The activity of the bank vole, clethrionqmys glareolus, and the long-tailed field mouse, apodemus sylvaticus

Greenwood, P.J.

The activity of the bank vole, Clethrionomys glareolus, and the long-tailed field mouse, Apodemus sylvaticus.

A dissertation submitted by P.J. Greenwood to the University of Durham, as part of the requirements for the degree of Master of Science.

Department of Zoology
Science Laboratories
South Road
Durham.

September 1974.

TABLE OF CONTENTS

LIST OF FIGURES

Page

LIST OF TABLES

INTRODUCTION

This study is a field investigation of the activity patterns of Clethrionomys glareolus (Schreber), the bank vole, and Apodemus sylvaticus (Linnaeus), the wood or long-tailed field mouse, recorded during the months of May, June and July 1974 in Houghall Wood, one mile south of Durham.

Numerous ecological studies have been made of both species particularly concerning population, movement and home range (e.g. Miller 1958, Kikkawa 1964, Tanton 1965, Ashby 1967), general ecology, including dietary and habitat preferences (e.g. Evans 1942, Miller 1954, Delaney 1957, Fullager, Jewell, Lockley and Rowlands 1960, Newson 1963, Crawley 1965, Drożdż 1966, 1967, Watts 1968) and metabolism and energy budgets (e.g. Grodziński and Górecki 1967, Górecki 1968). There have also been several studies of activity patterns; of Clethrionomys by Miller 1955, Brown 1956, Ostermann 1956, Saint-Girons 1960, 1961, Pearson 1962 and by Grodziński 1962, 1963, and of Apodemus by Elton, Ford, Baker and Gardner 1931, Miller 1955, Brown 1956, Ostermann 1956, Zollhauser 1958 and Saint-Girons 1959.

Nearly all published work related to the activity of small mammals has been carried out in the laboratory. Although laboratory studies allow considerable control over the major physical factors or "Zeitgeber" to which activity patterns are geared, information obtained in this way concerning wild species must be interpreted with care, however much it may provide information which is of value in interpreting field observations.

Only Elton et al. (1931), Brown (1956), and to a limited extent Kikkawa (1964), studied activity in the field in either Clethrionomys or Apodemus.

There is general agreement that Apodemus is either a predominantly or strictly nocturnal species. Concerning Clethrionomys there is less agreement. Barrett-Hamilton (1910-1921) first suggested that it is active at intervals throughout the day as well as night. Miller (1955), using single animals in a laboratory (16 hour day, 8 hour night), recorded 51.4% of total activity during the day and 48.6% during the night, and considered that Clethrionomys was showing some degree of nocturnal preference. Brown (1956) found in Silwood, Berkshire that Clethrionomys was mainly diurnal when Apodemus was present, but with overlap between them at dawn and dusk. Activity of Clethrionomys in June peaked well after sunrise and continued at a high rate throughout the day with no noticeable peak at sunset. Grodziński (1963) suggested that Clethrionomys was mainly nocturnal in summer, but diurnal in winter and spring and reached similar conclusions to both Saint-Girons (1960, 1961) and Pearson (1962). However Kikkawa (1964) considered that in Whytham Woods, Berkshire Clethrionomys was diurnal whilst showing marked peaks at dawn and dusk. Sewell (1973) again in a laboratory study found no correlation between activity peaks and dawn or dusk, and that activity, any short term rhythm apart, was evenly distributed throughout the 24 hour period.

Notwithstanding the obvious variation in results recorded for Clethrionomys, there has been little research conducted under natural environmental conditions. For this Miller (1955) considered that,

> "....of the various techniques that have been used to study animal activity a periodic trapping census is the only practical field method, since small mammals are impossible to keep under direct observation and in fact seldom seen except when trapped",

a technique used by Elton *et al*. (1931), Brown (1956), and Kikkawa (1964). Trapping has obvious limitations, the most important being that it immobilises the animal, although Harling (1971), using continuously recording traps, was able to overcome this problem in a study of *Peromyscus maniculatus*. However it did not solve the problem of dealing with individual, species and also possible seasonal variation in trap response (Tanton 1965, 1969), and interspecific competition for traps (Brown 1956).

