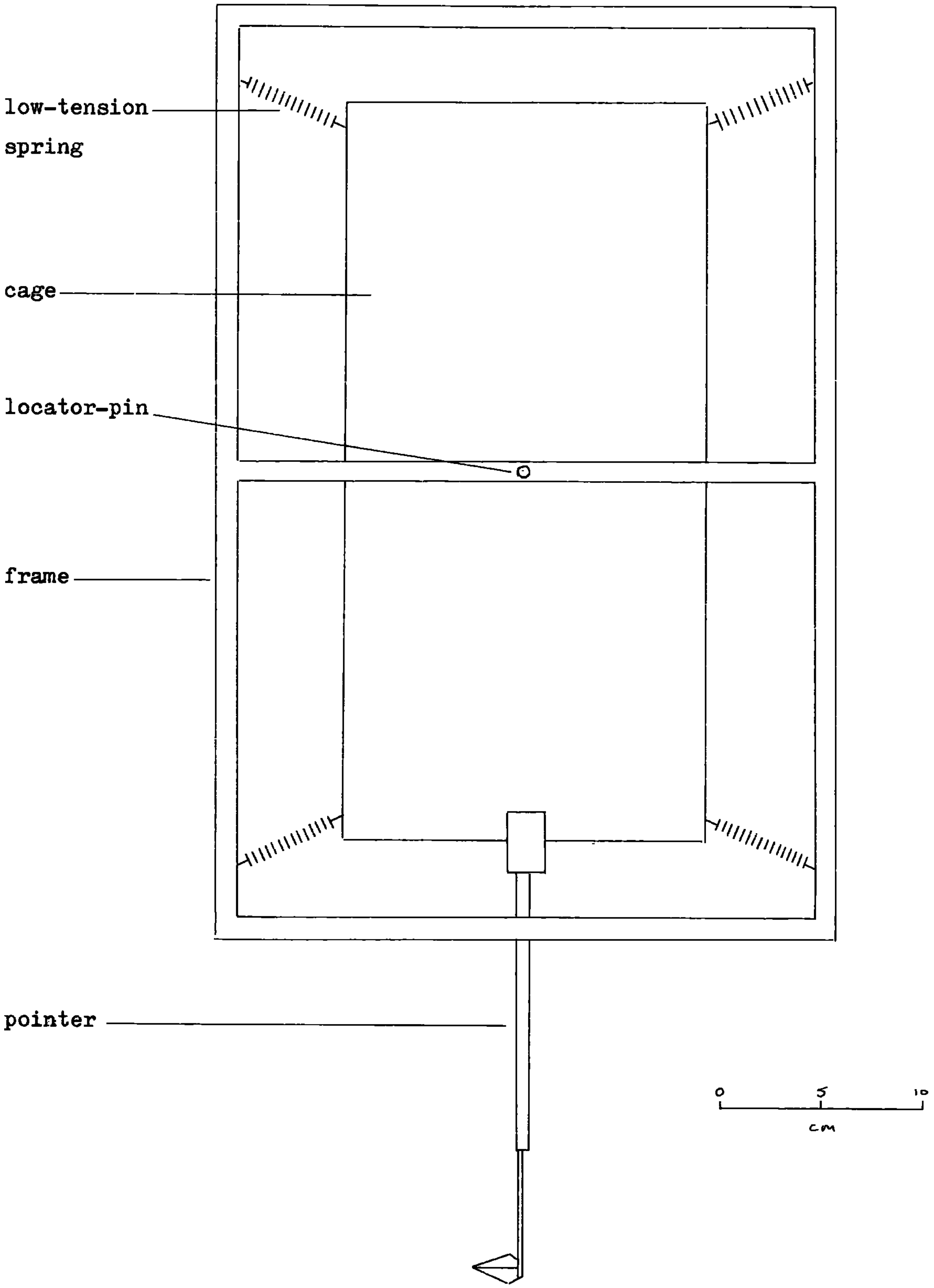


Fig 3. Actograph apparatus - from above.

voles were caught. A further trapping at the same site in early August, after the field study had ended, yielded one female and one male.

The captive animals were kept in large wire cages, approximately 60cm x 60cm x 45cm, when not in the actograph apparatus. Water was supplied in two pots and the animals were fed on carrot and grass, supplemented by clover. Bedding was provided in the form of straw and cotton wool. At the end of the study the animals were released at a stream (map ref NZ 405274) supporting a small population of water voles.

SECTION 4 RESULTS

4.1. Field Study

4.1.1. The Use of Baits by Other Animals

It became apparent during the preliminary baiting that water voles were not the only animals using the feeding stations. During daylight when baits were taken, individual pieces of carrot were removed completely and any remaining pieces of carrot were left unmarked. Observation had shown that water voles used the stations in this manner. However, during late dusk and darkness at several stations only a part of each piece of carrot, notably the centre, was taken and any remaining carrot tended to be shredded. On these occasions a piece of carrot very rarely disappeared completely and few pieces were left completely untouched. It was thought that Brown Rats, Rattus norvegicus, might be responsible. This was tested in three ways. It is thought that Arvicola rarely wanders far from the water's edge (Ryder 1962, Vincent 1974) and so a bait was set at the top of the bank, approximately 10m from the water, at a point where a rat had been seen earlier. Secondly observation was kept at one of the stations where the bait had been 'spoiled', and when an animal was heard a torch beam directed at the spot. Finally each station was checked for faeces and tracks, it being possible to identify Rattus by these characteristics (Lawrence and Brown 1973, Bang and Dahlstrom 1974). All three checks indicated that rats were present and using the baits and although none of the checks is sufficiently conclusive on its own to justify the association of spoiled baits and rat activity, the three taken together do indicate such an association.

Following this discovery the bait stations were checked at each visit for droppings, tracks and the appearance of bait which, together with the occasional observation, allowed a high degree of accuracy in identifying the animals using the baits. A note was kept of bait removal by Rattus in the hope of obtaining an activity pattern for this species. A watch was constantly kept for signs of animals other than Arvicola and Rattus utilising the feeding stations but no such evidence was found.

4.1.2. A Note on the Analysis of the Results

The frequency diagram of the number of baits taken for each hour (Fig 4) did not closely follow any of those distributions allowing transformation of the data and the application of parametric statistics. The closest approximation appeared to be to the Poisson distribution. The extent to which the data satisfied the Poisson model was tested by $\chi^2 = \frac{s^2(N-1)}{\bar{x}} = 657{\cdot}05$ with 143 df. With more than 100 df. exact values of χ^2 are not available in tables, but an approximation is obtained by looking up the probability of the expression $\sqrt{\chi^2} - \sqrt{2\mathrm{df.} - 1}$ in the table of the normal deviate. In this instance, when expanded, the expression gives a value of 19·37. The probability of a deviation as great as this is $<0{\cdot}0005$. Thus the data cannot be said to approximate to the Poisson distribution and transformation of them is not justified. Throughout the analysis therefore non-parametric statistics have had to be applied. Their use has been further necessitated by the fact that the absolute values of water vole activity increased during the period of study, apparently as a result of the recruitment of juvenile animals to the active population. An analysis based on ranking is thus more likely to be accurate.

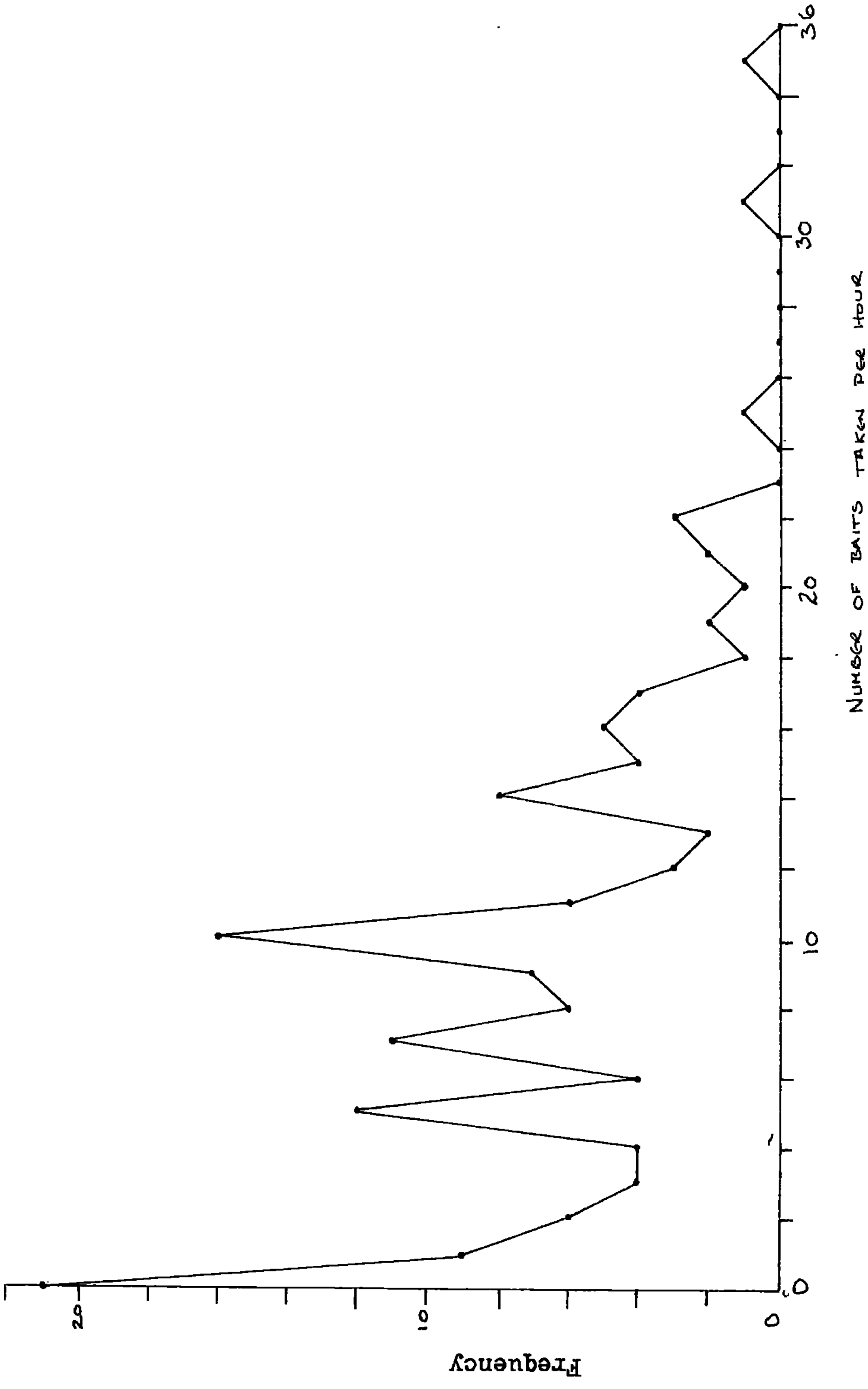
4.1.3. The Diel Pattern of Activity in Arvicola terrestris

The number of baits taken each hour by Arvicola during the six diel periods are given in Table I and represented as histograms in Fig 5. The agreement between these activity patterns was tested by the calculation of Kendall's Coefficient of Concordance, W, for which a value of 0·442 was obtained. The significance of this result was tested by calculating

$$\chi^2 = \frac{12(\sum r_a - \overline{\sum r_a})^2}{kn(n+1)} = 60{\cdot}92; \text{ with 23df. } p<0{\cdot}001$$

It may be concluded that there is close similarity between the activity

Fig 4. Frequency diagram of the number of baits removed by <u>Arvicola</u> in each hour.



observed and hence that during the period of the study the overall pattern of activity did not alter significantly.

Inspection of the histograms in Fig 5 indicates that major peaks of activity of Arvicola occurred just after sunrise and just before sunset, suggesting predominantly crepuscular activity. The diel period was divided into three periods based on light intensity;

i) Night - those hours during which no reading was obtained on the light meter (22:00-04:00).

ii) Day - those hours when light intensity was at a maximum (06:00-19:00).

iii) Dawn and Dusk - those hours when light intensity was rapidly increasing or decreasing (04:00-06:00 and 19:00-22:00).

The distribution of activity between these periods was tested by X^2 for each diel period and for the total results. The calculated values of X^2 are presented in table II. In all cases X^2 is significant at the 0·5% level. In each diel period the largest contribution to X^2 is from greater than expected activity at dawn and dusk, whilst in all except diel period III diurnal activity is very close to the expected value. It is apparent therefore that although the water vole population could be active at any time in the diel period, it was significantly more active at dawn and dusk than would be expected if activity were arrhythmic, and that nocturnal activity was correspondingly lower than expected.

The number of baits removed at each feeding station for each hour is given in Appendix A. It can be seen that at some stations the baits were very heavily utilised (eg station 7) and at others hardly at all (eg station 4). Under these circumstances it is possible that the distribution of activity observed was a reflection of the activity of a small number of individuals rather than the population as a whole. If however the activity pattern is common to the whole population the number of feeding stations used in each hour should give a similar pattern to the number of baits removed. There were insufficient stations for this to be tested for each diel period, but

TABLE I. The number of baits taken by <u>Arvicola</u> during each hour of the six diel periods.

BST	Diel Period I	Diel PeriodII	Diel Period III	Diel Period IV	Diel Period V	Diel Period VI	Total
00:00-01:00	0	0	0	10	1	2	13
01:00-02:00	8	0	10	5	5	15	43
02:00-03:00	0	4	10	10	10	7	41
03:00-04:00	0	5	1	0	6	7	19
04:00-05:00	5	10	15	21	14	9	74
05:00-06:00	17	7	21	16	31	9	101
06:00-07:00	7	8	7	25	16	2	65
07:00-08:00	9	0	2	0	11	18	40
08:00-09:00	1	8	0	15	13	4	41
09:00-10:00	5	0	6	14	17	14	56
10:00-11:00	4	2	10	9	14	10	49
11:00-12:00	5	7	0	2	12	14	40
12:00-13:00	0	0	3	5	1	3	12
13:00-14:00	7	0	1	6	0	5	19
14:00-15:00	3	20	14	0	4	11	52
15:00-16:00	1	9	5	14	8	17	54
16:00-17:00	0	1	2	8	5	17	33
17:00-18:00	10	10	6	9	8	7	50
18:00-19:00	10	10	11	16	16	10	73
19:00-20:00	13	16	22	22	3	22	98
20:00-21:00	10	9	10	15	35	19	98
21:00-22:00	7	7	19	11	12	12	68
22:00-23:00	0	7	14	10	11	11	53
23:00-00:00	5	0	0	1	5	1	12
TOTAL	127	140	189	244	258	246	1204

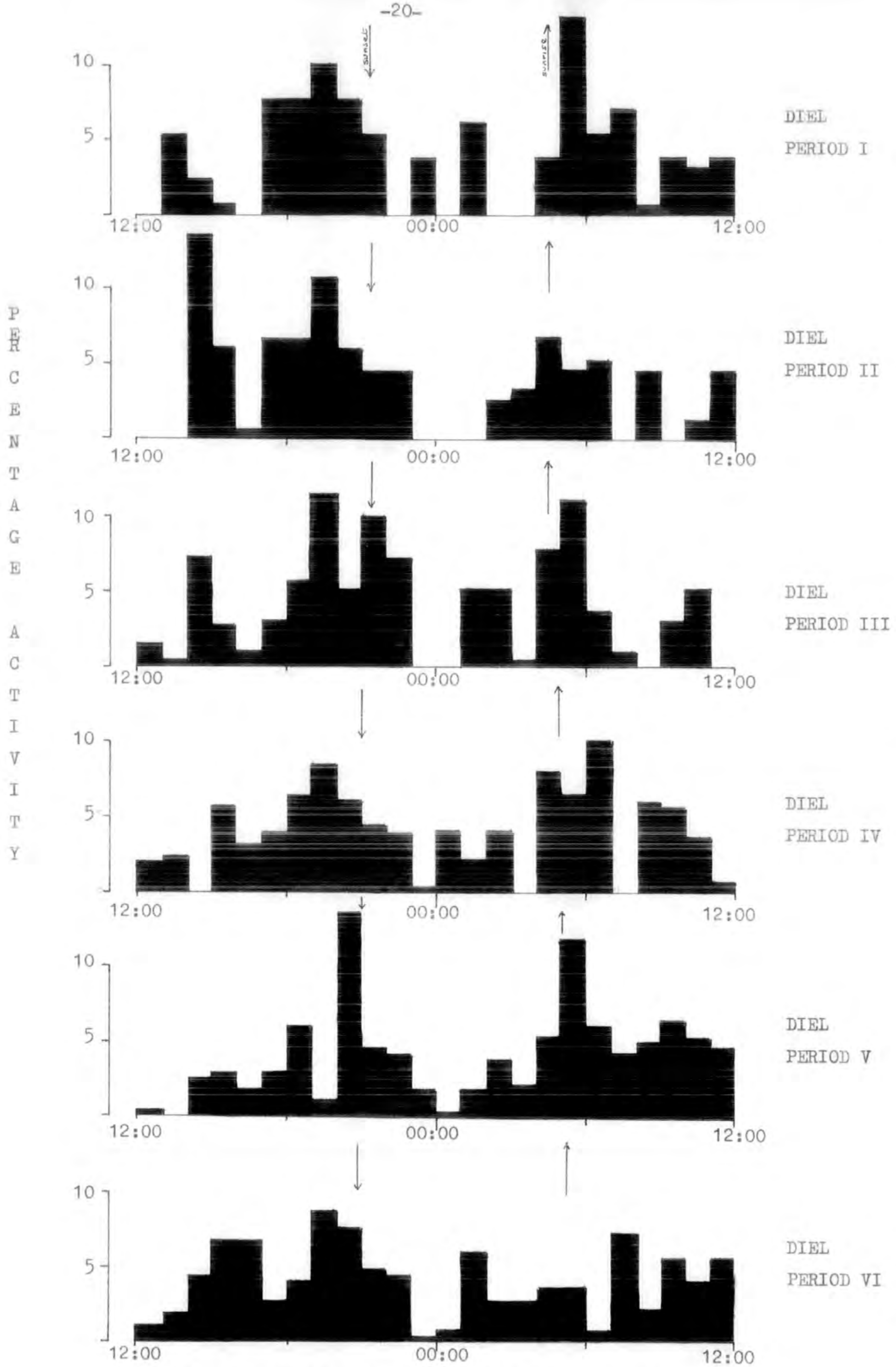


Fig 5. The field activity of Arvicola measured by bait removal.

(all times B.S.T.)

TABLE II. The distribution of field activity in <u>Arvicola</u>, as measured by bait removal, within six diel periods.

DIEL PERIOD	$\frac{(O-E)^2}{E}$ DAYLIGHT	$\frac{(O-E)^2}{E}$ NIGHT	$\frac{(O-E)^2}{E}$ DAWN AND DUSK	χ^2	p
1	0·71*	11·28*	26·00	37·99	$< 0{\cdot}001$
2	0·01*	10·31*	13·79	24·11	$< 0{\cdot}001$
3	12·01*	3·06*	55·25	70·32	$< 0{\cdot}001$
4	0·61*	10·25*	22·67	33·53	$< 0{\cdot}001$
5	1·61*	10·56*	31·13	43·30	$< 0{\cdot}001$
6	0·01*	5·82*	7·84	13·67	$< 0{\cdot}001$
1–6	6·74*	46·73*	136·52	189·99	$< 0{\cdot}001$

* signifies that the observed level of activity was less than the expected values.

For definitions of daylight, night and dawn and dusk see the text.

comparison can be made with the totals for all diel periods. The number of stations used in each hour have been summed and are presented in Table IIIa and represented as a histogram in Fig 6. The total baits removed are presented in Table IIIb and represented as a histogram in Fig 7. The degree of similarity between these two sets of data has been tested by calculating Spearman's Rank Correlation Coefficient, R_s, for which a value of 0·844 was obtained. The significance of this result was tested by the calculation of Student's t, $= R_s \frac{n-2}{1-R_s^2} = 7{\cdot}38$; with 22 df. $p < 0{\cdot}0005$. Similarly the distribution of activity measured by site utilisation is in agreement with that measured by bait removal ($\chi^2 = 21{\cdot}53$; with 2 df. $p < 0{\cdot}001$) the largest contribution to χ^2 being due to greater than expected crepuscular activity, whilst diurnal activity is very close to the expected value. The agreement between the two activity patterns is thus highly significant and it can be assumed that the pattern of activity obtained by bait removal is representative of that exhibited by the whole population, not just one or two individuals.

It was decided to test the distribution of activity at the five most utilised feeding stations to see what variation existed between smaller components of the population. Observation showed that one of the factors affecting the utilisation of stations was the distance of the nearest burrow system (see Section 4.1.4. and Discussion). It might be expected that most of the visits to a heavily used feeding station would be made by a small number of individuals, for example a family unit. The number of baits removed from these stations during the period of study are detailed in Table V, and the χ^2 values obtained are shown in Table IV below.

STATION	χ^2	p	MAXIMUM ACTIVITY
5	33·79	$< 0{\cdot}001$	Nocturnal
6	44·23	$< 0{\cdot}001$	Crepuscular
7	64·65	$< 0{\cdot}001$	Crepuscular
8	46·66	$< 0{\cdot}001$	Crepuscular
9	70·94	$< 0{\cdot}001$	Crepuscular

<u>TABLE IV.</u> The distribution of activity at the five most used feeding stations.

00:00 -01:00	01:00 -02:00	02:00 -03:00	03:00 -04:00	04:00 -05:00	05:00 -06:00	06:00 -07:00	07:00 -08:00	08:00 -09:00	09:00 -10:00	10:00 -11:00	11:00 -12:00
5	9	10	6	14	18	18	12	13	19	12	10
12:00 -13:00	13:00 -14:00	14:00 -15:00	15:00 -16:00	16:00 -17:00	17:00 -18:00	18:00 -19:00	19:00 -20:00	20:00 -21:00	21:00 -22:00	22:00 -23:00	23:00 -24:00
4	8	8	12	8	8	17	21	20	12	10	5

TABLE 111a The total number of feeding stations utilised by *Arvicola* in each hour of six diel periods.

00:00 -01:00	01:00 -02:00	02:00 -03:00	03:00 -04:00	04:00 -05:00	05:00 -06:00	06:00 -07:00	07:00 -08:00	08:00 -09:00	09:00 -10:00	10:00 -11:00	11:00 -12:00
13	43	41	19	74	101	65	40	41	56	49	40
12:00 -13:00	13:00 -14:00	14:00 -15:00	15:00 -16:00	16:00 -17:00	17:00 -18:00	18:00 -19:00	19:00 -20:00	20:00 -21:00	21:00 -22:00	22:00 -23:00	23:00 -24:00
12	19	52	54	33	50	73	98	98	68	53	11

TABLE 111b The total number of baits removed by *Arvicola* in each hour of six diel periods.

Fig 6. The total number of feeding stations utilised by <u>Arvicola</u> in each hour of the diel period. (all times B.S.T.)

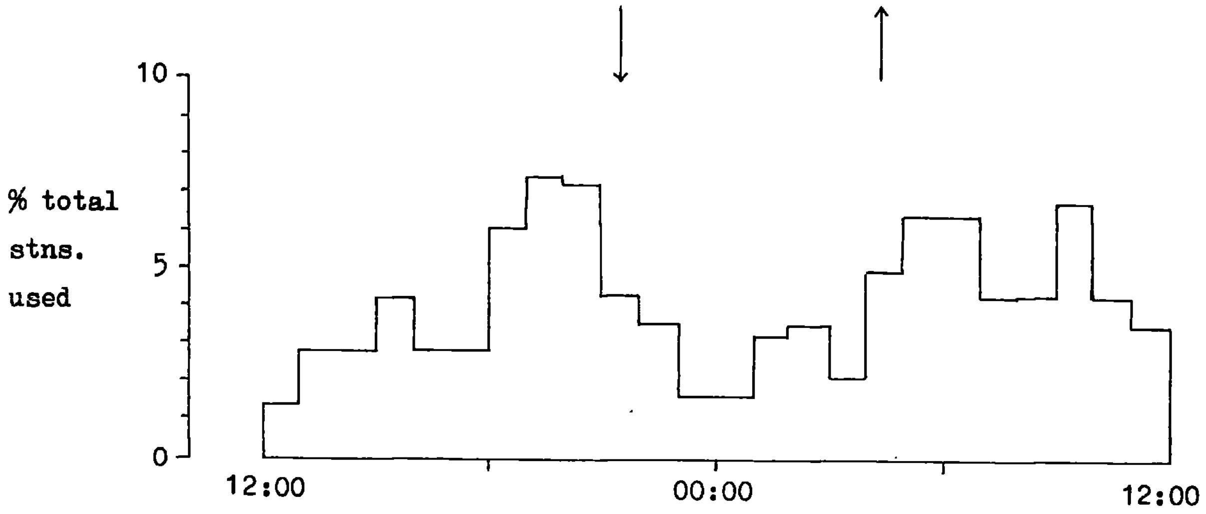


Fig 7. The total number of baits removed by <u>Arvicola</u> in each hour of the diel period. (all times B.S.T.)