Other field methods which have been used to study the activity or movement of small mammals include direct observation of *Arvicola amphibius* (Ashby, Harling and Whiles 1969), the use of tracking sheets to map the movements of *Apodemus sylvaticus* (Brown 1969), the frequency and time distribution of track marks in sand in a study of activity in *Peromyscus maniculatus* (Falls 1968), radioactive tagging of *Microtus agrestis* (Godfrey 1954), telemetry, the implantation of a radio transmitter into *Peromyscus* (Marten 1973), and the introduction of a thermistor probe into the nest of *Microtus agrestis* (Flowerdew 1973).

In this study evidence will be presented to show that observation at baited sites and the unobserved removal of a standard bait (dried peas) are satisfactory and inexpensive means of determining an index of above ground activity and its periodicity throughout the day in both *Clethrionomys* and *Apodemus*.

HABITAT and METHODS.

The investigation conducted in Houghall Wood involved both observation at a baited site and the collection of data from unobserved removal of dried peas from four sites. Peas were selected as a food due to their suitable size for counting compared with other artificial foods such as grain, and their availability compared with natural seeds. Removal was recorded in all instances at one or two hourly intervals depending on the number of sites it was possible to cover. Observation was carried out in six hourly periods and arranged so that the 24 hour period was recorded during three consecutive days.

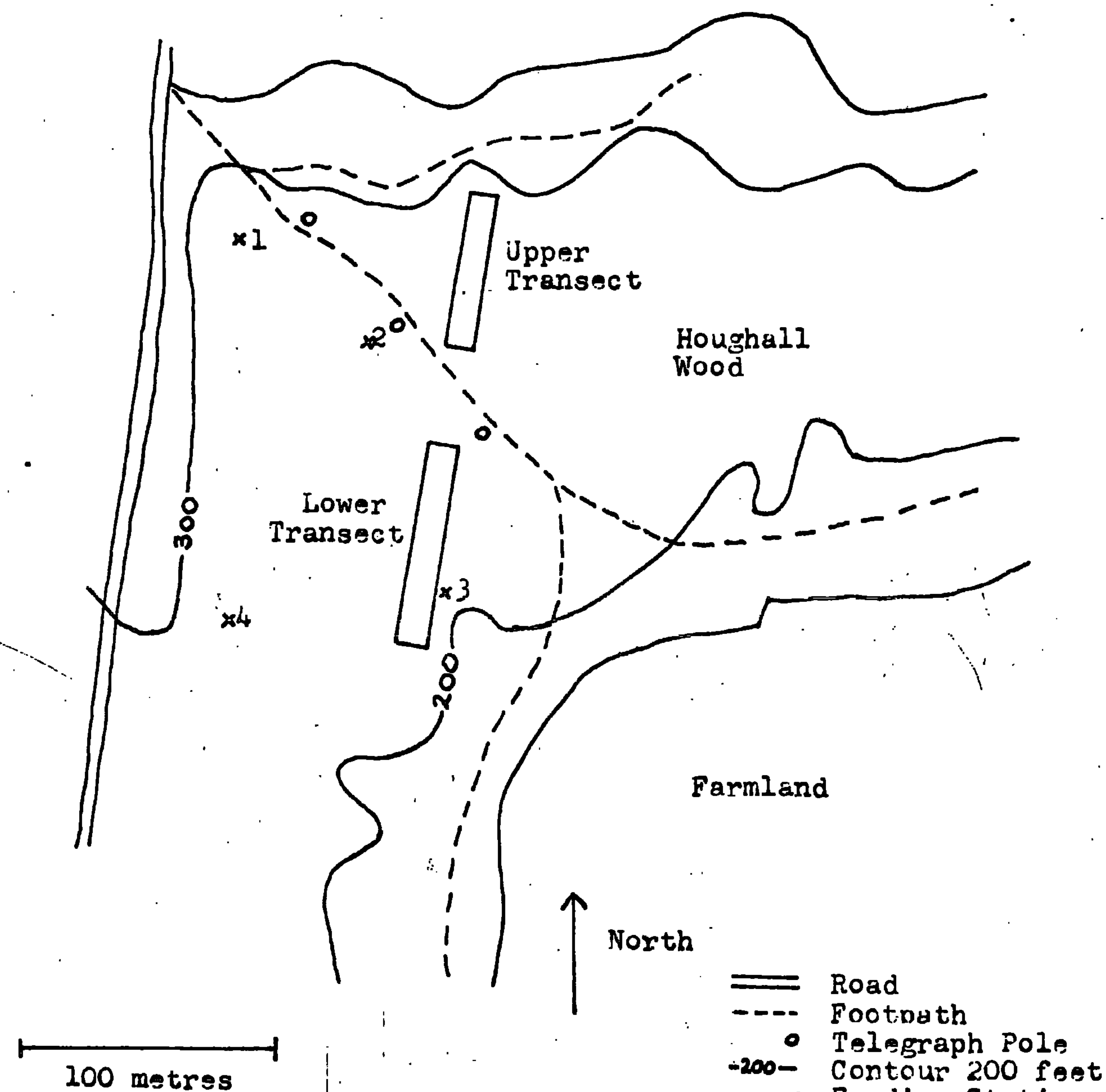
Study Area.

The work was carried out in a small section of mixed woodland close to the lower half of Transect 3 used by Ashby (I967) (see Figure I), O.S. map reference 276408. On ground sloping to the south, beech, *Fagus sylvatica*, sycamore, *Acer pseudoplanatus* and oak, *Quercus petrea*, are the dominant tree species providing a complete canopy cover over most of the area.

Initially four sites were selected for baiting with dried peas, each site being about IOO metres from any other. Site I lacked any ground vegetation cover but had a thick upper canopy cover of holly, *Ilex aquifolium*. Sites 2 and 3 had both a dense canopy of beech, sycamore and oak, and a ground cover of bramble, *Rubus fruticosus*, while Site 4 had a thin canopy of sycamore, no ground cover, but was close to a dense

Figure I.

Diagram of the section of Houghall Wood in which the investigation was conducted, showing the positions of the feeding stations and Transect 3, used by Ashby (1967).



area of bracken, Pteridium aquilinum. Sites I and 4 were near the upper section of the wood where drainage was good, whereas Sites 2 and 3 were situated close to the lower edge where conditions were more sheltered and often damp.

Method of Study.

The first part of the study involved the marking of some of those Clethrionomys and Apodemus individuals caught on Transect 3 during a routine census on 25 May. Five voles (four females, one male) and two female mice were given a distinctive mark to aid in the identification of individuals after release. A mixture of a commercial hair bleach (L'Oreal) and 20% hydrogen peroxide solution was brushed onto the hair of each animal and left for 30 minutes. To prevent the animals from removing the bleach they were confined in a small upturned plastic beaker. After half-an-hour the fur was thoroughly washed with tap water. The coat was allowed to dry before the animals were released back into the wood at their point of capture. The bleached fur was easily visible in both species.

Baiting of the sites began on 25 May. Approximately every six hours, 200 peas were put down in petri-dishes. Each dish was covered by a small wooden shelter, firstly to allow access only to small mammals and prevent peas being removed by Wood Pigeons, Columba palumbrus, and Jays, Garrulus glandrius, although neither were seen close to any site at ground level during the course of the study, and bird droppings were very infrequently recorded (5 occasions) within ½ metre of the sites, and secondly to shelter the peas from rain thus preventing them from softening and swelling. Squirrels, the only other possible removers of peas, were not present in the wood.

During the preliminary baiting period the largest number of peas was removed from site 3, so this site was selected for observation. Between 27-29 May and 3-5 June the removal of peas from site 3 was observed for two 24 hour periods. The 24 hour cycle was covered by regularly spaced observations of six hours duration, separated by twelve hour intervals during each period of three consecutive days. The site was watched from a distance of five metres. Records were made of all sightings of small mammals within a 50 square metre area in the vicinity of the feeding station, the approximate area visible to the observer. The species involved, the time of removal of peas from the petri-dish, the mode of approach and withdrawal of the animal to and from the site, and whether the individual was adult or juvenile, were noted on standard census sheets.