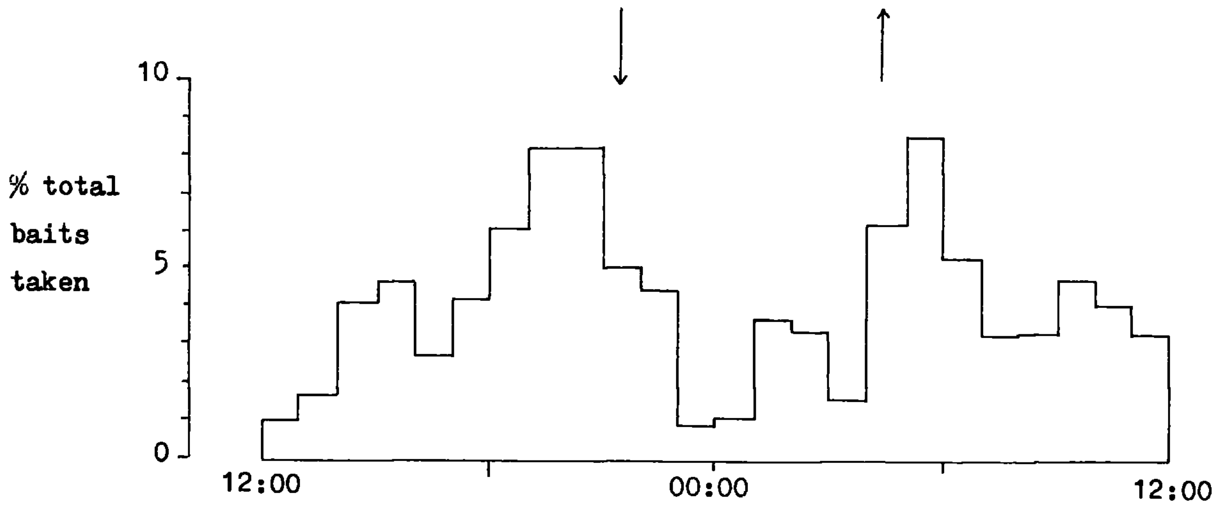


TABLE V. The total number of baits taken in each hour of six diel periods at each of the five most utilised feeding stations.

BST	SITE 5	SITE 6	SITE 7	SITE 8	SITE 9
00:00-01:00	1	0	6	0	2
01:00-02:00	3	0	15	5	0
02:00-03:00	17	1	11	5	0
03:-04:00	7	0	2	10	0
04:00-05:00	4	0	30	17	10
05:00-06:00	0	22	20	26	19
06:00-07:00	5	7	21	11	11
07:00-08:00	13	0	0	15	6
08:00-09:00	3	0	13	14	1
09:00-10:00	2	15	7	5	13
10:00-11:00	2	0	15	13	14
11:00-12:00	5	3	7	19	1
12:00-13:00	1	0	0	8	0
13:00-14:00	0	5	3	4	0
14:00-15:00	0	10	20	7	8
15:00-16:00	0	7	21	16	8
16:00-17:00	0	10	4	12	0
17:00-18:00	0	10	25	13	0
18:00-19:00	10	1	30	19	2
19:00-20:00	9	5	28	19	19
20:00-21:00	12	3	25	21	16
21:00-22:00	19	13	18	8	0
22:00-23:00	25	0	9	4	0
23:00-00:00	0	0	1	2	3

At all sites except station 5 nocturnal activity was much less than expected by chance and diurnal activity approximated to the expected values. At station 5 diurnal activity was much less than expected and both nocturnal and crepuscular activity were greater than expected, nocturnal activity being slightly greater than crepuscular activity.

The individual feeding stations do not show any great variation from the overall pattern of activity obtained and these results support the contention that the field population as a whole is exhibiting a crepuscular pattern of activity at the expense of nocturnal activity.

4.1.4. The Effects of Station Habitat on Bait Removal

In an effort to establish the extent to which choice of feeding station affected bait removal various physical parameters for each station were measured. These were selected on the basis of what the author considered might be important factors in *Arvicola's* choice of feeding area. All the factors nad previously been found to be of some importance in habitat selection in *Arvicola* (Ashby, Harling and Whiles, 1969, Zejda and Zapletl 1969). The parameters selected for measurement were;

Distance to nearest burrow entrance
Vegetative cover of station
Water depth at edge of bank
Water depth at 1m from bank
Distance of station from water's edge
Bottom type
Strength of current

Measurements were made after an extensive dry spell when the river was very low, and consequently water depths and current strengths are minimum figures and distance from the water's edge are maximum figures. As the measurements were made at the end of July, percentage vegetative cover will approximate to the maximum for the year. The results are presented for each site in Table VI.

FEEDING STATION	BOTTOM TYPE	% COVER	MAXIMUM DISTANCE TO WATERS EDGE (cm)	MINIMUM DEPTH AT WATERS EDGE (cm)	MINIMUM DEPTH 1M OUT FROM EDGE (cm)	MINIMUM CURRENT ($M. min^{-1}$)	MINIMUM OBS. DISTANCE TO BURROW (M)	TOTAL BAITS REMOVED
1	SILT	80	20	5	>100	< 1	-*	27
2	STONES + SILT	80	8	1	14	5	> 50	82
3	STONES	80	22	2	50	10	15	87
4	STONES	40	15	1.5	12	6	-*	15
5	SILT	40	7	1	>100	3	40	138
6	SILT	60	8	30	>100	4	60	112
7	STONES + SILT	40	15	20	>100	8	< 5	329
8	SILT	40	9	>100	>100	< 1	< 5	281
9	SILT	40	15	1	20	5	< 5	133

TABLE VI The habitat data for each feeding station
* Not ascertained

In the analysis of these results each factor was divided into two or three groups within the range of measurements obtained (eg percentage cover was divided into $<50\%$ and $>50\%$,) such that each station fell into one or other of these groups and the stations were evenly distributed between the groups, as far as possible without disrupting any natural divisions. The number of baits taken from all the stations in each group of a given parameter was tested against the number of baits taken from other groups of the same parameter by χ^2 and the results are presented in Table VII below.

<u>TABLE VII.</u> The Importance of Different Habitat Factors in Site Utilisation

PARAMETER	χ^2	p	GREATEST CONTRIBUTION TO χ^2	
Distance to nearest burrow entrance*	201·22	$< 0{\cdot}001$	< 5m	+
Vegetative cover	167·46	$< 0{\cdot}001$	$> 50\%$	-
Depth at water's edge	960·73	$< 0{\cdot}001$	> 10cm	+
Water depth at 1m	154·14	$< 0{\cdot}001$	< 1m	-
Distance to water's edge	375·61	$< 0{\cdot}001$	> 20cm	-
Bottom type	177·04	$< 0{\cdot}001$	Stony	-
Strength of current	1·36	$> 0{\cdot}2$	-	

*Not established for stations 1 and 4.

It can be seen that the two most important factors affecting the use of feeding stations are a comparatively great depth of water at the edge of the bank and a short distance from the station to the water's edge. The only factor measured that was of negligible importance was current strength.

4.1.5. The Diel Pattern of Activity in *Rattus norvegicus*

Although rats utilised baits throughout the period of study, they did so infrequently and insufficient data were obtained to give patterns of activity for each diel period. The total number of baits removed in each hour are given in Table IX and represented as a histogram in Fig 8. The distribution

00:00 -01:00	01:00 -02:00	02:00 -03:00	03:00 -04:00	04:00 -05:00	05:00 -06:00	06:00 -07:00	07:00 -08:00	08:00 -09:00	09:00 -10:00	10:00 -11:00	11:00 -12:00
2	7	9	5	1	0	0	1	0	0	0	0
12:00 -13:00	13:00 -14:00	14:00 -15:00	15:00 -16:00	16:00 -17:00	17:00 -18:00	18:00 -19:00	19:00 -20:00	20:00 -21:00	21:00 -22:00	22:00 -23:00	23:00 -24:00
0	1	0	0	0	0	0	0	2	4	6	11

TABLE V111 The total number of feeding stations utilised by *Rattus* in each hour of six diel periods.

00:00 -01:00	01:00 -02:00	02:00 -03:00	03:00 -04:00	04:00 -05:00	05:00 -06:00	06:00 -07:00	07:00 -08:00	08:00 -09:00	09:00 -10:00	10:00 -11:00	11:00 -12:00
10	24	43	22	5	0	0	9	0	0	0	0
12:00 -13:00	13:00 -14:00	14:00 -15:00	15:00 -16:00	16:00 -17:00	17:00 -18:00	18:00 -19:00	19:00 -20:00	20:00 -21:00	21:00 -22:00	22:00 -23:00	23:00 -24:00
0	6	0	0	0	0	0	0	6	9	27	48

TABLE 1X The total number of baits removed by *Rattus* in each hour of six diel periods.

Fig 8. The total percentage of feeding stations utilised by Rattus in each hour of the diel period. (all times B.S.T.)

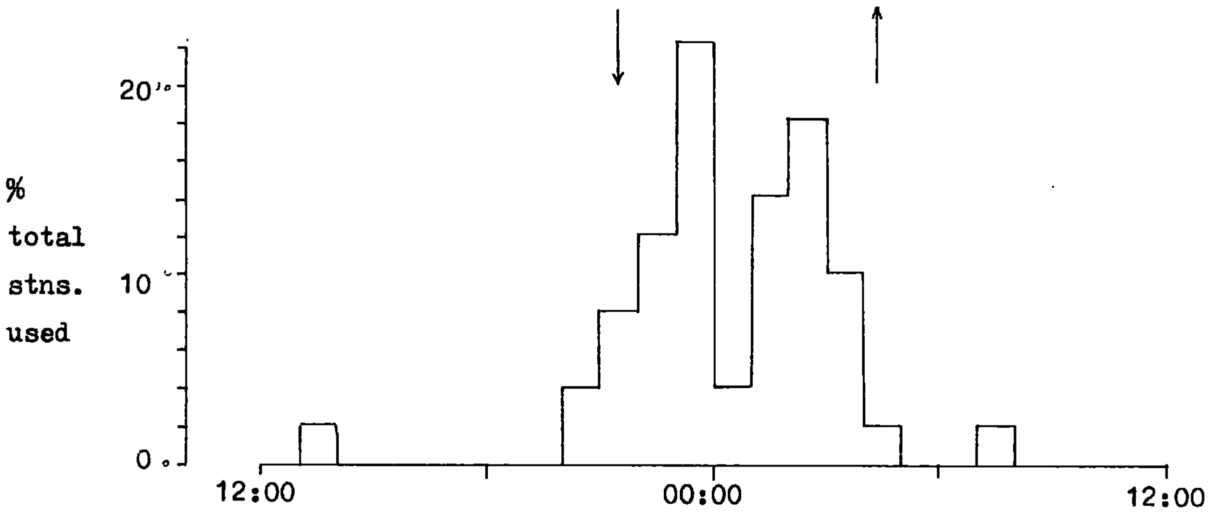
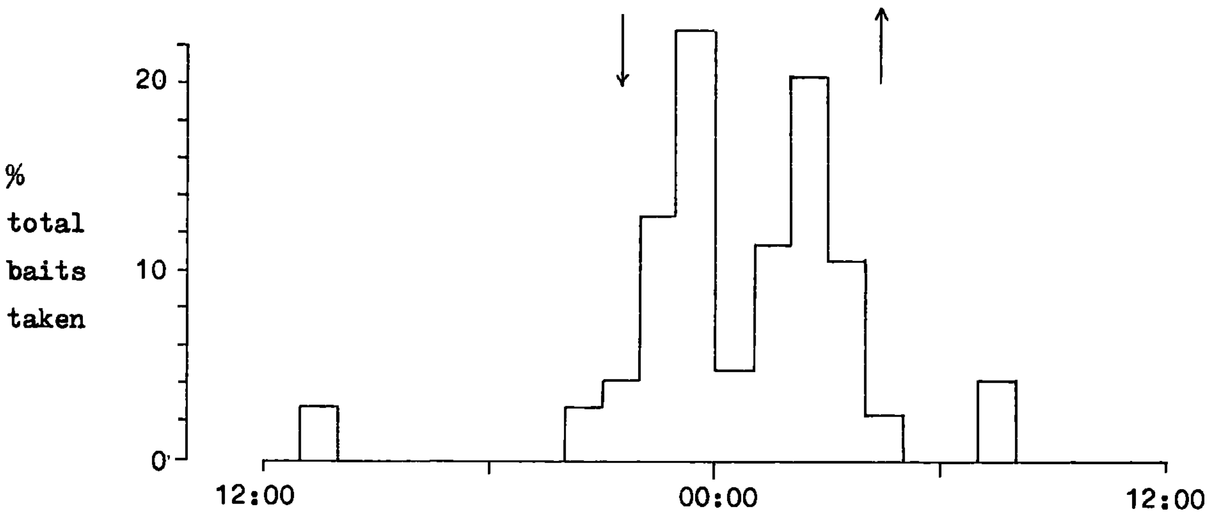


Fig 9. The total percentage of baits removed by Rattus in each hour of the diel period. (all times B.S.T.)



of activity was tested as before and a X^2 value of 384·24 obtained; with 2 df. $p < 0{\cdot}001$. The greatest contribution to X^2 comes from a much larger proportion of nocturnal activity than would be expected by chance. Crepuscular activity was slightly less than expected and diurnal activity much less than would be expected if activity were arrhythmic.

The total number of stations utilised in each hour are given in Table VIII and represented as a histogram in Fig 9. The agreement between these data and those obtained by bait removal was tested by the calculation of Spearman's Rank Correlation Coefficient, $R_s = 0{\cdot}824$, $t = 6{\cdot}822$; with 22 df. $p < 0{\cdot}0005$. Thus there is a highly significant agreement between the two sets of data and it would appear that the activity pattern obtained by bait removal is representative of the whole population.

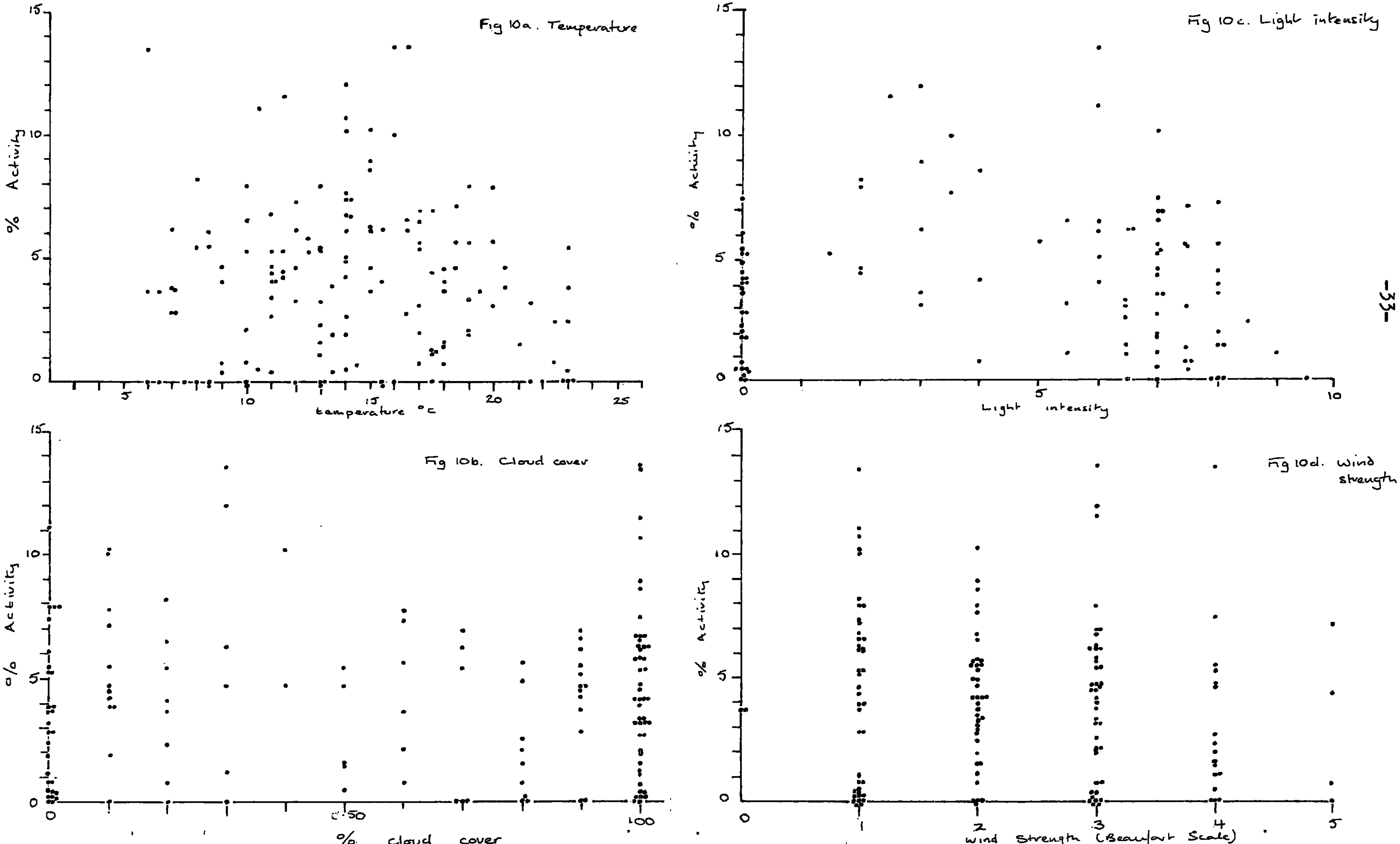
4.1.6. The Effect of Environmental Variables

Rain and human disturbance were negligible during the period of study and insufficient data were obtained to make any assessment of their effect. The values recorded for light intensity, cloud cover, wind strength and temperature ~~are given in Table X. These values have been~~ plotted against the corresponding number of baits taken are given in (Figs 10a-d). ~~and~~ It can be seen by inspection that none of the factors is producing a direct major response. This does not imply that the variables measured had no effect on activity. Table X gives the mean values for these parameters for each hour of the day and night. When the mean value of each factor for each hour of the diel cycle is plotted against the mean activity for the same times (Figs 11a-d) it is seen there is still no discernible relationship between temperature, cloud cover or wind strength and activity, but there does appear to be some non-linear correlation between light intensity and activity, more baits being taken at medi~~an~~um light intensities than when values are very low or high ~~(Figs 11a-d)~~. This result would be expected in a crepuscular animal, regardless of whether or not the animal is in fact responding directly to light intensity and it is not possible to fully assess the biological significance of this correlation on the basis of the limited information available.

TABLE X. The mean values of measured variables for each hour of the diel period.

	TEMPERATURE °C	LIGHT INTENSITY	CLOUD COVER %	WIND STRENGTH Beaufort
00:00 - 01:00	10·6	0	35	1·8
02:00	10·1	0	32	1·8
03:00	9·5	0	25	1·7
04:00	9·3	0	38	1·7
05:00	9·2	1	40	1·5
06:00	9·8	4·5	43	1·5
07:00	12·5	6	48	2
08:00	15	7·3	52	2·3
09:00	15·4	7·5	48	2·7
10:00	16·8	6	68	2·7
11:00	17·8	7·5	66	3
12:00	18·6	7	78	2·8
13:00	18·5	7·3	72	2·5
14:00	19·3	7·8	75	2·6
15:00	19·1	7·5	77	2·8
16:00	18·2	7	78	2·8
17:00	17·4	7	82	3
18:00	16·4	6·5	80	2·3
19:00	15·6	5·8	83	1·7
20:00	15·3	4	73	2·3
21:00	13·3	3·2	65	2·3
22:00	12·6	1·8	42	2·5
23:00	11·1	0	42	2·3
00:00	10·3	0	32	2

Figs 10a-d. Correlation of activity with environmental variables



Figs 11a-d. Correlation of activity with environmental variables (mean values)

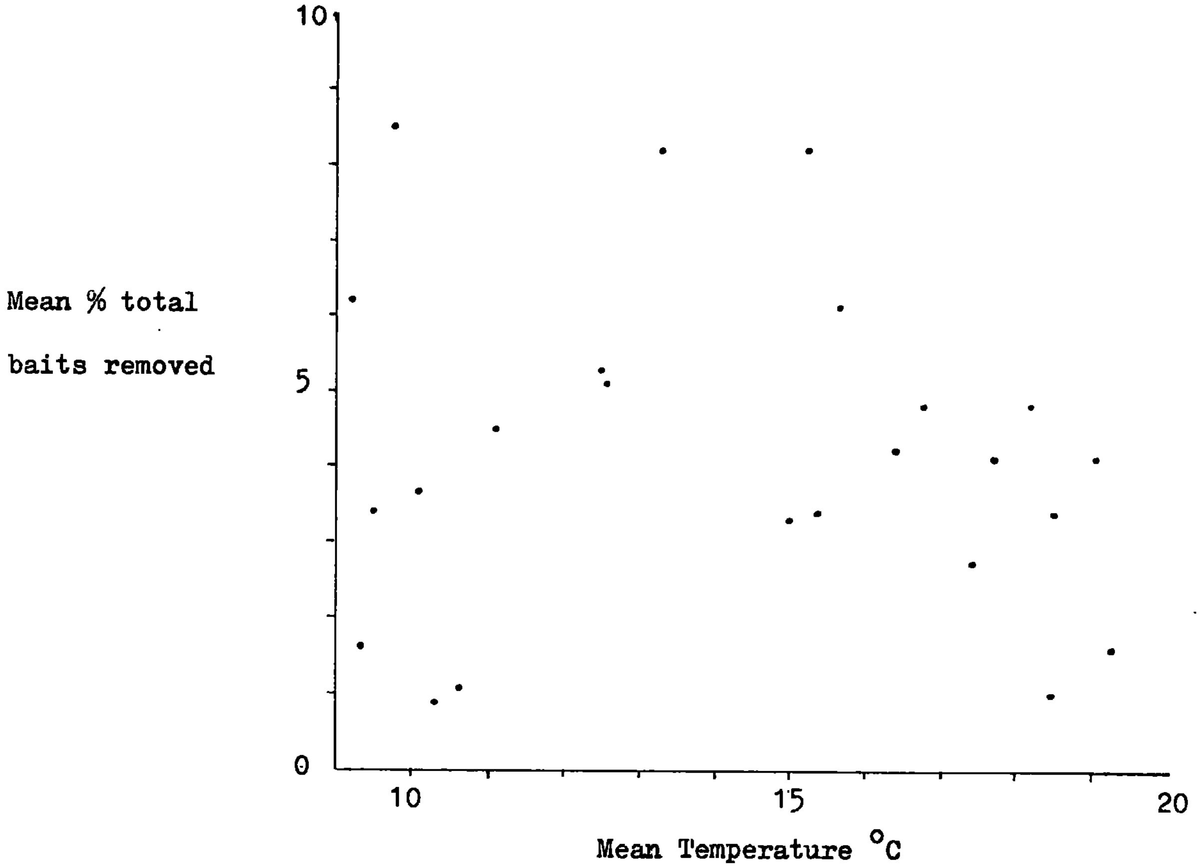


Fig 11a. Temperature.

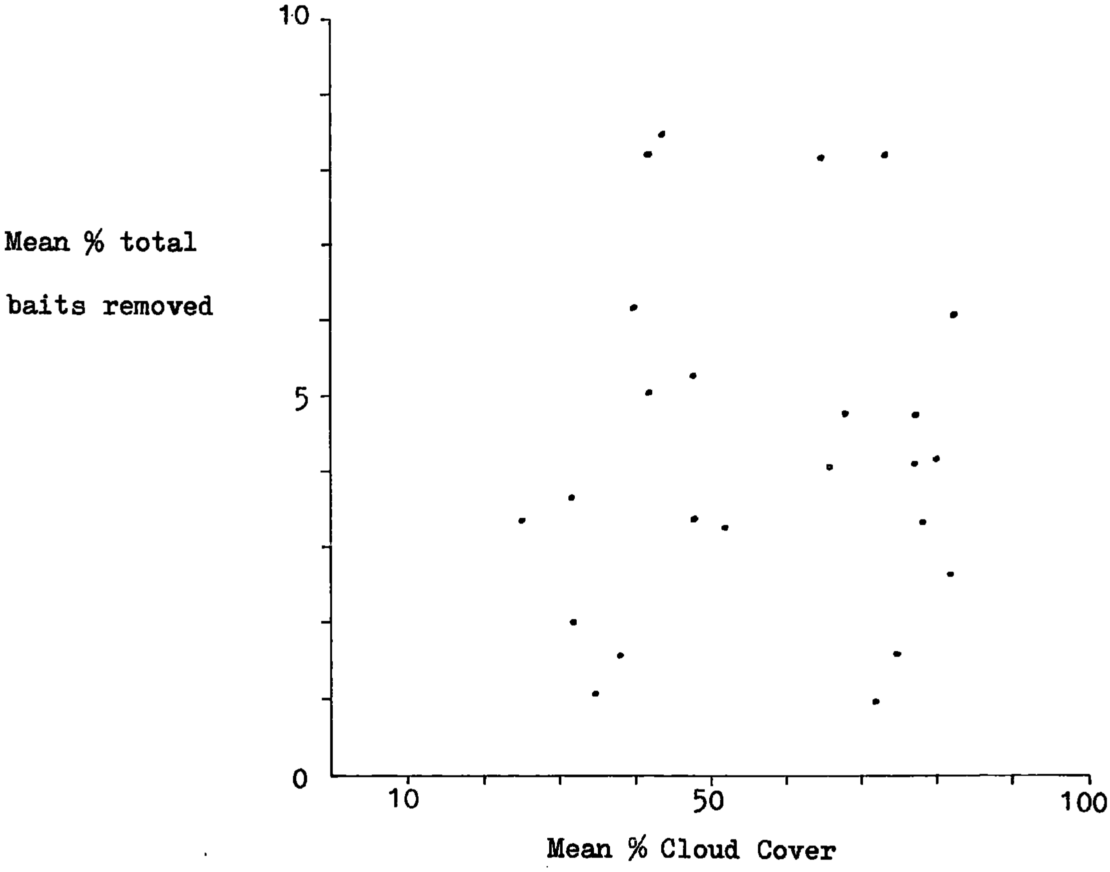


Fig 11b. Cloud cover.

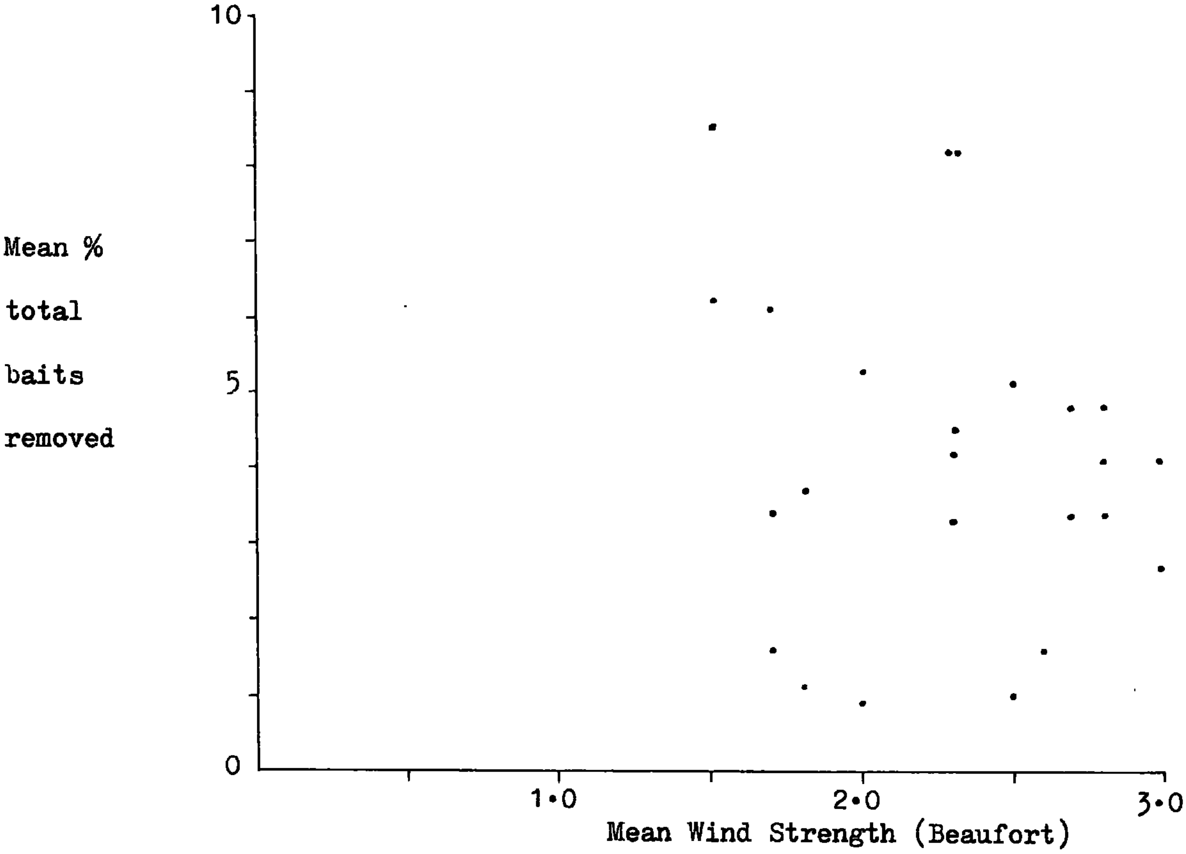


Fig 11c. Wind strength.

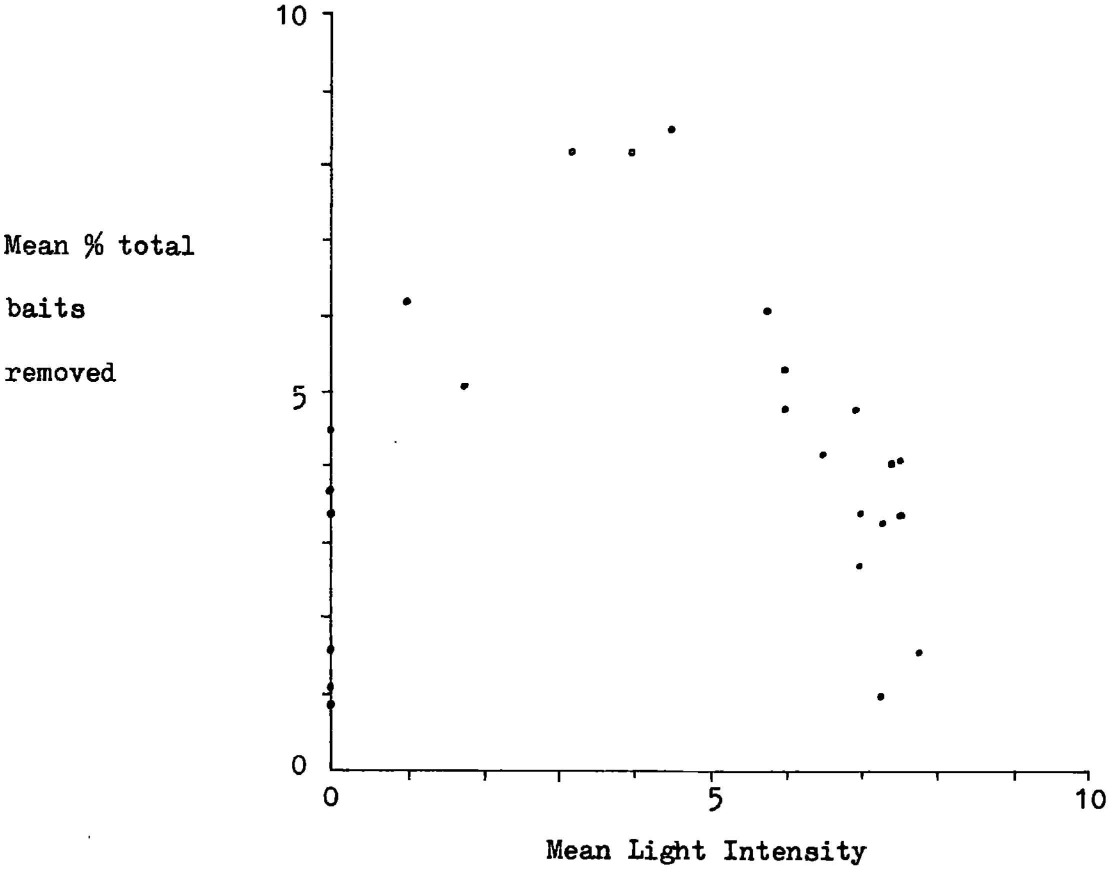


Fig 11d. Light intensity.

A clearer picture of the influence of the variables measured would be provided by plotting their values against activity seperately for each hour, but it was felt that this procedure was not justified with only six readings for each hour of the diel period.

4.1.7. Observation Data

The observations made at feeding station 7 were carried out between visits to the other feeding stations and thus account for approximately half an hour in each hour for which readings are expressed. Although it was possible to distinguish whether or not an animal was feeding, the number of baits taken could not be observed due to overhanging vegetation. Consequently this number refers to baits taken during the whole hour. This means that even if there was a perfect correlation between observed activity and bait removal the similarity between the two sets of data was likely to be only approximate. Bearing this in mind it was felt that if a relationship was found it would provide an indication of the validity of bait removal as an index of activity.

Observed activity has been expressed as an index, derived from the number of minutes during which animals were observed, divided by the total minutes of observation. The results are presented in Table XI and expressed as a scatter diagram in Fig 12. As might be expected there is a great deal of scatter, but it appears that there is some relationship between bait removal and observed activity. It was decided therefore to take average values for both sets of observations for each hour and these results are presented in Table XI and Fig 13. The degree of association was tested by the calculation of Spearman's Rank Correlation Coefficient, $R_s = 0{\cdot}867$, $t = 7{\cdot}88$; with 11 df. $p < 0{\cdot}0005$. It was felt that this result indicated a sufficiently close relationship to justify continuing with the method, but it was decided to carry out a more thorough check at a different station when observation could be continuous, allowing a more realistic comparison between observed activity and bait removal. These observations were made at station 8 in early August and the results are presented in Table XII

TABLE XI. The relationship between bait removal and observed activity: the preliminary observations at station 7.

BST	DIEL PERIOD I		DIEL PERIOD II		DIEL PERIOD III		MEANS	
	Baits Removed	Activity Index	Baits Removed	Activity Index	Baits Removed	Activity Index	Baits Rem.	Actvty Index
09:00–10:00	1	0•19			0	0•06	0•5	0•12
10:00–11:00	2	0•16			10	0•72	6	0•44
11:00–12:00	0	0•07			0	0•00	0	0•03
12:00–13:00	0	0•00			0	0•00	0	0•00
13:00–14:00	3	0•12			0	0•03	1•5	0•08
14:00–15:00	3	0•10	10	0•54	10	0•35	7•6	0•33
15:00–16:00	0	0•00	9	0•44	0	0•00	3	0•15
16:00–17:00	0	0•00	1	0•00	0	0•00	0•3	0•00
17:00–18:00	3	0•11	0	0•00	6	0•43	3	0•18
18:00–19:00	5	0•32	10	0•80	5	0•03	6•6	0•38
19:00–20:00			10	0•50	5	0•11	7•5	0•30
20:00–21:00	2	0•08	8	0•40	0	0•00	3•3	0•16
21:00–22:00	5	0•60	7	0•50			6	0•55

$$\text{Activity Index} = \frac{\text{Total animal-minutes observed}}{\text{Total minutes of observation}} \text{ in each hour}$$

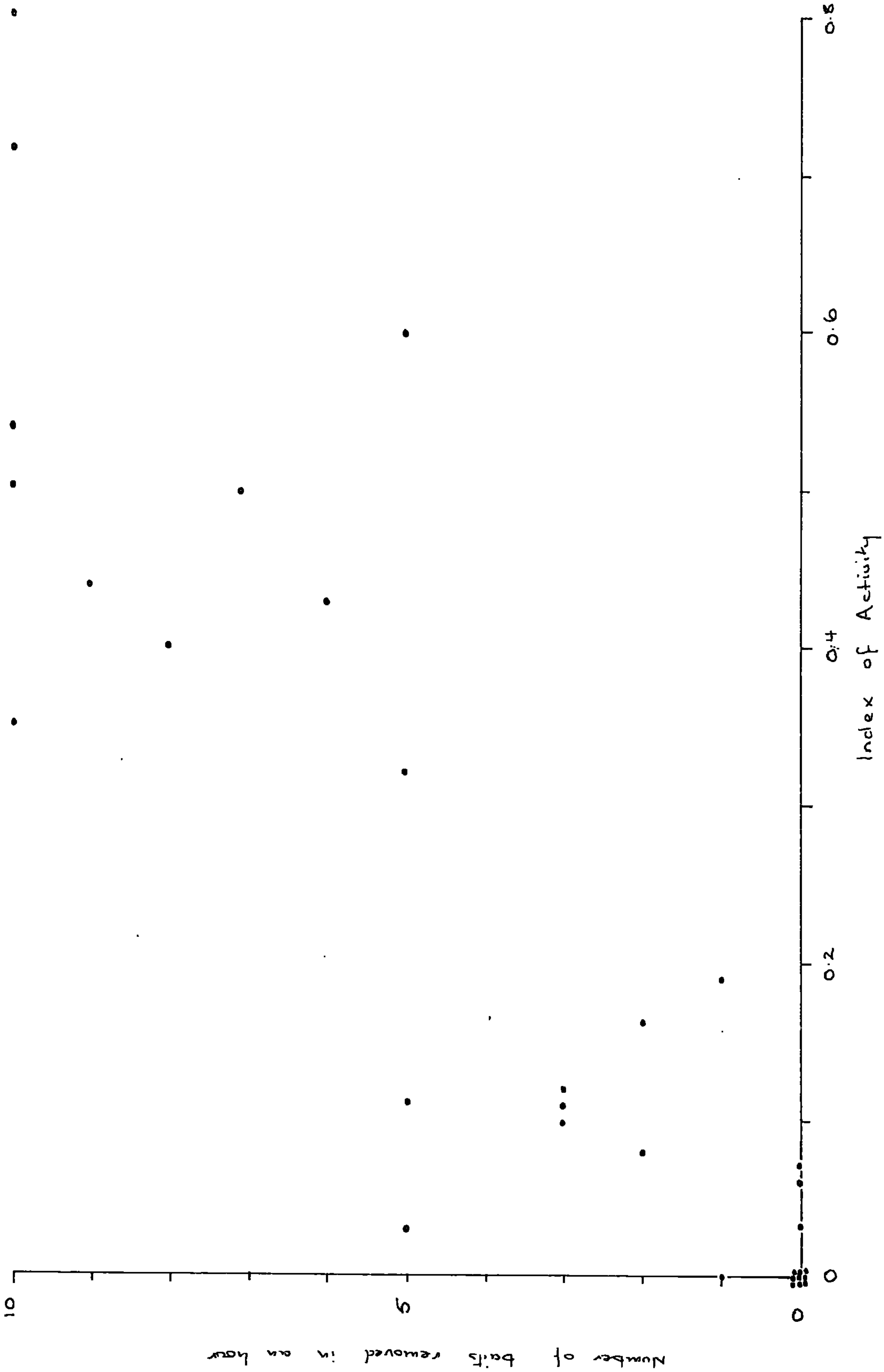


Fig 12. Total observation data at feeding station 7

Fig 13. Mean observation data at feeding station 7.

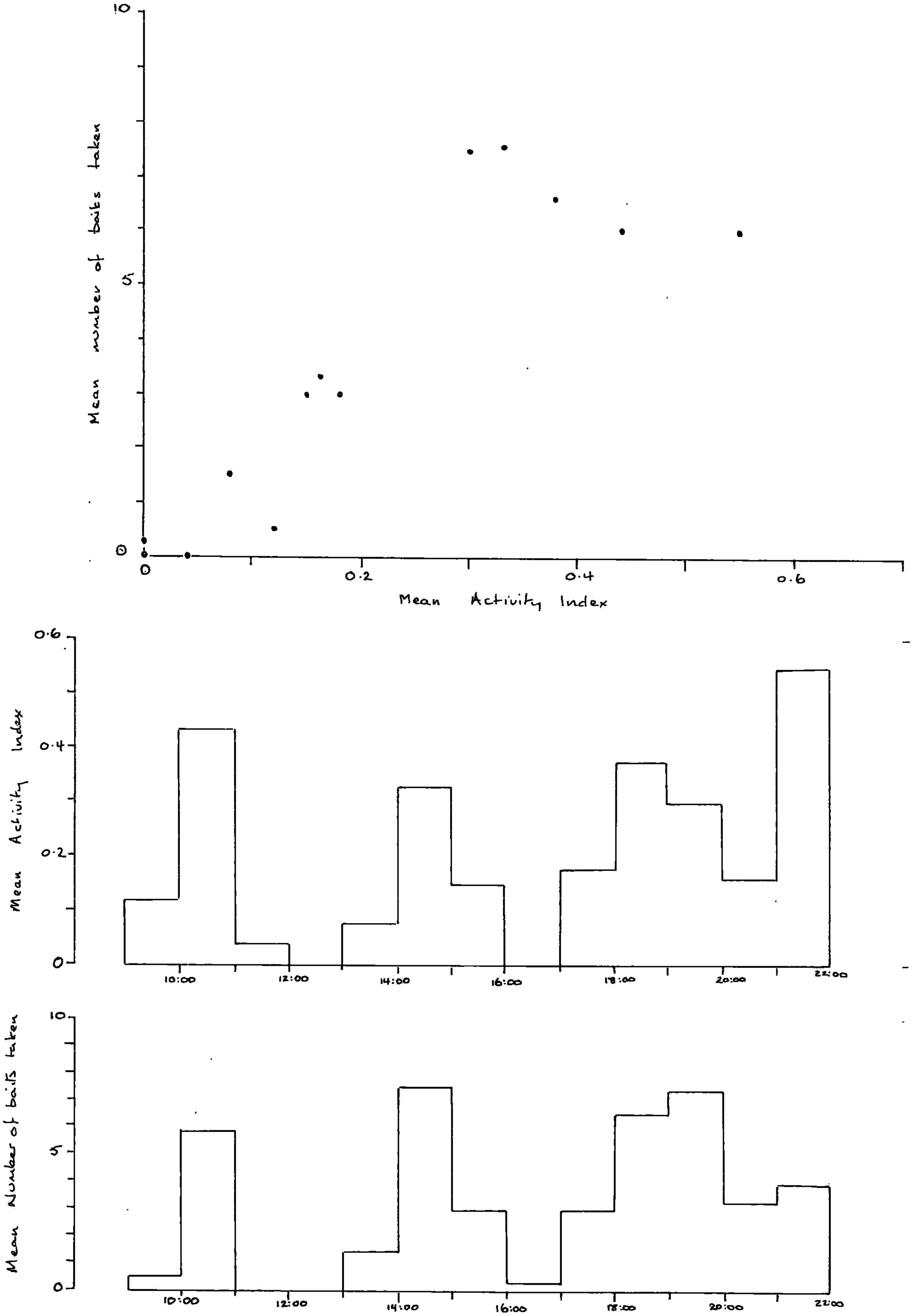
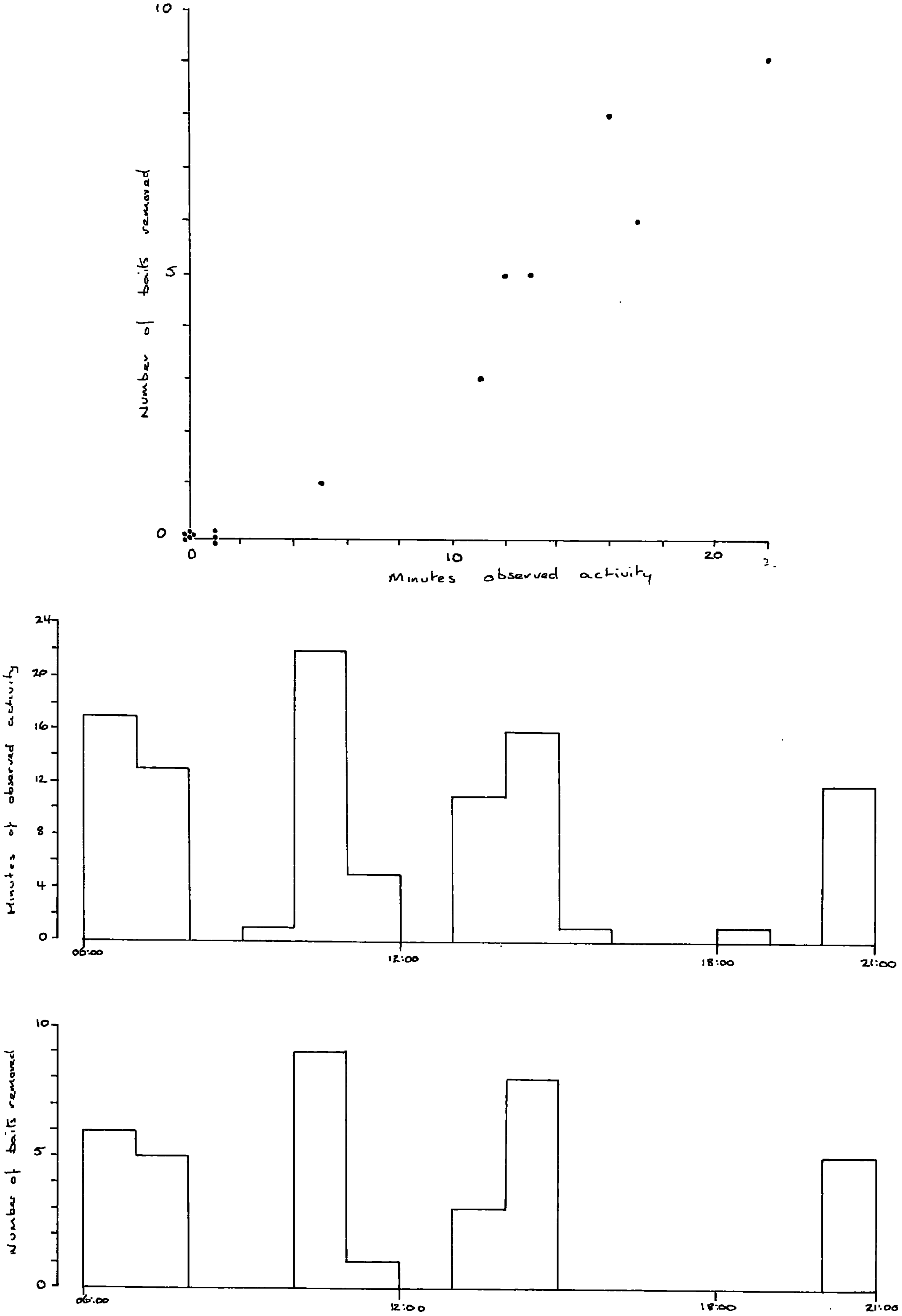


TABLE XII. The relationship between bait removal and observed activity: the observations at station 8.

BST	OBSERVED ACTIVITY (minutes)	BAITS REMOVED
06:00-07:00	17	6
07:00-08:00	13	5
08:00-09:00	0	0
09:00-10:00	1	0
10:00-11:00	22	9
11:00-12:00	5	1
12:00-13:00	0	0
13:00-14:00	11	3
14:00-15:00	16	8
15:00-16:00	1	0
16:00-17:00	0	0
17:00-18:00	0	0
18:00-19:00	1	0
19:00-20:00	0	0
20:00-21:00	12	5

Observations made 11 August - 19 August 1974.

Fig 14. Observation data from feeding station 8.



and Fig 14. The degree of association was tested as before, $R_s = 0{\cdot}83$, $t = 5{\cdot}38$; with 13 df. $p < 0{\cdot}0005$. It is therefore apparent that the number of baits removed from a feeding station is a substantially accurate reflection of the total activity that can be observed in the vicinity of that station.