Observation at night was at first carried out using a headlamp covered with a red filter connected to a car battery, but it appeared to disturb the animals and was replaced by a small hand torch covered with a deep red cellophane, giving a type of light not readily detected by mammals (Southern 1955, Finley 1959). This seemed to affect the animals less and on the second night of observation (4 June) visits to the site were more frequent.

The initial observations established that at site 3 93% of peas were taken, and 95% of sightings of Clethrionomys occurred between 04.00 hours and 22.00 hours B.S.T., the approximate hours of daylight during June. From IO-I9 June therefore a ten day continuous record of peas taken from all sites was noted every two hours between 04.00 hours and 22.00 hours. Every two hours the peas remaining at each site were removed, counted and replaced by a standard sample of 50 peas at sites I and 4, one of IOO peas at site 2 and of I50 peas at site 3, the number in all cases exceeding the number of peas taken in any two hour period during the day. Overnight, that is between 22.00 hours and 04.00 hours, 200 peas were deposited at all sites to determine the number of peas being taken by Apodemus. This procedure continued until 22.00 hours on I9 June when six Longworth traps, baited with peas and grain, were positioned around each site. These were checked on the following two days at 04.00 hours, I2.00 hours and 22.00 hours in an attempt to discover the number of individuals of both Clethrionomys and Apodemus visiting each site. No Microtus agrestis were observed or trapped at any of the four sites.

More observations at site 3 were carried out on 2I-23 June, 24-26 June, 4-6 July and 7-9 July. The mode of watching was similar to that prior to the IO day continuous record, in that to cover the 24 hour cycle in three consecutive days there were four 6 hour periods of observation, each followed by a twelve hour interval. Finally, in order to obtain information which was continuous throughout a 24 hour period, from 10-25 July, 6 periods, each covering 24 hours, were recorded at site 3. The procedure was to note the number of peas removed from the feeding station every hour. To offset the possible effect of inducing a surge of activity at the start of each baiting period, the site was prebaited with 300 peas six hours before the hourly visits began, while the time of commencement of each 24 hour check was six hours later than the time of beginning the preceding check, throughout the six day trial.

RESULTS

Section 1.

Results of the 10 day study, 10-19 June.

Data collected from observation at the end of May and beginning of June indicated that *Clethrionomys* and *Apodemus* were active together only to a very limited extent. Whereas 93% of peas taken by *Clethrionomys* were removed between 04.00 hours and 22.00 hours, the approximate hours of daylight (dawn 04.35 hours, dusk 21.33 hours), less than 5% of peas removed by *Apodemus* were taken during this period. The extent and fluctuations in bait removal were thus attributable to *Clethrionomys* during the daylight period and *Apodemus* during the six hour night. The full data are given in the Appendix, Tables 1-6.

Figure 2 shows the cumulative 10 day totals for the number of peas taken from each site during the successive two hour periods. It is evident that throughout the day there is some variation in the number of peas taken during each time period, when compared to any other. Rank correlations were calculated between all possible pairings of sites, to test the hypothesis that the fluctuations exhibited at each site were similar. In all cases there was no significant correlation ($p > 0.5$), and stressed the heterogeneity of the data. Major fluctuations in pea removal were shown only at site 3, and to a lesser extent at site 2.

The number of peas removed during the two hour periods

Figure 2. The number of peas taken from the four sites during each two hour period (04.00-22.00 hours), between 10 and 19 June.

+ Site 1, □ Site 2, △ Site 3, ○ Site 4.
04 equals 04.00-06.00 hours,
06 equals 06.00-08.00 hours etc.

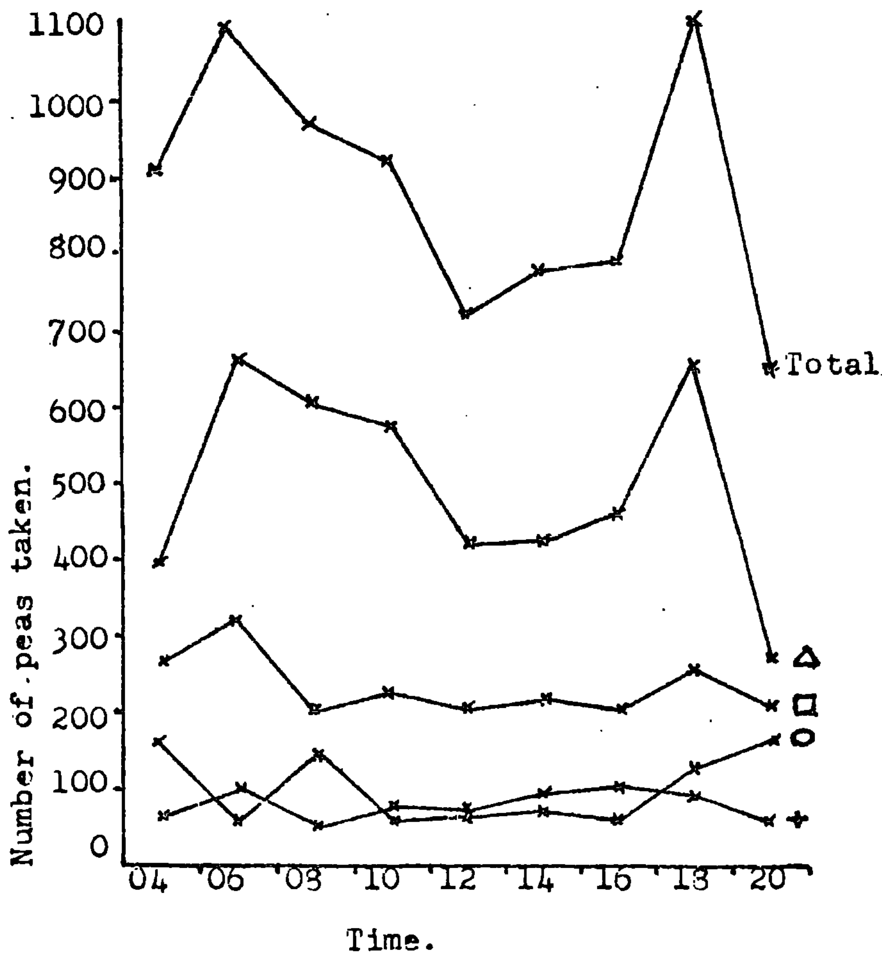