4.2 Laboratory Study

4.2.1. Representation of Data

Movements of the actograph cage registered as vertical deviations from a horizontal mark on the smoked paper. Two distinct types of activity could be distinguished. Strong movements of the cage produced marks approximately 2-3cm high, usually closely grouped together in blocks of varying length. Between these blocks the horizontal line produced during rest periods was frequently punctuated by small isolated marks approximately 0•5cm high. Observation showed that the major movements were the result of locomotory activity, feeding, grooming and exploration, whilst minor marks were caused by slight stirrings in the nest. The larger marks have been presumed to be equivalent to activity outside the nest and the minor movements ignored in comparison with field data. Where blocks of activity occur they often contain short periods of rest. These have been incorporated as part of the active period since in the field situation the animal is not constantly moving throughout the active period but frequently spends short periods immobile. The results as thus analysed do not therefore indicate the total period of time spent moving but the time during which activity occurs consistently.

The smoked paper revolved past the actograph pointer at a speed of 18•5mm per hour, and thus the smallest unit of time that can be isolated is slightly more than three minutes, corresponding to 1mm of movement of the drum. Activity is expressed to the nearest minute obtained by measuring along the horizontal axis in mm and multiplying by 3•25.

Results were obtained for five animals, each of which spent six diel periods in the actograph under natural daylight conditions, between July and early September. It would have been preferable for the laboratory study to run parallel with the field study, but this was impossible as the actographs had to be designed and constructed during the field study.

4.2.2. The Diel Pattern of Activity of *Arvicola* in the Laboratory

The activity of each animal for each diel period is given as minutes of activity per hour in Appendix B. The mean results for each individual are presented as minutes of activity per hour in Table XIII and Fig 15. The similarity of the patterns obtained between days for each animal was tested by calculating Kendall's Coefficient of Concordance, W, and the results are presented in Table XIV below.

TABLE XIV The Agreement Between Diel Activity Patterns Of *Arvicola*

INDIVIDUAL	W	χ^2	p
WF1	0•45	61•64	$< 0{\cdot}001$
WF2	0•31	42•09	$< 0{\cdot}01$
CM1	0•52	71•74	$< 0{\cdot}001$
WF3	0•60	82•20	$< 0{\cdot}001$
WM1	0•45	62•50	$< 0{\cdot}001$

These results indicate that although individuals may show slight variation in the timing of activity from day to day, over a period of just less than a week these differences are not significant.

The mean activity patterns for each animal, tested against each other for similarity by Kendall's Coefficient of Concordance, give values of $W = 0{\cdot}50$, $\chi^2 = 57{\cdot}83$; with 23 df. $p < 0{\cdot}001$. The agreement between the activity patterns of the animals is thus seen to be highly significant.

The distribution of activity within each diel period between night, dawn and dusk, and daytime, was tested by χ^2 for each animal. The results are given in Table XV below.

TABLE XIII. The mean number of minutes of activity per hour, recorded by the actograph, for individual <u>Arvicola</u> in the laboratory.

BST	WF1	WF2	CM1	WF3	WM1
00:00-01:00	43	41	48	52	43
01:00-02:00	40	24	25	14	52
02:00-03:00	10	58	25	45	52
03:00-04:00	42	50	52	59	54
04:00-05:00	44	14	60	31	37
05:00-06:00	11	29	54	3	20
06:00-07:00	4	38	18	13	25
07:00-08:00	21	11	4	26	25
08:00-09:00	45	17	40	11	7
09:00-10:00	30	35	52	25	28
10:00-11:00	1	29	34	20	23
11:00-12:00	21	21	6	4	9
12:00-13:00	40	6	10	27	21
13:00-14:00	36	31	25	18	31
14:00-15:00	13	10	50	9	18
15:00-16:00	5	18	25	17	29
16:00-17:00	10	24	9	8	23
17:00-18:00	21	21	12	25	15
18:00-19:00	10	19	20	17	33
19:00-20:00	18	16	18	23	22
20:00-21:00	16	10	21	13	17
21:00-22:00	30	29	45	41	51
22:00-23:00	17	60	50	59	53
23:00-00:00	44	60	60	58	31

Individuals are categorised according to origin (W = R. Wear, Durham, C = South Burn, Chester-le-Street), sex (M = male, F = female) and order of capture of each sex at each site. Categories are for identification purposes only.

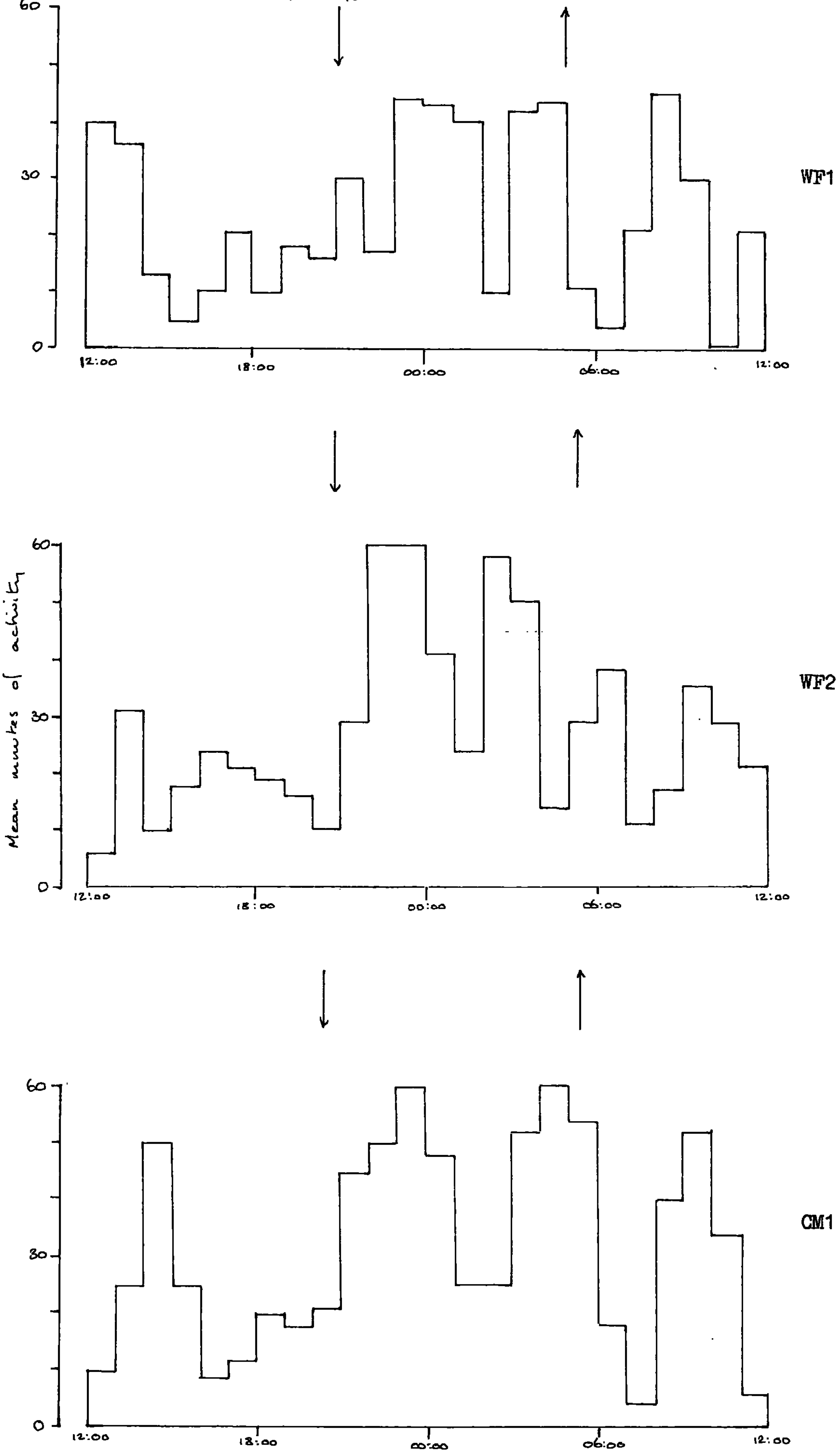


Fig 15. Mean activity patterns of individuals as recorded by actograph in the laboratory. (all times B.S.T.)

contd..

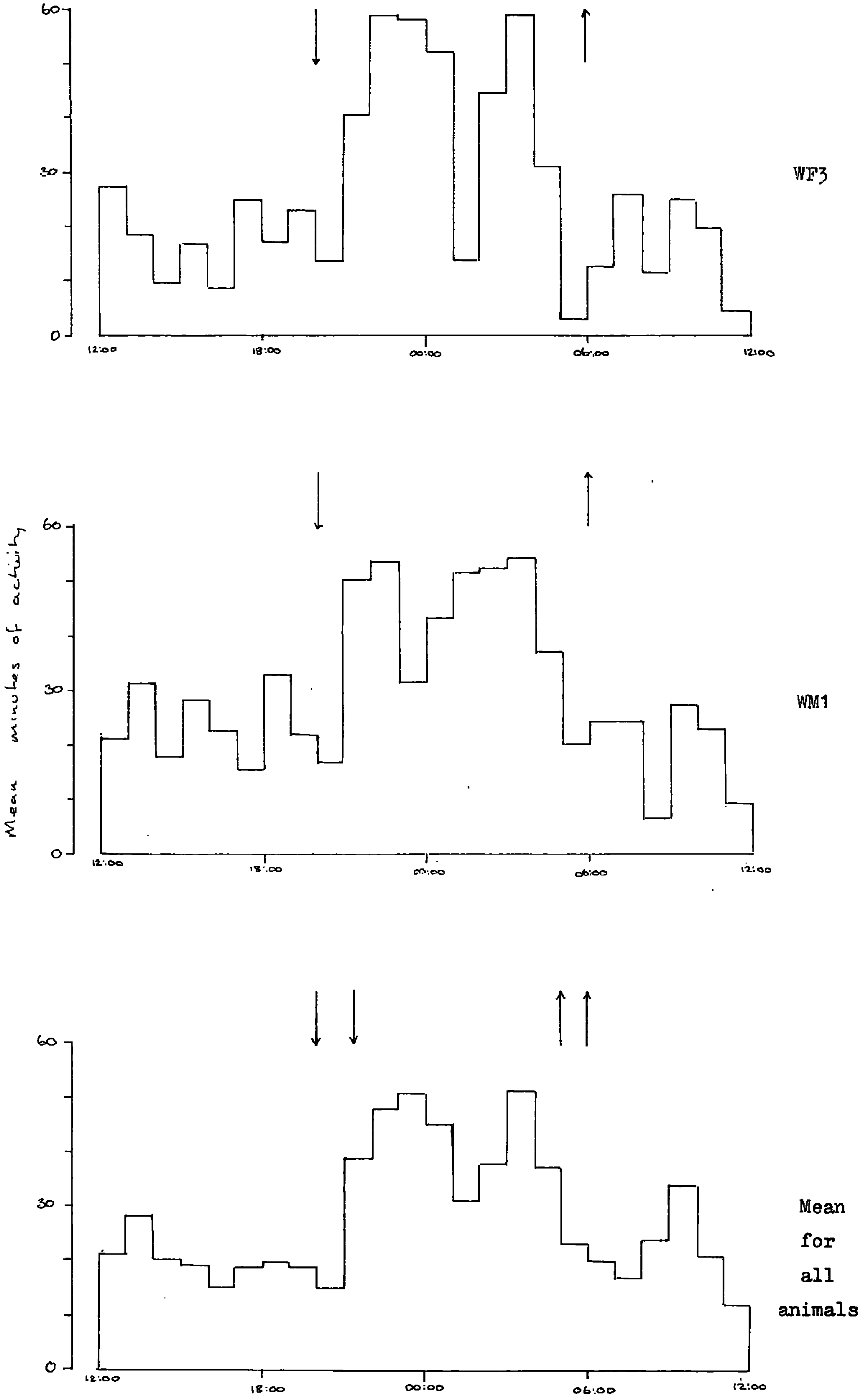


Fig 15. (contd). Mean activity patterns of individuals as recorded by actograph in the laboratory. (all times B.S.T.)

TABLE XV The Distribution of Activity of *Arvicola* in the Laboratory

INDIVIDUAL	DAY 1	DAY2	DAY 3	DAY 4	DAY 5	DAY 6
WF1	87·62*	19·86	12·25†	7·45▫	96·23	70·96
WF2	225·10	76·35	155·87	117·34	133·30	106·02
CM1	90·10	67·32	127·45	64·01	172·84	55·95*
WF3	110·70	243·70	145·80	146·20	232·40	197·30
WM1	69·88	97·90✳	123·90	132·90	172·90	173·10

The greatest contribution to X^2 is more than expected nocturnal activity except:

* More than expected crepuscular activity

✳ Less than expected crepuscular activity

$p < 0{\cdot}001$ except:

† $p < 0{\cdot}005 > 0{\cdot}001$

▫ $p < 0{\cdot}025 > 0{\cdot}02$

In all cases diurnal activity is less than expected and nocturnal activity is greater than expected. Of the thirty diel periods for which readings were taken, twenty eight showed a strong nocturnal trend and two, from the same animal, showed a crepuscular trend. It can be concluded therefore that in a very simple laboratory environment, under long-day summer light conditions, the animals under study showed a strongly nocturnal pattern of circadian activity. Further, the pattern exhibited was maintained by individuals over several days and the patterns exhibited by different individuals were significantly similar. Inspection of the histograms in Fig 15 shows that for all animals activity is not at a continuously high level throughout the night, but shows a persistent lull of 1-2hr partway through the dark period. In all animals except WM1 this lull occurs approximately between 01:00 and 03:00, but in WM1 it occurs between 23:00 and 00:00. Nocturnal activity is thus made up of two quite distinct peaks of activity, one after dusk and the second before dawn.

The total activity exhibited by each animal in each of the diel periods

TABLE XVI. The total activity exhibited by each individual in the actograph for each of six diel periods. (mins)

	DIEL PERIOD I	DIEL PERIOD II	DIEL PERIOD III	DIEL PERIOD IV	DIEL PERIOD V	DIEL PERIOD VI
WF1	523	571	567	623	571	567
WF2	604	754	668	599	685	724
CM1	761	782	794	816	741	676
WF3	586	644	637	614	627	604
WM1	884	571	621	814	652	770

is shown in Table XVI. The variation between days has been tested by X^2, the results being presented in Table XVII.

TABLE XVII The Variation in Total Activity Between Days in Arvicola.

INDIVIDUAL	X^2	p
WF1	8•75	$<0\cdot2 >0\cdot1$
WF2	28•95	$< 0\cdot001$
CM1	16•11	$< 0\cdot01 > 0\cdot005$
WF3	3•66	$> 0\cdot5$
WM1	104•31	$<0\cdot001$

It can be seen that in two individuals, WF2 and WM1, there is a highly significant variation in the total activity exhibited between days, whereas in the individuals WF1 and WF3 there is no such variation. Such lability existing within a population while the overall circadian rhythm remains unaltered, could be a factor of importance if it occurs in the field.

Activity at the individual level occurs in pulses, separated by periods of rest, as shown in the histograms of activity for each individual for each diel period (Figs 16-20). The length of each active period and rest period has been measured for each individual for each diel period. The results are presented in Appendix C. The mean results for the two components of the activity cycle are presented in tables XVIII and XVIX below.

TABLE XVIII The Mean Lengths of Active Periods in Arvicola (expressed in mins).

INDIVIDUAL	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	GRAND MEAN
WF1	119	110	119	111	118	117	116
WF2	97	65	104	86	108	104	96
CM1	152	152	152	149	143	130	146
WF3	82	104	109	96	89	104	97
WM1	114	77	128	165	109	128	122

Fig 16. Activity of WF1 for each of six diel periods in the laboratory.

(all times B.S.T.)

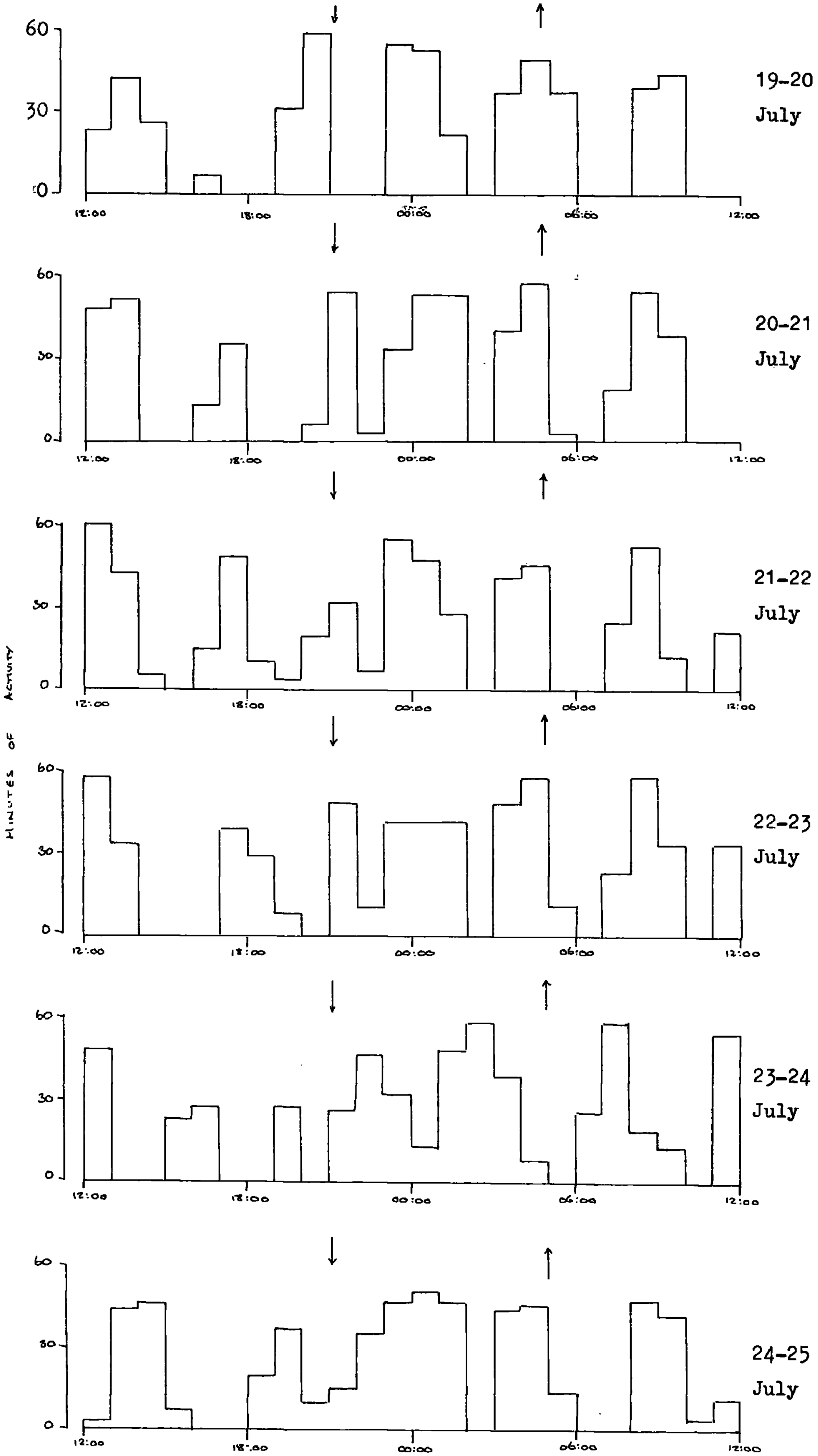


Fig 17. The activity of WF2 on each of six diel periods as recorded by actograph. (all times B.S.T.)

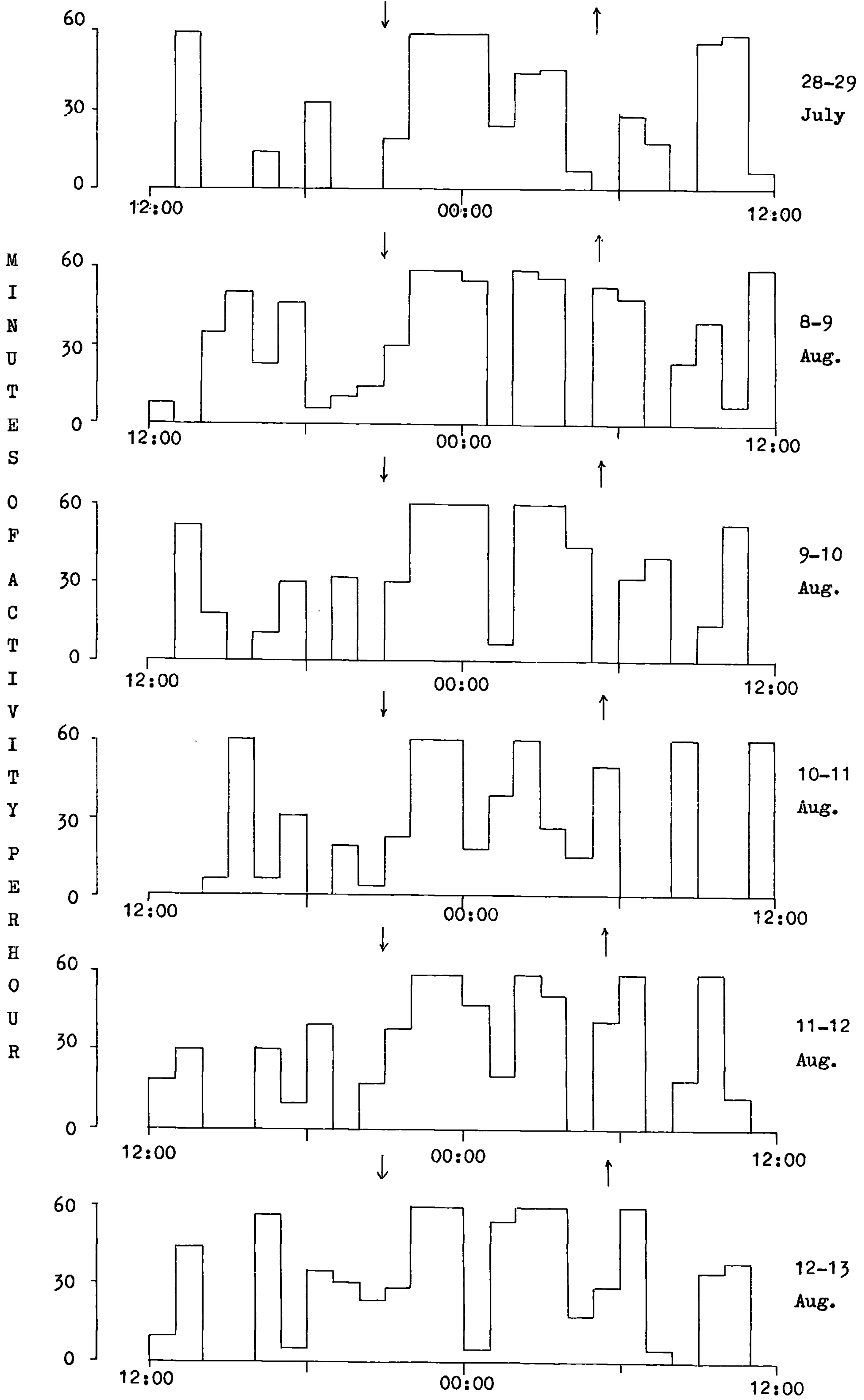


Fig 18. The activity of CM1 on each of six diel periods as recorded by actograph. (all times B.S.T.)