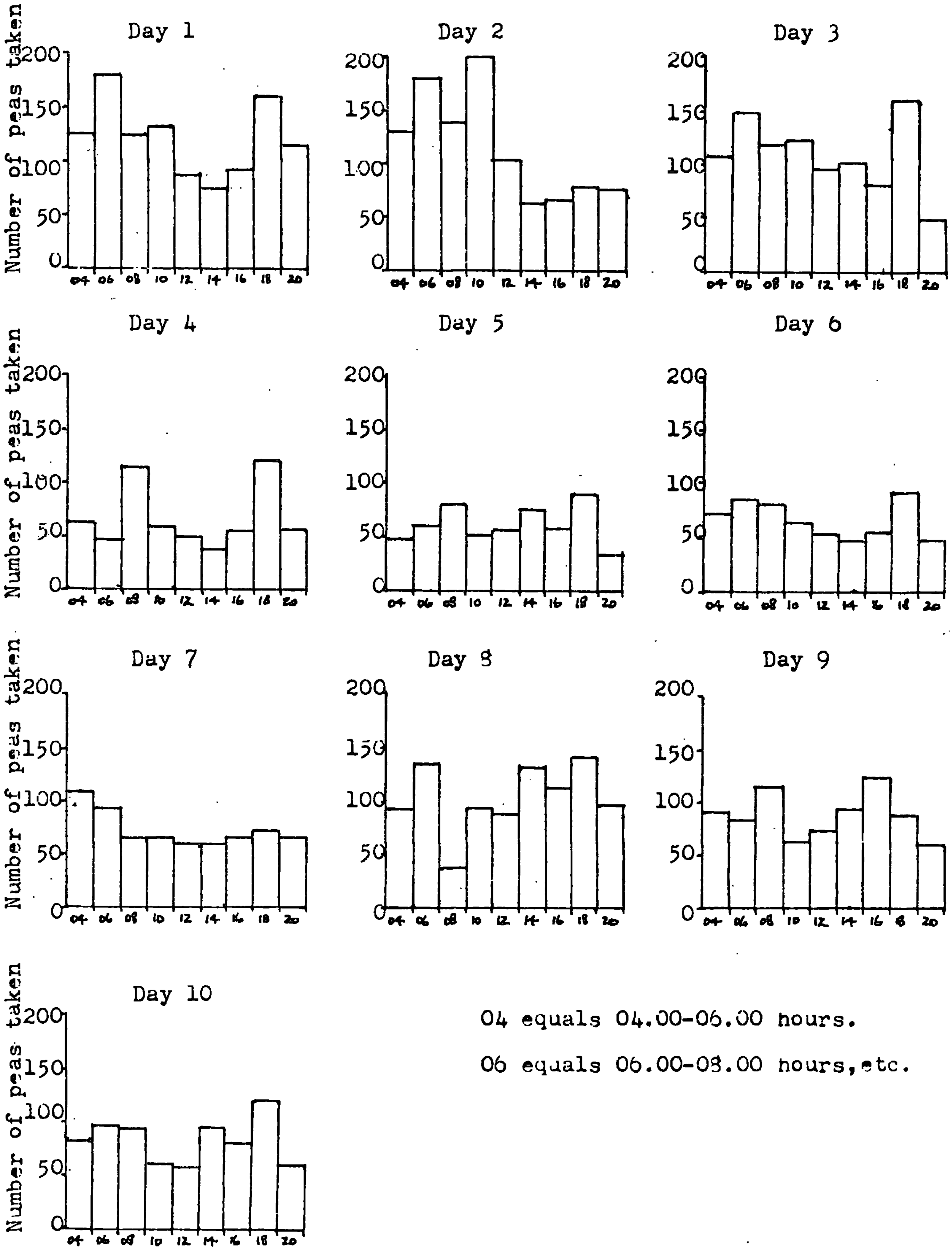