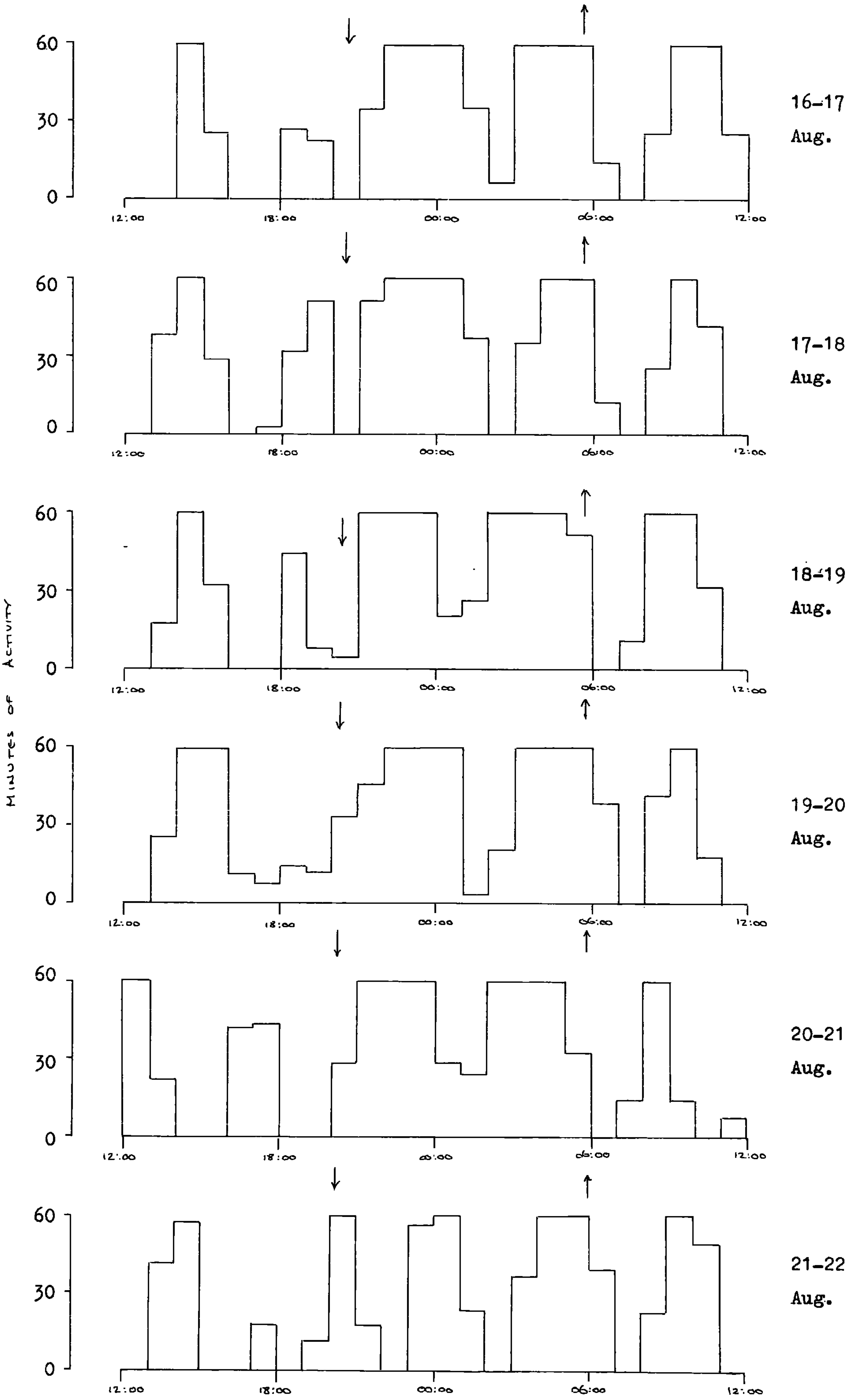


Fig 19. The activity of WF 3 on each of six diel periods as recorded by actograph. (all times B.S.T.)

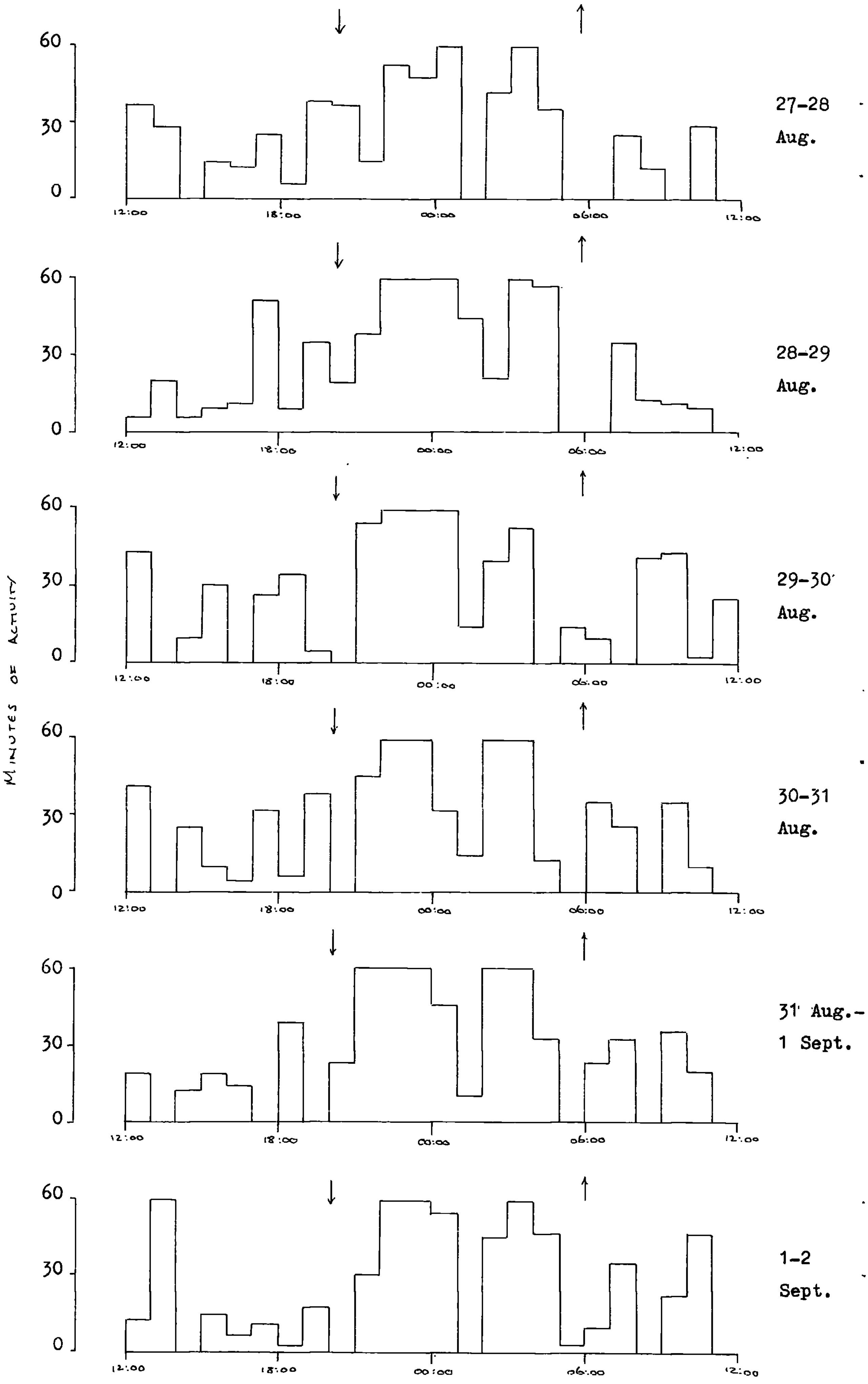


Fig 20. The activity of WM1 on each of six diel periods as recorded by actograph. (all times B.S.T.)

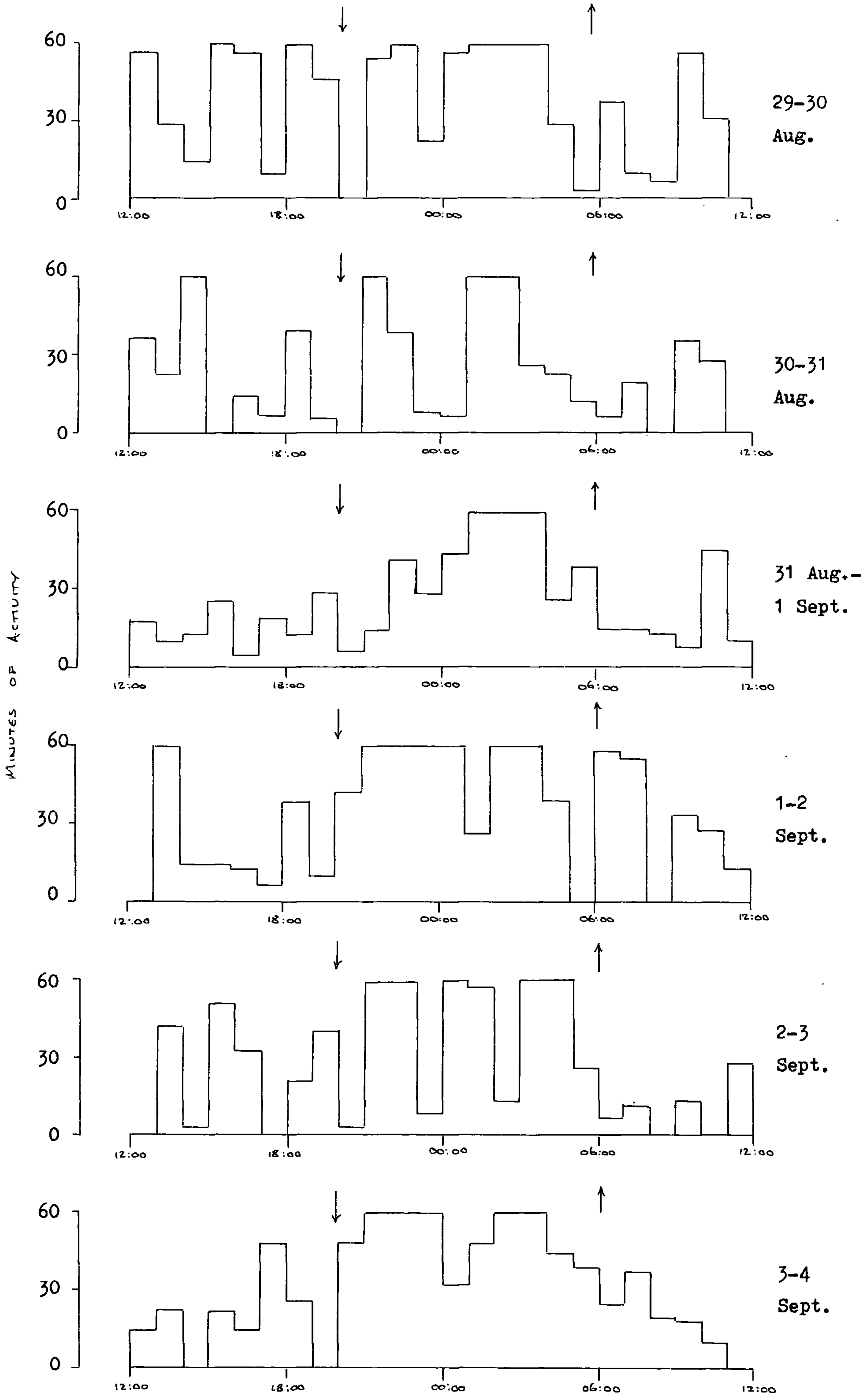


TABLE XVIX The Mean Lengths of Rest Periods of Arvicola (expressed in mins).

INDIVIDUAL	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	GRAND MEAN
WF1	131	131	122	106	137	136	127
WF2	117	112	108	99	112	131	113
CM1	123	119	119	173	131	122	131
WF3	100	85	140	107	105	118	108
WM1	115	182	186	142	214	56	144

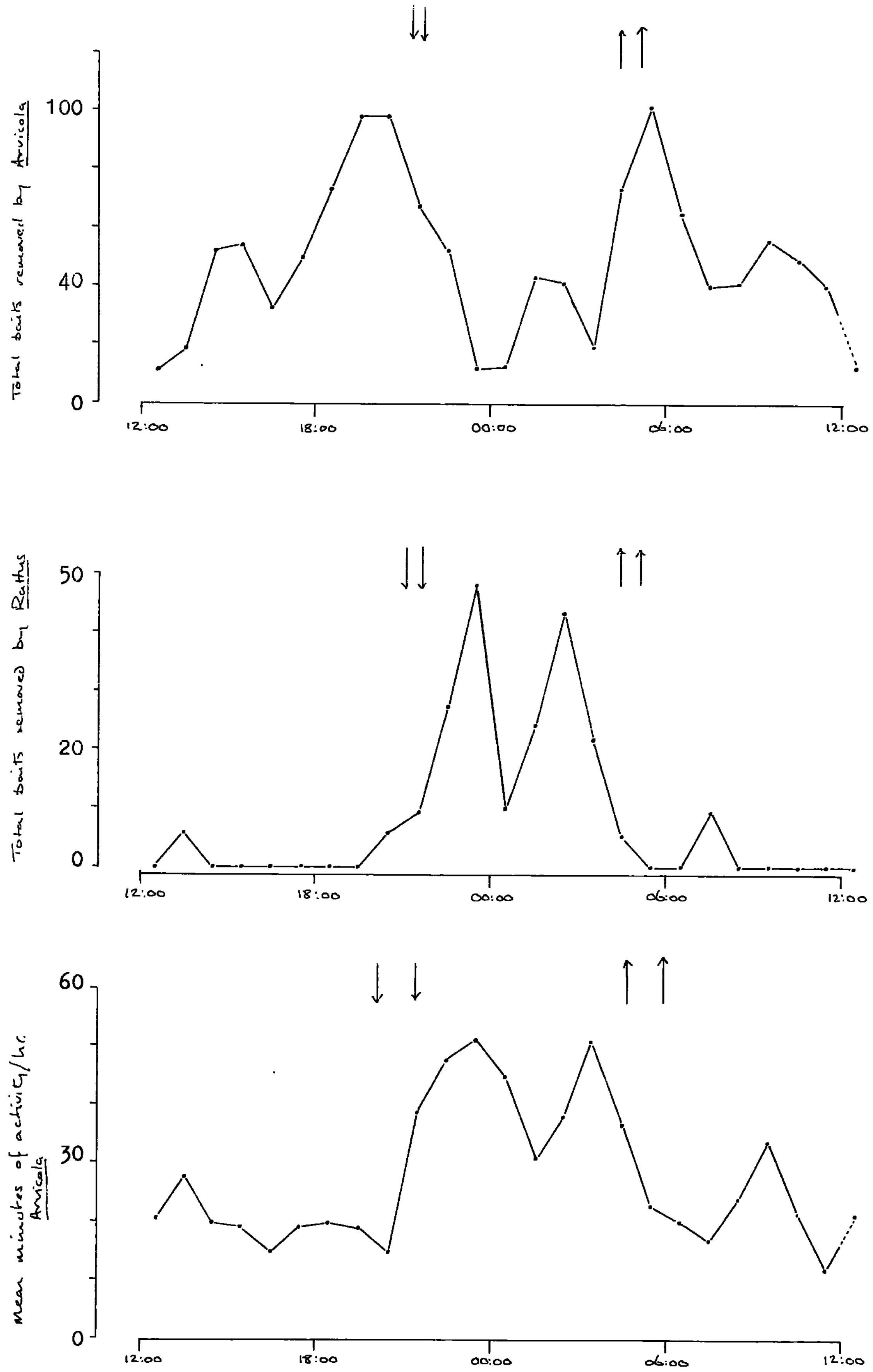
It can be seen from Appendix C that there is considerable variation in the duration of active and rest periods, both between diel periods and between individuals. Notwithstanding this variation, over a period of time for this group of animals where the overall patterns of activity are significantly similar, the data do indicate the possibility of a short-term rhythm of activity of approximately two hours rest, two hours activity, giving peaks of activity at approximately four-hour intervals.

4.3. Comparison of Laboratory and Field Results

The total pattern of activity exhibited by Arvicola as shown by bait removal in the field study was compared to the total pattern of activity obtained in the laboratory. Similarity was tested by calculating Spearman's Rank Correlation Coefficient, $R_s = 0{\cdot}25$, $t = -1{\cdot}21$; with 22 df. $p < 0{\cdot}1$. As would be expected from the separate analyses of these studies (Sections 4.1.3. and 4.2.2.) there is no significant level of similarity.

The mean pattern of activity obtained for Arvicola in the laboratory was also compared with the total pattern of activity exhibited in the field for the nocturnal period 21:00 - 05:00. Spearman's Rank Correlation Coefficient $R_s = 0{\cdot}517$, $t = 1{\cdot}598$; with 7 df. $p < 0{\cdot}1 > 0{\cdot}05$. Although not significant the result does indicate that there is greater similarity between the pattern of isolated Arvicola in the laboratory and Rattus in the field, than Arvicola in the laboratory and Arvicola in the field. The three activity patterns are represented graphically in Fig 21.

Fig 21. A comparison of the activity of Arvicola in the field (above) with Rattus in the field (middle) and Arvicola in the laboratory (below). (all times B.S.T.)



In this comparison it is worth briefly considering what effects the two species may be having on each other in their utilisation of stations. Both species made use of all the feeding stations at some point in the study, but activity was not evenly spread between stations. In part this was due to habitat differences, as demonstrated for Arvicola in Section 4.1.4.

Only one station was heavily used by both species (relative to the total number of baits taken by both species). This was station 9 at which Rattus removed 19·3% of all baits taken. Of the total baits taken by Arvicola at this station, 3·75% were removed during the hours of darkness.(% calculated from results in Appendix A).

Stations 7 and 8 were used heavily by Arvicola and lightly by Rattus, Rattus taking 2·99% and 2·50% of all baits taken at each site respectively. At these stations Arvicola removed 11·69% (station 7) and 9·52% (station 8) of all baits taken by the species, in the hours of darkness.

Stations 1 and 4 were used lightly by Arvicola and heavily by Rattus, Rattus taking 62·67% and 68·09% of all baits taken at each station respectively. Of the total baits removed by Arvicola at these sites, 37·03% (station 1) and 0·00% (station 4) were removed at night. The high nocturnal activity at station 1 by Arvicola was the result of only one nocturnal visit by this species and may thus be misleading.

Although these results have not been subjected to statistical analysis, due to an insufficiency of data at sites 1 and 4, it would appear that there is some influence by Rattus on the activity of Arvicola. At station 9, which was heavily used by both species, Arvicola exhibited much less nocturnal activity than at stations 7 and 8 which were little utilised by Rattus. At station 4, where Rattus was more active than Arvicola, the latter showed no nocturnal activity at all. The situation at station 1 is contrary to the general pattern, but as explained above may be misleading, and the overall trend of the results suggests some inter-specific relation.

4.4. Comparison of Results from the Present Study with those of Previous Studies

4.4.1. The Activity of Arvicola in the Laboratory

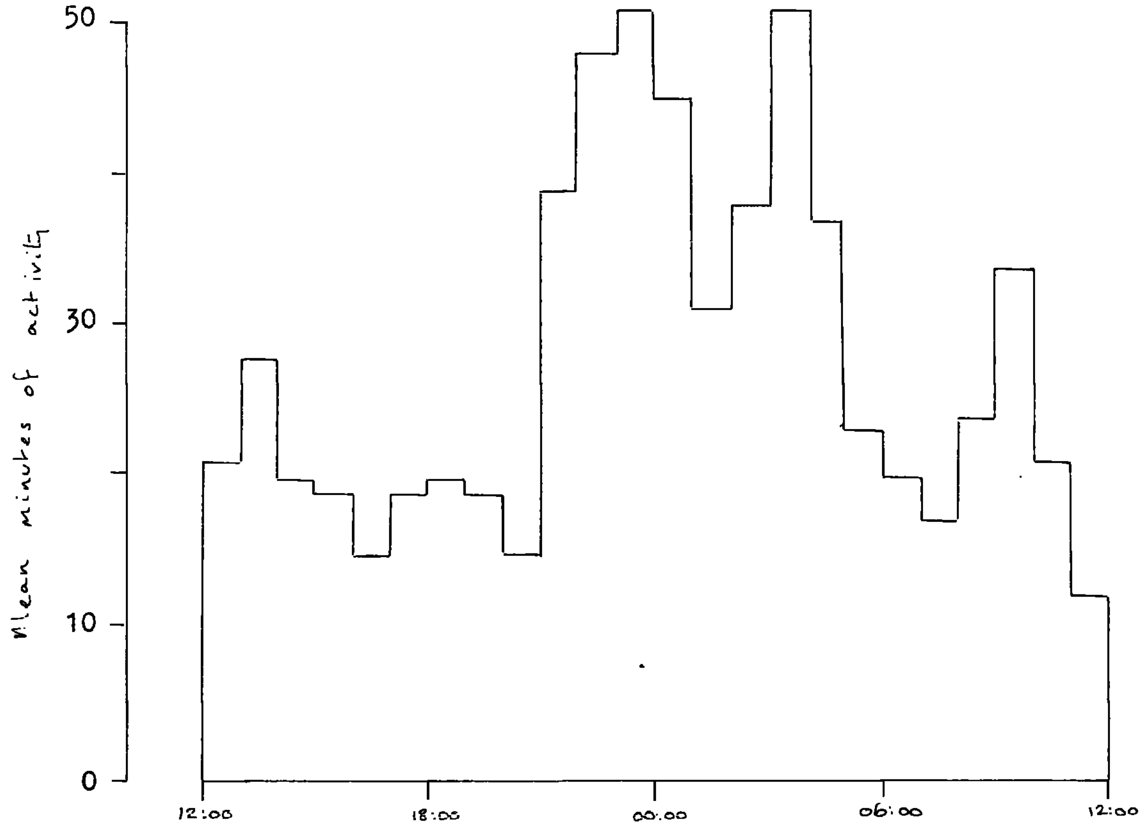
Duckett (1969) investigated the laboratory activity of Arvicola using animals drawn from the same population as was used in the present study. It was felt that a comparison of the two studies might provide an indication of the lability of the species' activity pattern over a period of time. The mean patterns of activity obtained for Arvicola in the present study was compared with the results obtained by Duckett under similar long-day light conditions. The studies differed in choice of method, Duckett using trip switches in runways. The two sets of results are presented in Table XX and represented as histograms in Fig 22. Comparison was made by the calculation of Spearman's Rank Correlation Coefficient, $R_s = 0{\cdot}85$, $t = 10{\cdot}29$; with 22 df. $p < 0{\cdot}0005$.

The activity pattern obtained for Arvicola in the laboratory in the present study is thus very similar to that obtained by Duckett and it may be assumed that this population has maintained a similar pattern of activity over a period of years. This does not necessarily infer that the field population would have maintained a particular pattern of activity for the same period.

4.4.2. The Activity of Rattus in the Field

Since the pattern of activity described for Rattus in the present study is based on quite limited data, it was felt that comparison with a previous study would be of value. The study of Chitty and Shorten (1946) was carried out on a comparable population, using a similar technique to that of the present study. Although they do not describe a circadian rhythm of activity as such, their results can be expressed in this manner and those obtained in July 1942 were compared with those of the present study as before. The two sets of results are presented in Table XXI and represented as histograms in Fig 23. $R_s = 0{\cdot}763$, $t = 3{\cdot}54$; with 9df. $p > 0{\cdot}001 < 0{\cdot}005$.

Fig 22. A comparison of the activity patterns exhibited in the laboratory by Arvicola in the present study (above) and that of M. J. Duckett (below). (all times B.S.T.) (Data of M. J. Duckett derived from Duckett (1969)). ↓ ↓ ↑ ↑



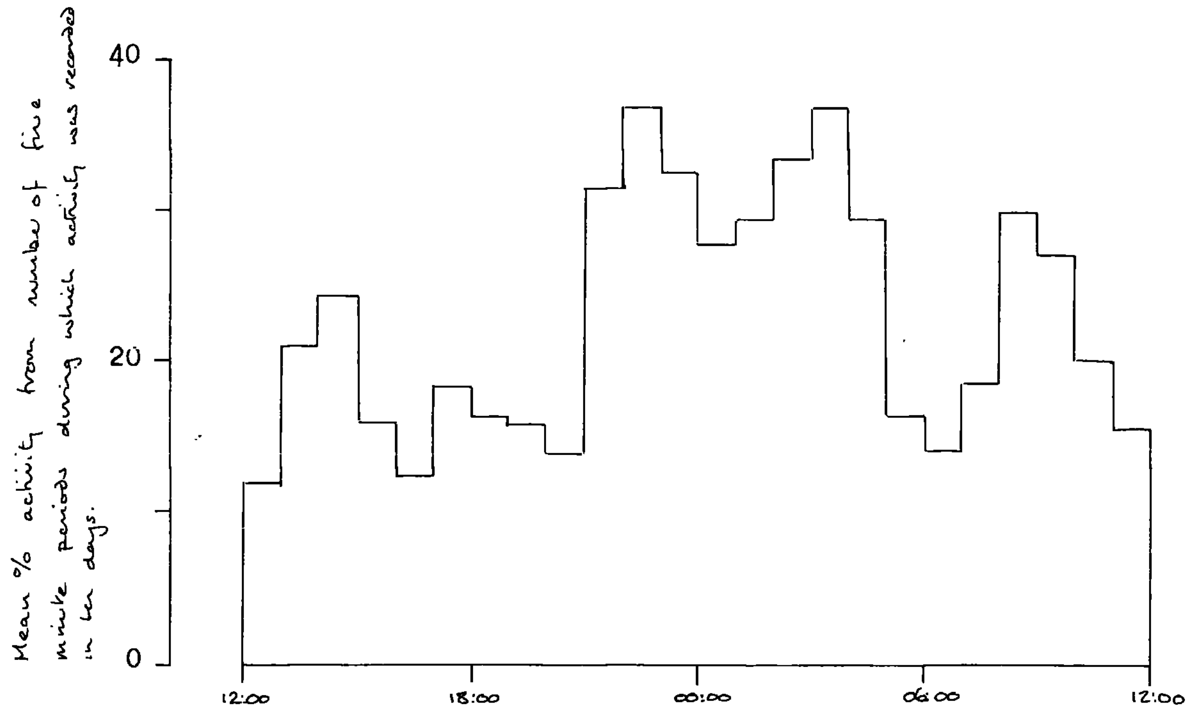


Fig 23. A comparison of the activity patterns exhibited in the field by <u>Rattus</u> in the present study (above) and that of Chitty and Shorten. (below). (all times B.S.T.) (Data of Chitty and Shorten derived from Chitty and Shorten (1946)).

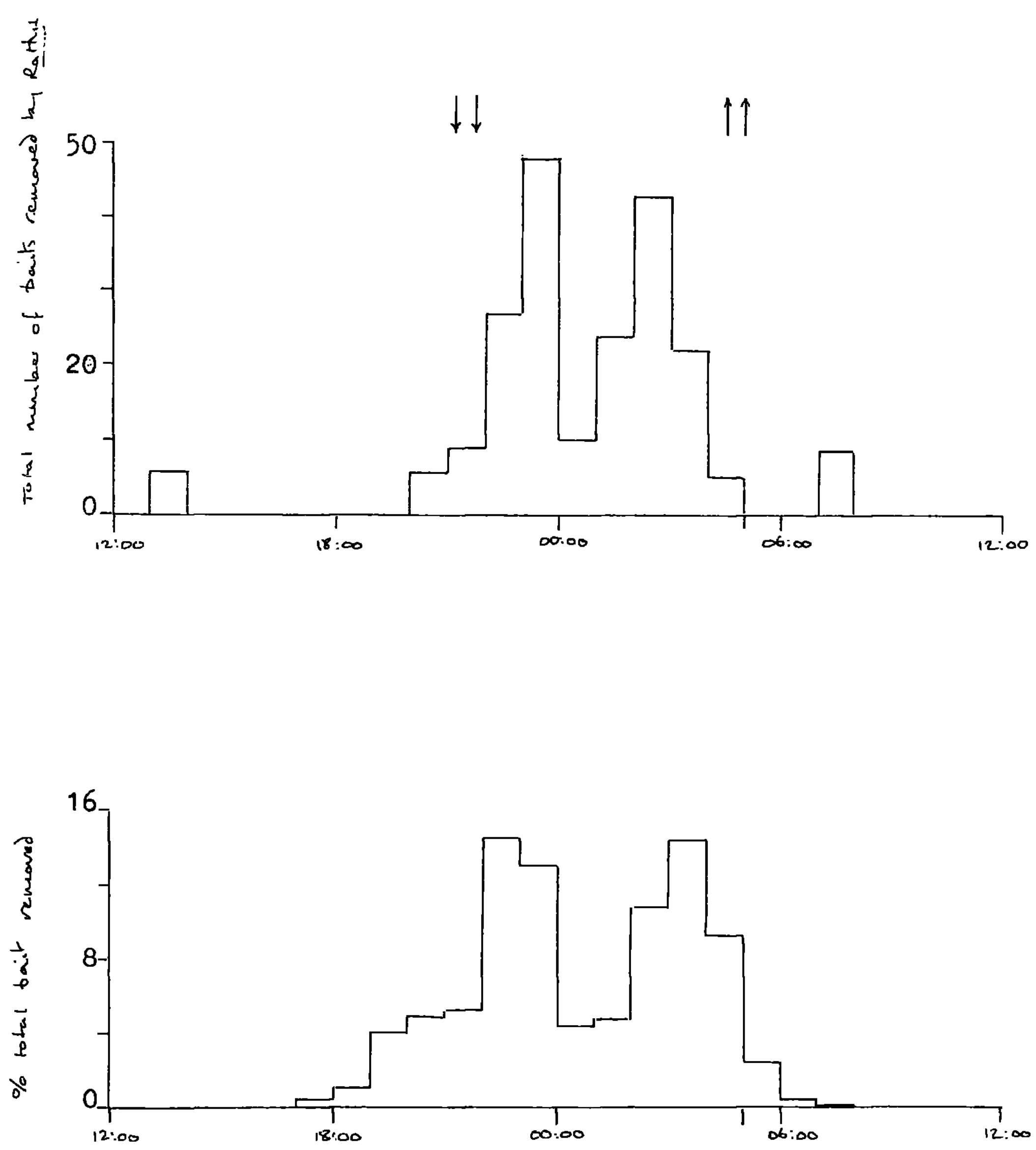


TABLE XX (left) . A comparison of laboratory activity in *Arvicola* in the present study with that of Duckett. (M.J. Duckett's data derived from Duckett (1969).

TABLE XXI(right) Comparison of *Rattus* field activity in present study with that of Chitty & Shorten. (Data from Chitty & Shorten (1946))

	ARVICOLA		RATTUS	
	Mean % activity (Duckett)	Baits rem. (Knight)	% bait rem. (Chitty & S.)	Baits rem. (Knight)
00:00-01:00	28	45	4•5	10
02:00	29•5	31	4•7	24
03:00	33•5	38	10•8	43
04:00	37	51	14•4	22
05:00	29•5	37	9•3	5
06:00	16•5	23	2•6	0
07:00	14	20	0•8	0
08:00	18•5	17	0•4	9
09:00	30	24	0	0
10:00	27	34	0	0
11:00	20	21	0	0
12:00	15•5	12	0	0
13:00	12	21	0	0
14:00	21	28	0	6
15:00	24•5	20	0	0
16:00	16	19	0	0
17:00	12•5	15	0	0
18:00	18•5	19	0•6	0
19:00	16•5	20	1•2	0
20:00	16	19	4•1	0
21:00	14	15	4.9	6
22:00	31•5	39	5•4	9
23:00	37	48	14•65	27
00:00	32•5	51	12•9	48

The distribution of activity in the nocturnal period, 20:00 - 06:00 is thus substantially similar in the two studies. Both studies recorded negligible activity during the remaining part of the diel cycle and the pattern of activity described for *Rattus* appears to be widespread in space and time.

SECTION 5 DISCUSSION

5.1. Introduction

Most studies of small mammal activity have, to date, been carried out under highly unnatural laboratory conditions. Where the aim of such a study is to investigate the physiological bases of active behaviour, as in Richter (1927) and in part Calhoun (1945), the relationship between laboratory and field conditions is of little importance. However many authors have carried out experiments under simplified laboratory conditions when attempting to correlate activity with physical environmental variables such as day-length and temperature (Davis 1933, Calhoun 1945, Miller 1955, Erkinaro 1961 and Kavanau 1963). The interpretation of such studies in terms of their ecological significance is very difficult, as indicated by Kavanau's (1969) study of the least weasel (Mustela rixosa) which under laboratory conditions is strongly nocturnal but in the field is active by both day and night or is largely diurnal. The limited value of isolated laboratory studies was emphasised by Enright (1970) when he said

" The greater part of the literature on endogenous rhythmicity - including contributions from some ecologists - appears to me to be largely, if not totally, irrelevent to ecology .... the observation under constant laboratory conditions of residual evidence of temporal adaptation, in the form of an endogenous rhythm, has only rarely led to any further understanding of the field situation. "

The same sentiment is expressed by Ashby (1972) when he concludes that "......... an advance in knowledge of the mechanisms determining the activity patterns of small mammals will require a greater emphasis on field observations of mammal behaviour and on laboratory experiments in which the variety of conditions found in nature is closely simulated."

Cloudsley-Thompson (1960) emphasises that information on the effects of environmental variables in the laboratory may be of little relevence to an understanding of the ecological components influencing activity in the field.

The constant emphasis on laboratory studies, in the light of the doubts expressed above and elsewhere in the literature, may be caused by the very restrictions of a laboratory environment, making it more amenable to control and manipulation of variables, and to the use by the researcher of automatic recording systems, thus releasing him for other duties. Simple field techniques can be time-consuming and laborious, while more elaborate techniques which automatically record field activity are often expensive and restricted in use to a very small section of the population under study.

5.2. The Measurement of Field Activity

Although trapping has frequently been used to study the periodicity of the activity of small mammals (Elton et al 1931, Van Wijngaarden 1954, Brown 1956, Kikkawa 1964, Bergstedt 1965 and Stoddart 1969) the technique is subject to several limitations, especially in the variation at both individual and population level in response to traps over a period of time.

Kikkawa (1964) and Tanton (1965) among others, have suggested that some individuals of populations of small rodents are highly prone to trapping whereas others are inherently trap-shy. Kikkawa (1964) found that individuals of Apodemus, with what he terms a "higher exploratory drive", entered traps more easily, as did socially dominant members of the population, whereas individuals with a low exploratory drive and sub-dominant individuals tended to be trap shy. Tanton (1965) reported that the possibility of capture for an individual remained constant throughout the trapping period used, of several weeks and this response was also found by Crowcroft and Jeffers (1961) in Mus and Rattus. Kikkawa (1964) however states that some trap-shy individuals gradually became accustomed to the traps and learnt to enter them. The latter author also showed that the experience of being trapped alters the reaction to traps at future encounters and that a trap-

-happy individual may become trap-shy and vice versa. Ashby (1967) reported that the effects of variations in individuals readiness to enter traps did not significantly affect the trappability of Apodemus and Clethrionomys with the spacing of traps he used, but that there was evidence that this did occur when the distance between traps was increased. In addition he always covered his traps with vegetation (Ashby pers. comm) I. Linn (pers. comm.) reports that Microtus enters Longworth traps more readily if the trap is covered with vegetative material, its unnatural surface thus being camouflaged. Rowe (1970) has demonstrated that the response of wild house mice (Mus musculus) to a trap is affected by whether or not the trap holds the odour of another individual, and that the response is further influenced by the sex of the previous occupant.

Tanton (1969) found fewer juveniles trapped than would be expected from the number of pregnancies recorded and the level of recruitment at the young adult weight. Kikkawa (1964) discovered that individual adults were more likely to be trapped at high population densities. Tanton (1965, 1969) and Bergstedt (1965) contend that seasonal variations in trapping frequencies arise as a result of fluctuations in the natural food supply. Southern (1973) reported that the proportion of a population of Apodemus trapped in a given period could vary by as much as 50% for unknown reasons.

Bergstedt (1965) reported that trap efficiency varied with the age of the traps, old traps being more effective than new traps. Sheppe (1965) found that on 84% of the occasions that Peromyscus leucopus left tracks at a station it left without entering the trap.

This heterogeneity in the response of small mammals to traps, at both the individual and population level, coupled with the seasonal variations in response, makes it necessary to interpret trapping data in terms of population activity with great caution.

Trapping is also disadvantageous in that it periodically immobilises the object of study and whilst it may provide an indication of the numbers of animals above ground in a given period, it in no way provides a measure of the intensity of activity. This problem has been overcome to some extent by Harling (1971) who in a study on Peromyscus maniculatus electronically monitored the triggering of traps, enabling release of the animals immediately after capture.

A further consideration in the present study was that the size of traps necessary to accommodate Arvicola was such that they were difficult to transport and to camouflage effectively and the likelihood of vandalism was high.

The application of radio-active isotopes to small mammal ecology has been reviewed by Bailey, Linn and Walker (1973). Although a useful tool in many circumstances, isotopes are more readily applicable to the identification of cryptic, stationary environmental components such as faeces and corpses, rather than in recording the above ground activity of small mammals. Their use is limited by virtue of the fact that only one animal may be followed at a time and then only if the habitat allows the observer to move freely in pursuit of the labelled individual and without disturbing its activities. Furthermore, when using radio-active chemicals there is always the risk of causing environmental contamination.

Of the more sophisticated techniques that of automatic photography, pioneered by Pearson (1959) and refined by Dodge and Snyder (1960), has the advantages that some qualitative aspects of activity may be recorded and that it is not very time-consuming. It is limited in application however to those animals that regularly use clearly defined runways.

The use of tracks to provide an index of activity has been described by several authors. Mayer (1957) and Sheppe (1965) provided an artificial surface of smoked paper, but Mayer's technique is laborious and inconvenient for extensive field investigation, especially when, as in the present study, burrow systems may have several entrances, some of which are underwater. Sheppe (1965) placed smoked paper in containers, but found greater variation in response to the containers than to traps and after the animals had become habituated to the containers in their environment they largely ignored them. The use of natural surfaces has the advantage of not interfering with the animals under study, but unless individuals leave very clear tracks identification may be difficult, especially at heavily utilised sites. The use of tracks presents the additional disadvantage of the need to define an arbitrary unit of activity which may be valid for the one study only.

Flowerdew (1973) has described the use of thermister probes placed in burrow nest chambers to record temperature changes with the animals presence or absence. The method has been used succesfully by Vincent (1974) in a study on Arvicola in outdoor enclosures. The technique makes the assumption that the animal is consistently active outside the nest and inactive in it. The value of the method in an extensive field study is reduced by the difficulties in accurately placing a sufficient number of thermister probes.

The use of telemetry (Cochran and Lord, 1963) is a potentially valuable technique but has the limitation of being more applicable to investigations of the activity of individuals rather than a population.

Emlen et al. (1957) suggest that dropping boards may be a potentially valuable technique in assessing field activity but a study by Duckett (1969) and the present study, indicate that for Arvicola at least use of dropping boards by the animal is too erratic to provide meaningful activity data.

Notwithstanding their limitations, each of the methods outlined above has a value or potential value in the field investigation of small mammal activity. For the present study however, where simplicity and cost were of major importance, it was felt that the development of bait removal as an additional technique was worth investigation. The method has not been used to any great extent previously as a measurement of activity. Hamilton (1937) used the technique in a supporting capacity in a study of the activity of Microtus pennsylvanicus by trapping; Chitty and Shorten (1946) were interested in establishing feeding activity in Rattus norvegicus as a measure of population density rather than in the timing of activity. In view of the assumptions the technique makes it was necessary to try and foresee any problems that may arise and test the validity of the method during the study.

The most fundamental assumption made is that a measure of feeding activity provides an accurate reflection of total activity. The theoretical reasoning behind this assumption has been argued briefly in Section 1, but by itself this is insufficient to justify the assumption that feeding activity is directly proportional to total activity. A number of studies (Crowcroft 1954, Kavanau 1969) have indicated that feeding activity provides a reliable index of total activity in laboratory conditions. Although it is possible that in a simple environment feeding activity may be stimulated by 'boredom effects' the potential for this to occur is more limited by physiological factors than in for example, the amount of spontaneous running or grooming activity. This contention is supported by a study by Blair (1951) in which he tracked Peromyscus polionotus in the field. He found that most movements were associated with feeding and food-gathering. The assumption of a direct relationship between feeding activity and total observed activity in Arvicola has been validated in the present study by observation of total activity concurrent with measurements of bait removal by the same animals. It seems reasonable to suppose that the same type of relationship will exist in other small herbivorous homeotherms.

Another assumption of the use of bait removal as a technique is that the introduction of an attractive food source will not effect a significant change in the animals feeding pattern. If the bait is sufficiently attractive it could stimulate feeding activity, either by increasing the amount of time spent feeding within the framework of the normal activity pattern, or by encouraging feeding at times the animal would not otherwise be active. Since the aim of the study was to obtain an index of actvity the former situation would have the lesser disruptive effect on the validity of the pattern obtained. An alternative problem was the possibility of habituation to the bait and that consequently removal would gradually decrease through the period of study. It was partly on account of these possibilities that the baits offered were insufficient to meet the calorific requirements of the animals under study and only laid down during those periods when measurements of activity were actually being made. This also provided a saving of materials and labour. In addition the onset of study periods during which measurements were taken was staggered as much as possible to reduce the overall effects of stimulation or habituation which may have occurred.

The results obtained do not show any evidence of either habituation or stimulation having occurred. If the animals were being stimulated to feed preferentially on the baits one would expect the number of baits taken to be low during the first few hours of any study period, and to increase thereafter as the animals discovered the food source and made additional use of it. In fact the mean number of baits taken during each succesive hour of a twelve hour study period fluctuated, with a minimum number of baits being taken in the seventh hour and a maximum in the eleventh hour after baiting commenced. If habituation were occuring either during a study period or during the course of the complete study, it would be expected that the number of baits taken would gradually decline. In fact over the course of the entire study the number of baits taken rose, associated with an increase in population density during the study due to an influx of juveniles.

Another difficulty that can be experienced with the use of bait removal is utilisation of the baits by species other than those under study. In the present study Rattus took baits originally intended for Arvicola. On the realisation that in nearly all cases it was possible to distinguish the species utilising baits with confidence, the study was extended to include Rattus. Much interesting additional material was thereby gained. In a very few instances it was not possible to identify the species responsible for removing baits; on these occasions the results had to be ignored. There was no evidence of the baits being utilised by other species, this possibly reflecting both the bait used and the size of the pieces offered. In other studies and at other times of the year the selection of species-specific bait might be more difficult.

Bait removal has been shown to provide a reliable index of activity in the field for small herbivorous homeotherms, both in the present study and one carried out concurrently on Apodemus and Clethrionomys (Greenwood 1974). It has the great advantages that it is convenient and inexpensive, provides a measure of the intensity of activity and also allows the concurrent observation of the qualitative aspects of activity. It does not provide a measure of actual activity, making comparison between studies difficult, and in common with many field techniques is time-consuming. It is felt however that it is a useful additional technique to be considered when field studies are made of small mammal activity.

5.3. The Effect of Station Habitat on Bait Removal

Of the factors measured, the two most important affecting site utilisation are a comparatively great depth of water at the edge of the bank and a short distance between the station and the water's edge. Since observation during the present study and in previous works (Barret-Hamilton and Hilton 1910-1921, Ryder 1962) showed that when disturbed Arvicola sought refuge in the water, the importance of these factors probably lies in ease of escape from predators. It would be expected that stations close to the burrow system would be more heavily utilised than stations further away and this is supported by the strong preference shown for stations within 5m of a burrow entrance. In entering the water the retreat of Arvicola is often aided by the disturbance of mud and silt from the bottom and whilst this may not be a deliberate action the selective advantage of this occurrence is apparent in obscuring the direction of retreat. This may explain why voles appear to avoid stations where the river bottom had no silt overlying the stones.

Although great vegetative cover may assist the vole in hiding from predators, it will also obscure the approach of those predators and it is possible that more open terrain is advantageous to the vole in spotting predators and making an escape into the water before they get too close.

The greater utilisation of stations where the water depth is greater than 1m at a distance of 1m from the bank is probably largely a reflection of the depth at the water's edge, rather than being of major importance in the feeding station selection by the vole.

Although Arvicola is a small animal it is a strong swimmer (Ryder 1962, and the present study; three animals were observed swimming across the river, one after heavy rain when the river was in flood) and consequently it might be expected that strength of current is of little importance in feeding station selection.

The above results emphasise the importance of considering the animals biology before setting up baiting stations in a study of this type. Such consideration may be of paramount importance in obtaining viable data, as heavily utilised stations are more likely to yield valid results than those visited only sporadically.

5.4. The Activity of Arvicola in the Field

Although compared to many species little work has been carried out on the activity of Arvicola, much of that which has been done has been carried out in the field.

Van Wijngaarden (1954) reported on the basis of a trapping technique in Holland that activity commenced at 04:00, remained comparatively constant until 16:00 and then rose to a peak at 21:00, with little activity during the hours of darkness. Using a similar technique Worral (Unpubl. Quoted in Southern, 1964) also found a peak of activity at dusk, the remaining activity being predominantly nocturnal and there being little activity during the day. Ashby, Harling and Whiles (1969) used an observational technique throughout the diel period but could discern no marked rhythm of activity, although there was evidence of lulls at midday and in the early evening. M. Creasy and M.J.Duckett (unpublished) made two studies in the same area as Ashby et al, at the same time of year, using tracks left on bankside mud as an index of activity. They found an overwhelming concentration of activity in the hours of darkness, with slight variations in the timing of peaks of activity between the two sites used. Stoddart (1969) reported a statistical preference for diurnal activity from trapping results. His use of only two trapping periods, the night-time one being twice as long as the day-time one, diminishes the value of his results for comparative purposes. Prior to these studies it seems to have been accepted that Arvicola was largely diurnal (Barret-Hamilton and Hinton 1910-1921, Ryder 1962, Corbett 1966) although no evidence was cited in support in these publications.

The present study established that the activity of a population of Arvicola during summer, was distributed throughout the diel period but with marked peaks of activity occurring at approximately dusk and dawn, and that nocturnal activity was considerably less than would be expected if activity were arrhythmic. It has also been demonstrated that this pattern is exhibited, albeit with some variability, in small units of the population. These results are in broad agreement with those of Van Wijngaarden (1954) but differ markedly from those of Worral (Southern, 1964), Ashby et al.(1969) and Creasy and Duckett (Unpubl.).

The great variation of activity patterns demonstrated in Arvicola populations from different places at different times, indicates that this species is capable of great lability in its daily pattern of activity. Ashby (1972) has pointed out that for small homeotherms

> "...... the pattern of activity of a given species in a given environment must be rigorously adapted to the conditions prevailing if it is to survive and reproduce."

Arvicola can occupy a wide range of habitats (Southern & Crowcroft 1956, 1964) and in continental Europe can have a much more terrestrial habit than is usual in the British Isles (Van den Brink 1967). Each type of habitat can vary quite widely in space and time and consequently different populations of Arvicola may be subject to quite different environmental pressures. This will apply to all species occupying a heterogenous habitat, but especially to those such as Arvicola that may fill largely different niches in different areas. The feeding requirements of Arvicola dictate that animals must be intermittently active throughout the diel period and hence will be faced with a greater variety of environmental pressures, both within the 24hr period, but particularly when viewed on an evolutionary time scale. Consequently selective processes will tend to favour those individuals capable of adopting different behavioural strategies to meet changing conditions. In a similar species where frequent feeding is not necessary to meet metabolic requirements, activity can be confined to a comparatively short period of the diel cycle. In such circumstances it might be expected that activity will take place at times when adverse environmental factors can be best avoided. The species will thus be subject to fewer direct environmental constraints and the ability to adopt alternative behavioural strategies will be less important, selective processes favouring those individuals whose activity coincides with the safest period of the diel cycle for individuals to be active.

5.5. The Activity of Rattus in the Field

As is the case with Arvicola, little work has been done on the activity of wild Rattus norvegicus. Barret-Hamilton and Hinton (1910-1921) states that the species is largely nocturnal but does not mention any evidence to support this contention. The data of Chitty and Shorten (1946), although not collected with the intention of defining the rat's activity pattern, can be reinterpreted to give such a pattern. When this was done for the period 10-20 July 1942 (the period corresponding most closely to that of the present study) a bi-modal pattern of nocturnal activity is obtained with peaks occurring approximately 1-2 hours before sunrise and 1hr after sunset. This study was made on a wild population of rats subject to little human disturbance, a similar situation to that of the present study. This showed a very similar bi-modal pattern of nocturnal activity. Both studies showed very little diurnal activity.

That two studies, widely separated in space and time, show such similar results could indicate that the activity pattern of Rattus norvegicus in the field situation is consistent. Although the rats used by Chitty and Shorten (1946) could be induced to feed at almost any time of the day, a strong hunger-stimulus was required to break the normal rhythm in undisturbed conditions. The evolutionary significance of such a restrictive activity pattern is difficult to assess, but clearly in such circumstances the species will be subject to fewer environmental constraints than a species such as Arvicola, which is more continuously active. One of the factors allowing a confined activity period is the intake of food of low bulk and high energy and protein content. Such food forms a large part of the diet of Rattus and other Muridae such as Apodemus (Drummond 1960). Advantage is conferred directly by the lower food intake required to maintain the metabolism, and also indirectly by the fact that energy expended in the process of accumulating a food store brings a proportionately higher return.