Figure 3. The number of peas taken from all sites during each two hour period from 10-19 June inclusive.



on each individual day is shown in Figure 3. The daily patterns of peaks and troughs do not appear to be consistent in timing from day to day. To test whether these fluctuations were correlated between days, the totals for the various days for each two hour period were ranked in decreasing order of the number of peas taken. Some of the days are more similar than would be expected by chance, to varying levels of significance.

Day 1 is similar to Day 3, (rs 0.79, d.f. 7, $p<0.02$), Day 6, (rs 0.75, $p<0.05$) and to Day 7, (rs 0.86, $p<0.01$).
Day 2 is similar to Day 6, (rs 0.83, $p<0.02$).
Day 3 is similar to Day 6, (rs 0.85, $p<0.01$) and to Day 7, (rs 0.66, $p<0.05$).
Day 6 is similar to Day 7, (rs 0.78, $p<0.02$).
Day 8 is similar to Day 10, (rs 0.71, $p<0.05$).

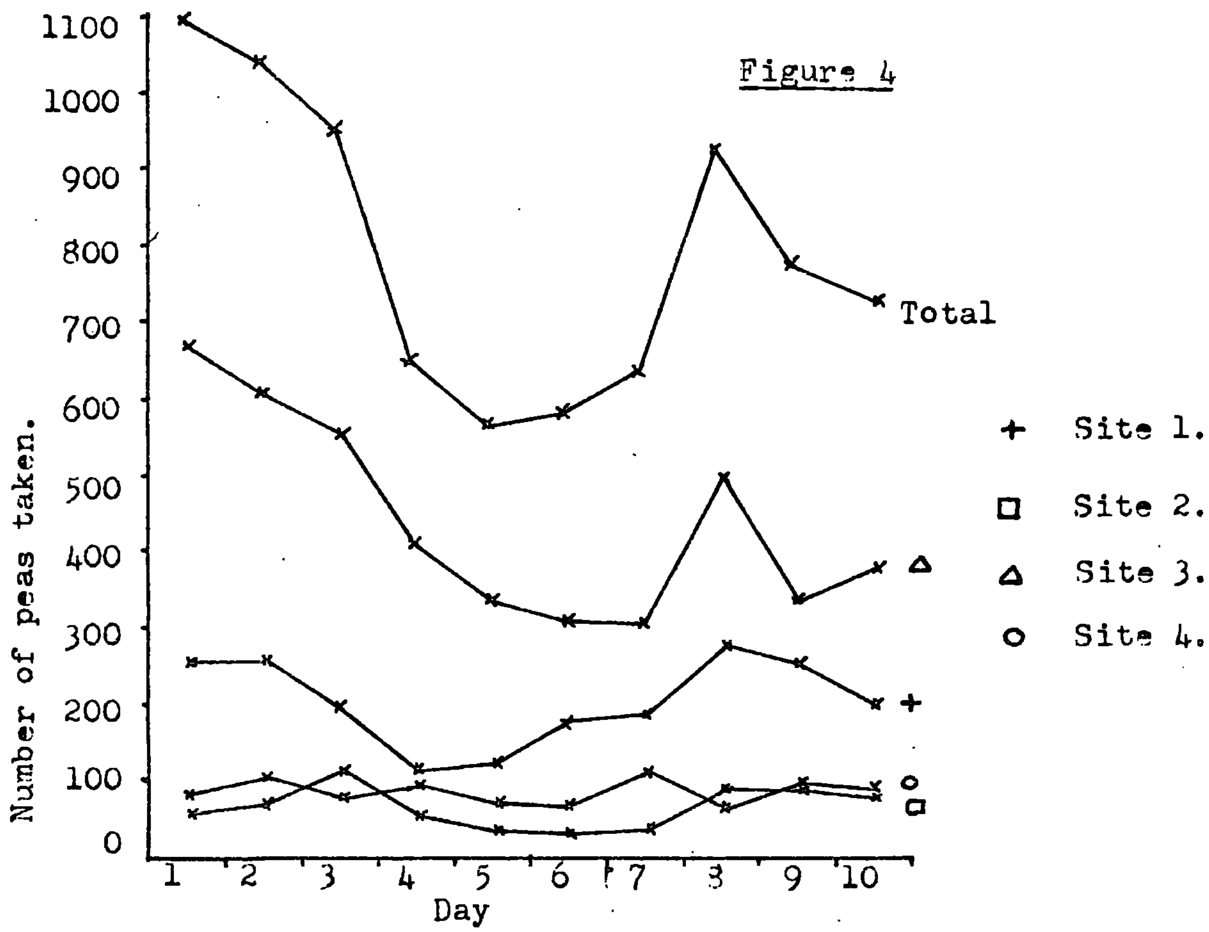
Notwithstanding these correlations, the overall pattern that emerges is one of inconsistent changes in the timing of increases and decreases in pea removal. This may be an accurate reflection of activity or alternatively an indication that a two hour period is insensitive, in that it is too long to show any regular short term changes in pea removal that may be occurring.