5.6. The Activity of Arvicola Under Artificial Conditions

The only previous laboratory study of Arvicola activity known to the author is that of Duckett (1969), which utilised a series of runs incorporating a trip mechanism. Duckett's results showed that although an individuals activity occurred in pulses throughout the diel period, by far the greater part of activity was concentrated into the hours of darkness. This trend was exhibited in both short-day and long-day conditions, but was especially noticable with a long-day, short-night cycle. Under these conditions

Duckett obtained a bi-modal nocturnal pattern of activity, exhibiting peaks 1•5hr after dusk and 1•5hr before dawn. The peaks were separated by a relative lull in activity which occurred halfway through the hours of darkness.

The present study, using actographs, demonstrated a very similar total pattern of activity, peaks occurring approximately 2•5hr after sunset and 1•5hr before dawn. These peaks were separated by a comparative lull in activity, approximately 5hr after sunset and 3hr before sunrise. Although there was some significant individual variation, the overall pattern of high nocturnal and low diurnal activity was generally maintained by different individuals over a period of days.

The animals used in the two studies came from the same geographical area, but were separated by approximately five generations (Stoddart, 1971). The results seem to indicate that Arvicola, from this site at least, has an endogenous rhythm of activity that is manifested by isolated individuals under laboratory conditions, when environmental variables are reduced and may (Duckett 1969) or may not (as in the present study) be manifested in the more complex field situation. Two recent studies (Lund 1970, Vincent 1974) have investigated the activity of Arvicola in small outdoor enclosures. Lund measured activity by means of a photo-electric cell whilst Vincent used thermister probes placed in the nest. In both studies seasonal variations in activity occurred. Lund found a strong diurnal trend in winter, often with peak activity at sunrise, and a more even distribution of activity between the hours of darkness and daylight during the summer months. Vincent observed a marked nocturnal tendancy during the summer, and a more or less even distribution of activity throughout the diel cycle in the winter months.

5.7. An Overall View of Activity in Arvicola

The experiments carried out in the present study and the studies of other workers outlined above, fall naturally into two sub-divisions;

i) studies of activity in a natural situation

ii) studies of activity in artificial situations

The former studies describe the activity that occurs in the field, where the animal is subject to a wide variety of environmental pressures, but do little to explain the reasons for the manifestation of a particular pattern of activity. The latter studies, by manipulating the variables to which the animals are exposed, help to provide some information on which factors may modify the activity of Arvicola in field situations.

The investigations carried out under artificial conditions include two laboratory studies (Duckett, 1969 and the present study) and two enclosure studies (Lund 1970, Vincent 1974). With the exception of Lund (1970) all these studies were carried out in the Durham area and all gave broad agreement in the pattern of activity exhibited by Arvicola during the summer months (May-August). In the present study and that of Duckett (1969) the animals came from the same site on the R. Wear, or very close to it, and might be expected to contain much of the same genetic material. Both studies utilised extremely simple laboratory conditions, but measured activity in different ways. Nevertheless the similarity of the patterns obtained is highly significant.

In Vincent's (1974) study, animals from a site approximately 15 miles away were used, and although over a long period of time there is likely to be some interchange of genetic material between this population and the R. Wear population, the genotypes of individuals from these two populations might be expected to show greater variation than is exhibited between individuals from the R. Wear population. In addition Vincent (1974) measured the activity of Arvicola in outdoor enclosures which provided a more complex environment than that of the laboratory studies. Despite these differences in genetic make-up and experimental conditions, Vincent's results for the summer months are closely approximated to those obtained in the laboratory.

The investigation carried out by Lund (1970) took place at Lyngby, Denmark, about 2^{o}N and 10^{o}E of Durham. The population from which his experimental animals were drawn has presumably been genetically isolated from the Durham population for 5,000-10,000 years, since the separation of the British Isles from continental Europe. Lund's results do not agree with those of Vincent or the two laboratory studies. Whilst this may be attributable in part to differences of climate and daylength, it does not seem likely that this is sufficient to explain such a marked variation in the activity patterns exhibited.

It may be postulated that the activity rhythms exhibited by the animals from Durham under artificial conditions, are the expression of an evolutionary template of activity which has evolved in response to unknown but particular selection pressures, and is entrained by the regularly fluctuating cycle of light intensity. This template will not be constant throughout the species, since it will have evolved in response to different selective pressures in different populations. Populations closely identified in time and space, with regular interchange of genetic material, will have very similar templates of activity, whilst populations widely separated in space and time and habitat, are likely to exhibit greater variability in the expression of such templates. Populations separated spatially and temporally, but occupying similar habitats, historically and in present day characteristics, will be expected to possess similar templates of activity. In an animal whose energy requirements dictate intermittent activity throughout the diel cycle, exposure to the pressures of selective processes will be at a maximum, necessitating great flexibility in behavioural strategy. Variation in selective pressures and hence in the behavioural strategies adopted to compromise with them, will have led to the evolution of activity templates tailored to the environmental history of a particular population. The presence of such a template would explain the very close similarity in the patterns of activity shown by Arvicola under highly simplified laboratory conditions, the approximate similarity to this pattern shown by animals from the other Durham site and the contradictions posed by the activity patterns of animals in Denmark.

Although the factors contributing to the evolution of a template of activity may be varied, it is possible that the rhythm of activity exhibited may be phased by the probability of a single environmental stimulus occurring at a particular time. A 'Zeitgeber' of this nature must be predictable and not subject to excessive, short-term variation within the normal cycle; long-term variations however, achieved by small daily changes in the timing of the 'Zeitgeber', allow entrainment of the system to the new conditions. In the case of Arvicola there are indications that a rapid change in light intensity at dawn and dusk may act as a 'Zeitgeber' (Duckett, 1969, the present study) although Vincent's (1974) results do not wholly support this notion.

The type of evolutionary template postulated would not dictate the exact timing of activity in an individual under field conditions, but would act as a substrate on which exogenous environmental stimuli would act, thus allowing flexibility of response to the conditions prevailing. It follows that, at both individual and population level, the species will be attempting to 'fit' essential behavioural activities into the framework of the evolutionary template, the acuity of such a fit being dependant upon the countering effects of prevalent environmental stimuli. If such a situation does exist it would provide a possible explanation for the apparently contradictory patterns of activity found in different field studies.

Although several of the field studies carried out on the activity of Arvicola agree in showing crepuscular and/or nocturnal peaks of activity, each study reported a pattern of activity that did not agree with the results of other studies, and none of the studies showed complete agreement with the evolutionary template postulated. Insufficient information is given in the report of Worral's study (Southern 1964) to comment on which factors are affecting activity in the field, or on how closely the evolutionary template of her population may agree with that of the Durham population. The studies carried out in Durham however do offer the opportunity to consider the environmental factors contributing to the field activity pattern.

In the present study it has been shown that the pattern of activity exhibited in the laboratory during the summer months by Arvicola is strongly nocturnal, with a low level of intermittent activity throughout the rest of the diel cycle. An almost identical pattern of activity was obtained by (Duckett 1969) using animals from the same site five years previously. The present study also showed that Rattus norvegicus exhibited a pattern of activity in the field which is strikingly similar to that exhibited by Arvicola in the laboratory, and that the pattern of activity obtained for Rattus in the field in Durham is almost identical to that obtained by Chitty and Shorten (1946) for a wild rat population over thirty years ago in a different part of the country. This latter correlation indicates that the evolutionary template of activity is quite rigidly adhered to by this species, and must have arisen in response to a factor that is constant over the areas covered by the studies. That such a restricted pattern of activity is possible is probably a result of this species omnivorous diet, which contains a much higher proportion of nutritionally valuable material in relation to bulk than that of Arvicola. In this situation activity can be concentrated into that part of the diel cycle most advantageous to the survival of the individual, reducing the variety of environmental variables to which the species is exposed. Selective processes will tend to favour animals that adhere to the evolutionary template of activity. For activity to occur outside the framework of the template would require a major change in the timing of stimuli operating for and agaist the animals survival prospects. Whilst this may happen several times to an individual (eg the period immediately after a juvenile leaves the nest, or when a food supply runs out) a sufficiently strong 'blanket' stimulus affecting the whole population will be a rare event. It must also be remembered that for much of the year a nocturnal pattern of activity will be much less restrictive than during the period of the present study.

It appears therefore that whereas the field activity pattern of Arvicola is geared to flexibility of response within the framework provided by the evolutionary template of activity, the field activity of Rattus appears to be geared to a stricter adherence to a very similar template of activity. In the present study both animals were present on the banks of the river, and despite some indications of minor differences of habitat, both utilised baits at all the stations used in the study. In these circumstances, where thereis a demonstrable sympatric spatial distribution and, one would expect, some degree of overlap in food sources, Rattus has retained a bi-modal nocturnal peak of activity whereas Arvicola exhibits a pattern of activity with very low nocturnal and very high crepuscular activity. It is suggested therefore that the activity pattern exhibited by Arvicola in this field study has resulted as a response to the rigidly adhered to pattern of Rattus, and that the peaks of activity occurring at dawn and dusk in Arvicola in the field are the equivalent of the peaks occurring during the hours of darkness in the laboratory. The use of different sites by the two species, considered briefly in Section 4.3., tends to support this hypothesis. This situation would suggest that the activity of Rattus has acted analagously to a wedge in 'holding apart' the peaks of activity in Arvicola, which nevertheless remain as close to their original positions as the prevalent conditions (ie the presence of Rattus) allow.

The reason for the disruption of Arvicola's pattern of activity, rather than that of Rattus, is that Arvicola is geared to a labile pattern of activity and Rattus to a rigid pattern as outlined above.Further, it is likely that Rattus, the more powerful animal as an adult, is the more aggressive species. Lorenz (1966) has reported on work that has demonstrated inter-familial aggression in Rattus norvegicus. It seems reasonable to suppose that this aggression would be extended to Arvicola. This suggestion is supported by Ryder (1962) who contends that Rattus norvegicus is the greatest enemy of Arvicola, predating the young and 'attacking adults on sight'. If this is the case, then a population of Arvicola spatially sympatric with a population of Rattus would be expected to modify its pattern of activity to achieve the greatest possible degree of temporal separation, allowing for the effects of other environmental variables and the framework of the evolutionary template of activity.

M. Creasy and M.J. Duckett (Unpubl.) in a field study on the same site and at the same time of year as that of the present study, reported Arvicola to be showing a very strongly nocturnal pattern of activity and little crepuscular or diurnal activity. In the light of the present study there are two possible explanations for their results.

The method they used was to assess the intensity of tracks lefton patches of bankside mud, and it is possible that they failed to differentiate tracks of Arvicola and those of Rattus. The tracks and trails of these species are very similar, but can be differentiated if clear impressions are left (Lawrence and Brown 1973). Harling and Ashby however (pers. comm.) report that at the time of the study activity of Rattus near the study area was concentrated at a pig-farm, further downstream, with no general utilisation of the river banks by this species. Creasy and Duckett themselves indicate that they looked for signs of Rattus throughout the period of their study, but failed to identify any. It seems reasonable to suppose therefore that at that particular time Rattus was not present at the study site, and the pattern of activity obtained is that of Arvicola, which approximates quite closely to that found for the same species in the laboratory. Unfortunately Creasy and Duckett used a four-hour time interval in their study, and this makes comparison of the exact patterns between the studies difficult. A parallel study by the same authors at a small side stream near Pity Me, four miles from the main site, also indicated a prevalence of nocturnal activity, but the trend was less pronounced.

Ashby et al (1969) observed a population of Arvicola on a side stream close to the site used in the other two studies, and reported an arrhythmic pattern of activity. This study was carried out a year previously to that of

Creasy and Duckett and therefore it would be expected that the population would have a very similar pattern of activity to that obtained by Creasy and Duckett. That such a trend is not shown might be attributable to a number of factors, not least of which is that the idea of an evolutionary template of activity is invalid, and that the activity exhibited is purely a response to immediate conditions. However the close agreement between the results of Duckett (1969), the laboratory results of the present study and the similarity of Vincent's (1974) results appear to provide strong evidence of the presence of such a template. Further, laboratory work on other small mammals has established the presence of an endogenous rhythm of activity in many species (Johnson 1926, Davis 1933, Crowcroft 1954, Erkinaro 1961) suggesting the presence of an evolutionary template of activity to be widespread.

It is suggested that the discrepancy of the results of Ashby et al (1969) compared to those of other studies, arises from the cumulative effect of a multiplicity of factors. Some of the factors which may have contributed to the pattern of activity exhibited include the difference of habitat, which approximates more closely to the optimum for Arvicola (Zejda and Zapletl 1969) than the main river site and the greater amount of bankside cover available on the side stream. A further factor which might possibly have affected the pattern of activity obtained is a major difference in population size. On the continent populations of Arvicola may fluctuate from year to year in the same manner as other Microtinae (Zverev 1928), although not to such a great extent as related species (Lund 1970). Whilst such fluctuations in the British Isles are muted by comparison, there is some evidence that they can occur (Southern and Crowcroft 1956). It is possible that if the population was high at the time Ashby et al carried out their study this could be sufficient to disrupt the normal approximate adherence to an evolutionary template of activity. Certainly, whilst Ashby et al (1969) reported no difficulty in observing Arvicola at the time of their study, Ashby (1972) mentions several unsuccessful watches for water voles the following year and Duckett (1969) had to abandon an attempt to assess field activity by observation because of a lack of sightings. In the present study, although Arvicola was frequently observed, most sightings were in relation to activity at baited sites. From the initial sighting it was usually possible to locate the burrow(s), aiding further observation. Whilst no attempt was made to measure population size it was certainly less than peak densities reported by Mehl (1950), Van Wijngaarden (1954) and Pestikov (1963), all quoted in Lund (1970). Since it is impossible on the evidence available to either verify or invalidate the effect of possible factors contributing to the results of Ashby et al (1969), the explanations offered must remain speculative until further work has clarified the issue.

5.8. The Effect of the Physical Environment on Activity

Field studies of small mammal activity have tended to try and establish a correlation between changes in the level of activity and concurrent fluctuations in such physical variables as light intensity and temperature Hicks 1949, Brown 1956, Gentry and Odum 1957, Kikkawa 1964 and the present study). It is often presumed that the physical factor most closely correlated with the pattern of activity is causally related to it. This approach poses several problems of interpretation, some of which have been pointed out by Enright (1970).

The causal relationship of activity to fluctuations in a physical variable assumes a simple stimulus-response system. Since the patterns of activity exhibited appear to be a compromise between the evolutionary template of the species and the prevailing environmental conditions, any correlation between activity and fluctuations in a physical variable is likely to provide only a partial explanation of the factors controlling activity. Whilst such a correlation may indicate how a particular pattern of activity is controlled, it may give no information as to why activity occurs when it does. As Enright (1970) has pointed out, a pattern of activity that has evolved or is expressed as an adaptive function to one environmental variable, may be entrained by an entirely different variable. The present study has highlighted this problem by suggesting the possibility that although activity in Arvicola was being entrained by a rapid change in light intensity, any such entrainment was probably an adaptive response to avoid Rattus.

A further problem in correlating activity with physical variables is that the immediate response by the population to the prevailing conditions is often assumed. Whilst in many cases this assumption may be valid, there is no reason to suppose that the relationship may not be complicated by delayed responses. Furthermore, since many of the physical parameters measured are not independant of each other (eg cloud cover and rainfall), it may be difficult to determine the contribution of a single factor in the control of a pattern of activity.

Notwithstanding the difficulties of associating physical variables with the overall pattern of activity exhibited, many authors have demonstrated that such variables may modify the existing pattern, both in the laboratory and in the field. Brown (1956) found that heavy rainfall reduced activity in Microtus agrestis at exposed sites, whilst Gentry and Odum (1957) obtained larger catches of Peromyscus polionotus on warm cloudy nights than cold clear nights. Hicks (1949) reported that temperature, wind speed, cloudiness and precipitation modified activity in the Western Fox Squirrel (Sciurus niger rufiventer), but found difficulty in isolating the effects of inter-connected variables. Other workers (Nikolaev and Chertova 1962, Kikkawa 1964) have also commented on the modifying effects of weather on the activity of Arvicola and Apodemus and Clethrionomys respectively. Jahoda (1973) showed a difference in the levels of activity of Onychomys leucogaster breviauritus between the time of the new moon and the time of the full moon.

Given environmental variables have not always been found to modify the activity of small mammals. Johnson (1926), in a laboratory study on Peromyscus leucopus and P. maniculatus, could not find any evidence that humidity or temperature changes affected activity. Vincent (1974) tried to correlate a number of variables with activity in Arvicola, but found no significant correlations during late spring and summer, although he did observe that activity was reduced on bright sunny days. In the present study there was no evidence of any modifying influence by the variables measured, although it is recognised that data obtained were insufficient to assess fully the import of variables on the activity observed.

It is feasible that the more or less physical structure of the environment may influence the pattern of activity exhibited, in addition to physical variables that might fluctuate quite rapidly within a short time period such as weather and light intensity. Heterogeneity in the physical structure of an individual's environment is likely to result in a spatial rather than temporal modification of its activity. If for example, avoidance of diurnal, predatory birds, hunting by sight were important, the individual might be expected to be active in those parts of its range with dense overhead cover rather than more exposed areas. By spatially distributing its activity in this way the timing of activity need not be disrupted. In different populations of the same species however, there may be fundamental differences in the degree of cover available, and whilst this may be compensated for to some extent by differences in the density of the population, adaptation might also be achieved by a modification of the activity pattern. Hamilton (1937) did not find any evidence that availibility of cover affected activity in Microtus p. pennsylvanicus. However such a possibility should not be excluded when comparing activity patterns of different populations of other species, especially those such as Arvicola which show great lability in their patterns of activity. This possibility has previously been suggested by Southern (1964) and Ashby (1972) as an explanation of divergent results obtained for Clethrionomys and Arvicola respectively.

5.9. The Community Aspect of Activity

Whilst many observers of small mammal activity have attempted to isolate the modifying effects of physical variables, little attention has been devoted to considering activity in relation to the community of which the population is a part. Some early workers considered how predator-prey interactions may produce modifications to a species activity pattern (Hamilton 1937), but the realisation that closely related species may affect the timing of activity in each other is comparatively recent.

Miller suggested (1955) that " the role of activity in the community relations of the wood mouse and bank vole is an extremely critical one and that it is an important feature of any competition between them", but did not comment on the possibility of either species adapting its pattern of activity in response to that of the other species. Brown (1956) noted that *Clethrionomys* was not trapped overnight when *Apodemus* was active. Cloudesly-Thompson (1960) speculated that asynchronous patterns of activity in closely related species may reduce competition resulting from interference. Andrzejewski and Olszewski (1963) reported that *Apodemus flavicollis* was dominant over *Clethrionomys* in the free-living condition, but it was not until Bergstedt's (1965) study that the interaction of two ecologically closely related species was shown to lead to the modification of the activity of one of them, *Clethrionomys* tending to become diurnal in the presence of a high population density of *Apodemus*. Greenwood (1974) confirmed such a relationship between *Apodemus* and *Clethrionomys*, and the present study provides strong evidence that *Arvicola* modifies its activity in the presence of *Rattus*.

To produce modifications of activity, two species need not be closely related. Knorre and Knorre (1959) (quoted in Ashby 1972) observed a major response in the activity of the moose, *Alces alces*, to the presence or absence of midges, diurnal activity being negligible in their presence whilst in midge-free localities *Alces* was intermittently active throughout the diel cycle.

The manner in which predators and prey may influence each others activity has not yet been systematically been investigated, although Rue (1967) reported that the mink, Mustela vison, normally arrhythmic in the field, has become almost exclusively nocturnal where hunted and trapped by man. Other species which man consistently 'predates' may respond in a similar manner. Intermittent disturbance by man may also influence the expression of an activity pattern, although the limited observations of the present study do not suggest that this is the case in Arvicola, which sought cover when disturbed by boats or people, but reappeared within minutes of their passage. Harling (pers. comm.) observed a similar response in Arvicola.

A final community aspect of activity is that of intra-specific relationships. Kikkawa (1964) suggests that competition may affect activity. It seems reasonable to suppose that at high population densities some individuals may be forced to be active outside their normal pattern of activity, and that this might modify the exhibited population activity to some extent. Vincent (1974) has shown that social facilitation increases activity in Arvicola but within the framework of the normal pattern of activity. It is felt that under normal conditions inter-specific reactions are more likely to influence activity in a given species than intra-specific reactions.

5.10. Conclusion

It was known that the pattern of activity exhibited by the water vole, Arvicola terrestris, is extremely labile, varying both between different natural habitats and between the field situation and laboratory conditions. The present study has confirmed this situation and may have provided a partial explanation for some of the variability shown. It has demonstrated the importance of considering community inter-actions when the ecological adaptations of a particular pattern of activity are being evaluated, and suggests that previous observers have underestimated the complexity of factors acting together to produce a particular pattern of activity. It is believed that whilst the study may have helped illuminate some aspects of the activity of Arvicola terrestris, any claim to understanding these patterns can only come after much more extensive field and laboratory work has been completed.

SUMMARY

1 The techniques available for both field and laboratory studies of small mammal activity are described.

2 The activity of Arvicola has been monitored under natural conditions on the banks of the R. Wear, close to Durham, and in the laboratory. Measures of activity in the field have been by the rate of disappearence of carrot from baiting stations. Activity of isolated individuals in the laboratory was monitored by the use of actographs.

3 The newly developed method of bait removal as an index of activity is described. Not new

4 A crepuscular pattern of activity was demonstrated in Arvicola in the field, both at the population level and within small sections of the population.

5 The effects of feeding-station habitat on bait removal were assessed.

6 A nocturnal pattern of activity has been observed in Rattus norvegicus, which also utilised the study area.

7 Cloud cover, wind speed and temperature were not found to modify activity in Arvicola. A possible relationship between light intensity and activity was observed.

8 A close agreement between bait removal and total observed activity in Arvicola has been demonstrated.

9 A nocturnal pattern of activity in Arvicola in laboratory long-day, short-night conditions has been confirmed.

10 The patterns of activity obtained in the field for Arvicola and Rattus have been compared with the pattern of activity obtained in the laboratory for Arvicola.

11 A comparison of the results obtained in the present study and those of some other workers is made.

12 The techniques used in the present study were compared with other techniques.

13 The patterns of activity exhibited under different conditions by Arvicola in this and previous studies, and the pattern of activity exhibited by Rattus in this and a previous study were discussed.

14 An explanation was offered for the field activity observed in Arvicola in this study that allows for the differing patterns obtained in previous studies.

15 The effect of the physical environment on small mammal activity was discussed.

16 The manner in which community relationships have been shown to modify activity was discussed, and further effects were speculated.

17 It was concluded that the pattern of activity exhibited by a given population of small mammals is the result of more complex inter-actions than had previously been thought.

18 The need for further studies of the field activity of small mammals has been demonstrated.

ACKNOWLEDGEMENTS

I would like to extend my thanks to Professor D. Barker, for the provision of facilities, Dr K. R. Ashby, for his very helpful criticisms and general encouragement, and Mr P. J. Greenwood for many rewarding discussions. The work was carried out whilst the author was in receipt of a grant from the Natural Environment Research Council.

REFERENCES

Andrzejewski, R. and Olszewski, J. (1963). Social behaviour and interspecific relations in Apodemus flavicollis and Clethrionomys glareolus. Acta. Theriol. 7 : 155 - 168.

Ashby, K. R. (1967). Studies on the ecology of field mice and voles (Apodemus sylvaticus, Clethrionomys glareolus and Microtus agrestis) in Houghall Wood, Durham. J. Zool. Lond. 152:389-513.

Ashby, K. R. (1972). Patterns of daily activity in mammals. Mamm. Rev. 1: 171-185.

Ashby, K. R., Harling, J. and Whiles, D. (1969). Observations on the distribution and activity of water voles (Arvicola amphibius amphibius) in Old Durham Beck, Durham. J. Zool. Lond. 158: 209-214.

Bailey, G. N. A., Linn, I. J., and Walker, P. J. (1973). Radioactive marking of small mammals. Mamm. Rev. 3: 11-23.

Bang, P. and Dahlstrom, P. (1974). Guide to animal tracks and signs. London: Collins.

Barret-Hamilton, G. E. H. and Hinton, M. A. C. (1910-1921). A history of British mammals. London: Guerney & Jackson.

Bergstedt, B. (1965). Distribution, reproduction, growth and dynamics of the rodent species Clethrionomys glareolus(Schreber), Apodemus sylvaticus (Linne) and Apodemus flavicollis(Melchior) in southern Sweden. Oikos 16: 132-160.

Blair, W. F. (1951). Population structure, social behaviour and environmental relations in natural populations of the beach mouse, Peromyscus polionotus leucocephalus. Contr. Lab. Vert. Biol. Univ. Mich. 48: 1-47.

Browman, L. G. (1943). The effect of controlled temperature upon the spontaneous activity rhythm of the albino rat. J. Exp. Zool. 94: 477-489.

Brown, L. E. (1956). Activity of the small mammals Apodemus, Clethrionomys and Microtus. Proc. zool. Soc. Lond. 126: 549-564.

Brown, L. E. (1969). Field experiments on the movements of *Apodemus sylvaticus*L. using trapping and tracking techniques. *Oecologia (Berl)* *2*: 198-222.

Calhoun, J. B. (1945). Diel activity patterns of the rodents *Microtus ochrogaster* and *Sigmodon hispidus hispidus*. *Ecology* *26*: 251-273.

Chitty, D. and Shorten, M. (1946). Techniques for the study of the Norway Rat (*Rattus norvegicus*). *J*. *Mammal*. *27*: 63-78.

*Chou, Y. (1963). *Statistical analysis*. New York: Holt, Rinehart & Wilson.

*Clarke, G. M. (1969). *Statistics* *and* *experimental* *design*. London: Arnold.

Cloudsley-Thompson, J. L. (1960). Adaptive functions of circadian rhythms. *Cold* *Spring* *Harb*. *Symp*. *Quant*. *Biol*. *25*: 345-356.

Cochran, W. W. and Lord, R. D. (1963). A radio-tracking system for wild animals. *J*. *Wildl*. *Mgmt*. *27*: 9-24.

Corbet, G. B. (1966). *The* *terrestrial* *mammals of* *western* *Europe*.London: Fouliu.

Crowcroft, P. (1954). The daily cycle of activity in British shrews. *Proc*. *zool*. *Soc*. *Lond*. *123*: 715-729.

Crowcroft, P. (1959). A simple technique for studying activity rhythms of small mammals by direct observation. *Acta*. *Theriol*. *3*: 105-110.

Crowcroft, P. and Jeffers, J. N. R. (1961). Variability in the behaviour of wild house mice (*Mus musculus* L.) towards live traps. *Proc*. *zool*. *Soc*. *Lond*. *137*: 373-382.

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

Dodge, W. E. and Snyder, D. P. (1960). An automatic camera device for recording wildlife activity. *J*. *Wildl*. *Mgmt*. *24*: 340-342.

Drummond, D. C. (1960). The food of *Rattus norvegicus* in an area of seawall, saltmarsh and mudflat. *J*. *Anim*. *Ecol*. *29*: 341-347.

Duckett, M. J. (1969). Activity in the water vole. Unpublished thesis. *Univ*. *Durham*.

---

* Not mentioned in text.

Elton, C., Ford, E. B., Baker, J. R. and Gardner, A. D. (1931). The health and parasites of a wild mouse population. Proc. zool. Soc. Lond. 1931: 657-721.

Emlen, J. T., Hine, R. L., Fuller, W. A. and Alfonso, P. (1957). Dropping boards for population studies of small mammals. J. Wildl. Mgmt. 21: 300-314

Enright, J. T. (1970). Ecological aspects of endogenous rhythmicity. Ann. Rev. Ecol. Systm. 1: 221-237.

Erkinaro, E. (1961). The seasonal changes in the activity of Microtus agrestis. Oikos 12: 157-162.

*Fitter, R., Fitter, A. and Blamey, M. (1974). The wild flowers of Britain and northern Europe. London: Collins.

Flowerdew, J. R. (1973). A new method for recording the activity of small mammals in the field. J. Zool. Lond. 171: 449-455.

Gentry, J. B. and Odum, E. P. (1957). The effect of weather on the winter activity of old-field rodents. J. Mammal. 38: 72-77.

Godfrey, G. K. (1954). Tracing field voles (Microtus agrestis) with a Geiger-Muller counter. Ecology 35: 5-10.

Godfrey, G. K. (1955).A field study of the activity of the mole (Talpa europaeus). Ecology 36: 678-685.

Greenwood, P. J. (1974). The activity of the bank vole, Clethrionomys glareolus, and the wood mouse, Apodemus sylvaticus. Unpublished thesis. Fac. Sci. Univ. Durham.

Hamilton, W. J. (1937). Activity and home range of the field mouse, Microtus pennsylvanicus pennsylvanicus. Ecology 18: 255-263.

Harling, J. (1971). A technique for precisely timing captures of Peromyscus maniculatus. Can. J. Zool. 49: 1275-1277.

Hicks, E. A. (1949). Ecological factors affecting the activity of the western fox squirrel, *Sciurus niger rufiventer* (Geoffroy). *Ecol. Monogr.* *19*: 287-302.

Holišová, V. (1970). Trophic requirements of the water vole, *Arvicola terrestris* Linn. on the edge of stagnant waters. *Zool. Listy.* *19*: 221-233.

Jahoda, J. C. (1973). The effect of the lunar cycle on the activity pattern of *Onychomys leucogaster breviauritus*. *J. Mammal.* *54*: 544-549.

Johnson, M. S. (1926). Activity and distribution of certain wild mice in relation to biotic communities. *J. Mammal.* *7*: 245-277.

Kavanau, J. L. (1963). Continuous automatic monitoring of the activities of small captive animals. *Ecology* *44*: 95-110.

Kavanau, J. L. (1966). Automatic monitoring of the activities of small mammals. 99-146 (Chapter 5) In: Watt, K. E. F. (Ed) *Systems analysis in ecology*. New York: Academic Press.

Kavanau, J. L. (1969). Influences of light on activity of small mammals. *Ecology* *50*: 548-557.

Kaye, S. V. (1960). Gold-198 wires used to study movements of small mammals. *Science* *131*: 824

Kikkawa, J. (1964). Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. *J. Anim. Ecol.* *33*: 259-299.

Knorre, E. P. and Knorre, E. K. (1959). (Materials on some characteristics of moose physiology). *Trudy Pechoro-Ilychskogo Gosudarstvennogo Zapovednika* No 7: 133-167.

Lawrence, M. J. and Brown, R. W. (1973). *Mammals of Britain: their tracks, trails and signs*. London:Blandford.

Lockie, J. D. (1966). Territory in small carnivores. *Symp. zool. Soc. Lond.* *18*: 143-165.

Lorenz, K. (1966). On aggression. London: Methuen & Co.

Lund, M. (1970). Diurnal activity and distribution of Arvicola terrestris in an outdoor enclosure. EPPO. Public Service A. No. 58: 147-158.

Mayer, W. V. (1957). A method for determining the activity of burrowing animals. J. Mammal. 38: 531.

Mehl, S. (1950). Die wuhlmaus. Biol. Zentralanst. Braunschweig. Flugblatt. 2C: 1-10

Miller, R. S. (1955). Activity rhythms in the wood mouse, Apodemus sylvaticus and the bank vole, Clethrionomys glareolus. Proc. zool. Soc. Lond. 125: 505-519

Nikolaev, A. S. and Chertova, O. S. (1962). Effect of weather factors on the activity of the water rat. Problemy Zool. Issled. V. Sibiri: 172-173. Russian trans. prog. (R.T.S. 5296).

Pearson, O.P. (1959). A traffic survey of Microtus reithrodontomys. J. Mammal. 40: 169-180

Peshkov, B. (1963). The biotopes and feeding habits of the water vole (Arvicola terrestris) in the flood plain of the Lena River. (Transl.) From: REF. ZH.BIOL. No. 141240, 1964.

Richter, C. P. (1927). Animal behaviour and internal drives. Q. Rev. Biol. 2: 307-343.

Rowe, F. P. (1970). The response of wild house mice to live traps marked by their own and by a foreign mouse odour. J. Zool. Lond. 162: 517-

Rue, L. L. (1967). Pictorial guide to the mammals of North America. New York: Crowell.

Ryder, S. R. (1962). Water voles. London: Sunday Times Book Publications.

Saint-Girons, M. C. (1960). Le rhythme nychthemeral d'activité du campagnol roux, Clethrionomys glareolus(Schreber) 1780. I-Les males. Mammalia 24: 516-532.

Saint-Girons, M. C. (1961). Le rhythme nychthemeral d'activité du campagnol roux, *Clethrionomys glareolus*(Schreber)1780. II- Les femelles. *Mammalia* *25*: 342-357.

Sewell, P. I. V. (1973). *Activity patterns and behaviour of Clethrionomys glareolus*. Unpublished thesis, *Fac*. *Sci*. *Univ*. *Durham*.

Sheppe, W. (1965). Characteristics and uses of *Peromyscus* tracking data. *Ecology* *46*: 630-634.

Shirley, M. (1928). Studies in activity I. consistency of the revolving drum method in measuring the activity of the rat. *J*. *Comp*. *Psychol*. *8*: 23-28.

Southern, H. N. (1964). *The handbook of British mammals*. Oxford: Blackwell.

Southern, H. N. (1973). A yardstick for measuring populations of small rodents. *Mamm*. *Rev*. *3*: 1-10.

Southern, H. N. and Crowcroft, P. (1956). Terrestrial habits of the water vole. *Proc*. *zool*. *Soc*. *Lond*. *126*: 166-167.

Stoddart, D. M. (1969). Daily activity cycle of the water vole (*Arvicola terrestris*). *J*. *Zool*. *Lond*. *159*: 538-540.

Stoddart, D. M. (1971). Breeding and survival in a population of water voles. *J*. *Anim*. *Ecol*. *40*: 487-494.

Tanton, M. T. (1965). Problems of live-trapping and population estimation for the wood mouse, *Apodemus sylvaticus*. *J*. *Anim*. *Ecol*. *34*: 1-22.

Tanton, M. T. (1969). Estimation and biology of populations of the bank vole (*Clethrionomys glareolus*)and wood mouse (*Apodemus sylvaticus*). *J*. *Anim*. *Ecol*. *38*:

Van den Brink, F. H. (1967). *A field guide to the mammals of Britain and Europe*. London: Collins.

Vincent, M. A. (1974). *Energy utilisation and activity patterns of the vole, Arvicola terrestris amphibius*. Unpublished thesis. *Fac*. *Sci*. *Univ*. *Durham*.

Wijngaarden, A. van. (1954). Biologie en Bestrijding van de Woelrat, *Arvicola terrestris terrestris* in Nederland. *Eindhoven Meded*. *plziektenk*, *Deinst Wageningen*. 1-147.

Zejda, J. and Zapletl, M. (1969). Habitat requirements of the water vole (*Arvicola terrestris* Linn.) along water streams. *Zool*. *Listy*. *18*: 225-238.

Zverev, M. (1928). (Mass increase of steppe lemmings and water voles in Siberia). *Zashch. Rast*. *Vredit*. *5*: 104-105. (Quoted in Vincent 1974).

APPENDIX A

Number of baits removed by Arvicola
at each feeding station for each diel period

DIEL PERIOD I

FEEDING STATION

	1	2	3	4	5	6	7	8	9	TOTAL
JUNE 13										
00:00 - 01:00										
02:00		2			1		5			8
03:00										
04:00										
05:00							5			5
06:00		4				3	5	5		17
07:00						4		3		7
JULY 12										
07:00 - 08:00	1				2			3	3	9
09:00									1	1
JUNE 14										
09:00 - 10:00						2	1	2		5
11:00							2	2		4
12:00					5					5
13:00										
14:00	1					1	3	2		7
15:00							3			3
16:00	1									1
17:00										
18:00				2			3	5		10
19:00							5	5		10
JUNE 12										
19:00 - 20:00		5				5	2	1		13
21:00		5					5			10
22:00				2			5			7
23:00										
00:00								2	3	5
TOTAL	3	16		4	8	15	44	30	7	127

DIEL PERIOD II

FEEDING STATION

	1	2	3	4	5	6	7	8	9	TOTAL
JUNE 19										
00:00 - 01:00										
02:00										
03:00							4			4
04:00								5		5
05:00							10			10
06:00								7		7
07:00							8			8
08:00										
09:00							7	1		8
JULY 12										
09:00 - 10:00										
11:00								2		2
12:00	1					3		3		7
JUNE 17										
12:00 - 13:00										
14:00										
15:00						10	10			20
16:00							9			9
17:00							1			1
18:00						10				10
19:00							10			10
20:00		3					10	3		16
21:00					1		8			9
JUNE 18										
21:00 - 22:00							7			7
23:00							4	3		7
00:00										
TOTAL	1	3			1	23	88	24		140

DIEL PERIOD III

FEEDING STATION

	1	2	3	4	5	6	7	8	9	TOTAL
JUNE 21										
00:00 - 01:00										
02:00							10			10
03:00					10					10
04:00								1		1
05:00							8	7		15
06:00						9	4	8		21
07:00						1	3		3	7
08:00							1	1		2
09:00										
JUNE 25										
09:00 - 10:00	4								2	6
11:00							10			10
12:00										
13:00								3		3
14:00						1				1
15:00							10	4		14
16:00								5		5
17:00						2				2
18:00							6			6
19:00							5	4	2	11
20:00					7		5	10		22
21:00					1			6	3	10
JUNE 20										
21:00 - 22:00						6	6	7		19
23;00					9		5			14
00:00										
TOTALS	4				27	19	73	56	10	189

DIEL PERIOD IV

FEEDING STATION

	1	2	3	4	5	6	7	8	9	TOTALS
JULY 17										
00:00 - 01:00		4	5		1					10
02:00		5								5
03:00		5			5					10
04:00										
05:00		7						7	7	21
06:00						1	3	2	10	16
07:00					2	2	10	3	8	25
08:00										
JULY 26										
08:00 - 09:00	1	3					6	5		15
10:00	1					7	6			14
11:00					2				7	9
12:00								2		2
13:00								5		5
14:00			6							6
15:00										
16:00	1		1				9	3		14
17:00						8				8
18:00							9			9
19:00	1		2		3		10			16
20:00		5	3				3	3	8	22
JULY 16										
20:00 - 21:00		2	6					7		15
22:00		1			10					11
23:00			4		6					10
00:00		1								1
TOTALS	4	33	27		29	18	56	37	40	244

DIEL PERIOD V

		FEEDING STATION									
		1	2	3	4	5	6	7	8	9	TOTALS
JULY 22											
00:00 -	01:00			1							1
	02:00		3			2					5
	03:00					2	1	7			10
	04:00					2			4		6
	05:00		5			4		2	3		14
	06:00			10			4	8		9	31
	07:00		3	1	4	1		2	5		16
AUG 1											
07:00 -	08:00			4		3			4		11
	09:00		2	2		3			6		13
	10:00			1	1	2	6		3	4	17
	11:00			1					6	7	14
	12:00			4					7	1	12
JULY 25											
12:00 -	13:00					1					1
	14:00										
	15:00		4								4
	16:00	1					7				8
	17:00	1							4		5
	18:00								8		8
	19:00	2		3		7	1		3		16
JULY 21											
19:00 -	20:00									3	3
	21:00			8		4		10	4	9	35
	22:00						7		5		12
	23:00		2	9							11
	00:00			5							5
TOTALS		4	19	49	5	31	26	29	62	33	258

DIEL PERIOD VI

FEEDING STATION

	1	2	3	4	5	6	7	8	9	TOTALS
JULY 30										
00:00 - 01:00									2	2
02:00	10							5		15
03:00		1	1					5		7
04:00					5		2			7
05:00		1					5		3	9
06:00						5		4		9
07:00					2					2
08:00					8			7	3	18
09:00		1						3		4
10:00	1			6					7	14
11:00			4				3	3		10
12:00							7	7		14
AUGUST 1										
12:00 - 13:00			3							3
14:00						3		2		5
15:00								3	8	11
16:00			1					8	8	17
17:00		5					4	8		17
18:00							7			7
JULY 19										
18:00 - 19:00		3						7		10
20:00			2		2		8	2	8	22
21:00					6	3	2	4	4	19
22:00					9			3		12
23:00					10			1		11
00:00							1			1
TOTALS	11	11	11	6	42	11	39	72	43	246

APPENDIX B

Minutes of activity recorded by the actograph for each individual for each of six diel periods

WF1

	19.7.74 - 20.7.74	20.7.74 - 21.7.74	21.7.74 - 22.7.74	22.7.74 - 23.7.74	23.7.74 - 24.7.74	24.7.75 - 25.7.74
00:00 - 01:00	53·5	53·5	47	42	13	50·5
02:00	21	53·5	27·5	42	48·5	47
03:00	0	0	0	0	58·5	0
04:00	37·5	40·5	40·5	48·5	39	44
05:00	48·5	58·5	45·5	58·5	8	45·5
06:00	37·5	3	0	11·5	0	13
07:00	0	0	0	0	26	0
08:00	0	19.5	24·5	23	58·5	0
09:00	39	55	52	58·5	19·5	47
10:00	44	39	11·5	34	13	40·5
11:00	0	0	0	0	0	3
12:00	0	0	21	35·5	55	11·5
13:00	23	48·5	60	58·5	48·5	3
14:00	42	52	42	34	0	44
15:00	26	0	5	0	0	47
16:00	0	0	0	0	23	6.5
17:00	6·5	13	15	0	27·5	0
18:00	0	35·5	48·5	39	0	0
19:00	0	0	10	29	0	19·5
20:00	31	0	3	8	27.5	37.5
21:00	58·5	6·5	19·5	0	0	10
22:00	0	55	32·5	48·5	26	15
23:00	0	3	6·5	10	47	35·5
00:00	55	34	55	42	32·5	47
TOTALS	523	570·5	566·5	622·5	571	567

WF2

	28.7.74 – 29.7.74	8.8.74 – 9.8.74	9.8.74 – 10.8.74	10.8.74 – 11.8.74	11.8.74 – 12.8.74	12.8.74 – 13.8.74
00:00 - 01:00	60	53•5	60	18	48•5	5
02:00	24•5	0	6•5	39	21	55
03:00	45•5	60	60	60	60	60
04:00	47	57	60	26	52	60
05:00	8	0	44	15	0	18
06:00	0	53•5	0	50•5	42	29
07:00	29	48•5	32•5	0	60	60
08:00	18	0	40•5	0	0	5
09:00	0	24•5	0	60	19•5	0
10:00	57	40•5	15	0	60	35•5
11:00	60	8	53•5	0	13	39
12:00	6•5	60	0	60	0	0
13:00	0	8	0	0	19•5	10
14:00	60	0	52	0	31	45•5
15:00	0	35•5	18	6•5	0	0
16:00	0	50•5	0	60	0	0
17:00	15	23	11•5	6•5	31	57
18•00	0	47	31	31	10	5
19:00	34	6•5	0	0	40•5	55•5
20:00	0	11•5	32•5	19•5	0	31
21:00	0	15	0	4	18	24•5
22:00	19•5	31	31	23	39	29
23:00	60	60	60	60	60	60
00:00	60	60	60	60	60	60
TOTALS	604	753•5	668	599	685	724

CM1

	16.8.74 - 17.8.74	17.8.74 - 18.8.74	18.8.74 - 19.8.74	19.8.74 - 20.8.74	20.8.74 - 21.8.74	21.8.74 - 22.8.74
00:00 - 01:00	60	60	21	60	29	60
02:00	35•5	37•5	27•5	3	24•5	23
03:00	6•5	0	60	21	60	0
04:00	60	35•5	60	60	60	37
05:00	60	60	60	60	60	60
06:00	60	60	52	60	32•5	60
07:00	15	13	0	39	0	39
08:00	0	0	11•5	0	14•5	0
09:00	26	26	60	42	60	23
10:00	60	60	60	60	14•5	60
11:00	60	42	32•5	18	0	48•5
12:00	26	0	0	0	8	0
13:00	0	0	0	0	60	0
14:00	0	39	18	26	23	42
15:00	60	60	60	60	0	58•5
16:00	26	29	32•5	60	0	0
17:00	0	0	0	11•5	42	0
18:00	0	3	0	8	44	18
19:00	27•5	32•5	45•5	15	0	0
20:00	23	52	8	13	0	11•5
21:00	0	0	5	34	29	60
22:00	35•5	52	60	45•5	60	18
23:00	60	60	60	60	60	0
00:00	60	60	60	60	60	57
TOTALS	761	781•5	793•5	816	741	675•5

WF3

	27.8.74 - 28.8.74	28.8.74 - 29.8.74	29.8.74 - 30.8.74	30.8.74 - 31.8.74	31.8.74 - 1.9.74	1.9.74 - 2.9.74
00:00-01:00	60	60	60	32·5	45·5	55
02:00	0	44	14·5	15	10	0
03:00	42	21	40·5	60	60	45·5
04:00	60	60	53·5	60	60	60
05:00	35.5	57	0	13	32·5	47
06:00	0	0	15	0	0	3
07:00	0	0	10	35·5	23	10
08:00	26	35·5	0	26	32·5	35·5
09:00	13	13	42	0	0	0
10:00	0	11·5	44	35·5	35·5	23
11:00	29	10	3	10	19·5	47
12:00	0	0	26	0	0	0
13:00	37·5	6·5	44	42	19·5	13
14:00	29	21	0	0	0	60
15:00	0	6·5	10	26	13	0
16:00	15	10	31	10	19·5	15
17:00	13	11·5	0	5	14·5	6·5
18:00	26	52	27·5	32·5	0	11·5
19:00	6·5	10	35·5	6·5	39	3
20:00	39	35·5	5	39	0	18
21:00	37·5	19·5	0	0	23	0
22:00	15	39	55	45·5	60	31
23:00	53·5	60	60	60	60	60
00:00	48·5	60	60	60	60	60
TOTALS	586	643·5	636·5	614	627	604

WM1

	29.8.74 – 30.8.74	30.8.74 – 31.8.74	31.8.74 – 1.9.74	1.9.74 – 2.9.74	2.9.74 – 3.9.74	3.9.74 – 4.9.74
00:00 – 01:00	57	6·5	44	60	60	32·5
02:00	60	60	60	26	57	48·5
03:00	60	60	60	60	13	60
04:00	60	26	60	60	60	60
05:00	29	23	26	39	60	44
06:00	3	13	39	0	26	39
07:00	37·5	6·5	15	58·5	6·5	24·5
08:00	10	19·5	15	55	11·5	37·5
09:00	6·5	0	13	0	0	19·5
10:00	57	35·5	8	34	13	18
11:00	31	27·5	45·5	23	0	10
12:00	0	0	10	18	27·5	0
13:00	57	37·5	18	0	0	14·5
14:00	29	23	10	60	42	23
15:00	15	60	13	15	3	0
16:00	60	0	26	15	50·5	21
17:00	57	15	5	13	32·5	14·5
18:00	10	6·5	19·5	6·5	0	48·5
19:00	60	39	13	39	21	26
20:00	47	5	29	10	40·5	0
21:00	0	0	6·5	42	3	48·5
22:00	55	60	14·5	60	58·5	60
23:00	60	39	42	60	58·5	60
00:00	23	8	29	60	8	60
TOTALS	884	570·5	621	814	652	769.5

APPENDIX C

The lengths of active and rest periods of <u>Arvicola</u> in the actograph

ACTIVE PERIODS (mins)

	DIEL PERIOD I	DIEL PERIOD II	DIEL PERIOD III	DIEL PERIOD IV	DIEL PERIOD V	DIEL PERIOD VI
WF1	71	103	62	39	114	68
	143	71	159	54	202	247
	159	159	127	188	107	120
	101	104	101	133	114	91
	126	114	143	136	55	117
		107	79	152		
				73		
WF2	36	39	36	65	123	45
	204	62	208	71	185	203
	114	159	136	156	115	167
	49	130	99	178	104	73
	127	71	91	94	66	73
	55	70	55	71	75	65
		55		50	88	
		65				
CM1	52	68	52	71	216	91
	251	269	204	230	236	136
	208	169	256	240	89	195
	162	130	162	120	91	130
	86	122	26	81	84	99
WF3	39	46	41	39	34	208
	39	39	250	201	41	152
	41	263	91	149	248	36
	198	136	88	49	159	55
	136	36	75	42	51	71
					57	
WM1	133	45	75	284	84	70
	120	101	250	185	117	263
	136	123	58	114	119	175
	253	76		78	162	70
	94	42			62	63
	84					