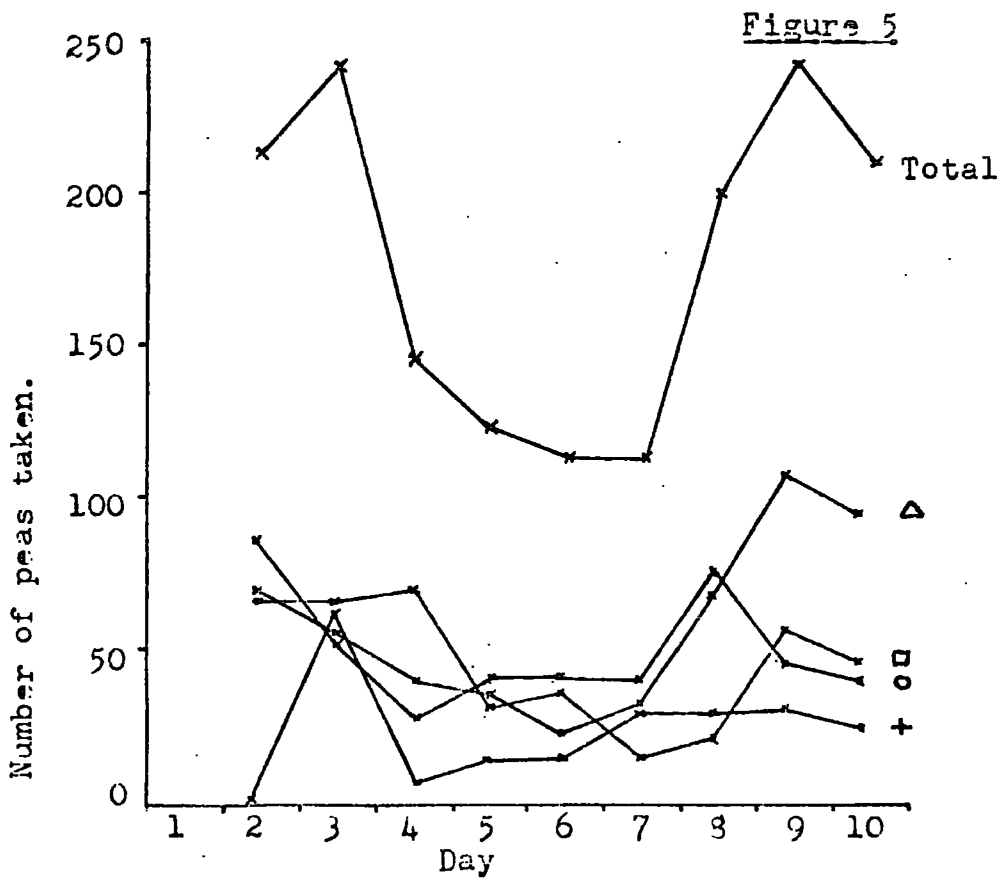
Variation in the number of peas taken from day to day, and between sites.

Figure 4 is the total number of peas removed from each site between 04.00 hours and 22.00 hours for each day. Figure 5 is the equivalent totals between 22.00 hours and 04.00 hours.

Figure 4: The number of peas taken/day between 04.00-22.00 hours at sites I-4 on successive days from IO-I9 June.

Figure 5: The number of peas taken/day between 22.00-04.00 hours at sites I-4 on successive days from II-I9 June.





Clethrionomys took very different numbers of peas from the four sites, 8% being from site 1, 26% from site 2, 55% from site 3, and 11% from site 4. Those removed by Apodemus were taken more evenly, 26% from site 1, 14% from site 2, 33% from site 3, and 27% from site 4.

Some reduction in the rate of removal was noted at all sites over the 10 day period. As the sites were prebaited for two days, this reduction might be due to satiation. The increase in consumption in the last three days, compared with the previous four days would however suggest that satiation was not a major factor.

Influence of environmental factors on the removal of peas.

In an attempt to account for some of the variation in the number of peas removed and the similarity between the variation recorded for both Clethrionomys and Apodemus, rank correlations were calculated for the number of peas taken on each day and various environmental factors, rainfall, hours of sunshine, maximum temperature and mean cloud cover. The resulting data are given in Table 1.

There are no significant correlations ($p > 0.05$) between any one of the physical factors looked at, and the number of peas removed on the day concerned.

Peas taken: Increasing rainfall (r_s 0.61, d.f. 8, $p > 0.1$).
Peas taken: Decreasing hours of sunshine (r_s 0.3, $p > 0.1$).
Peas taken: Decreasing maximum temperature (r_s 0.47, $p > 0.1$).
Peas taken: Increasing mean cloud cover (r_s 0.33, $p > 0.1$).

Table 1.

The number of peas taken/day from all sites between 04.00-22.00 hours for ten days commencing 10 June, and various physical factors recorded on those same days.

Day:	Total peas taken.	Rain mms.	Sun hours.	Mean cloud cover.	Temp. max. C.
1	1082	3.6	3.9	8	14.6
2	1034	0.1	8.1	3.5	14.5
3	947	0.0	6.3	5	19.0
4	635	0.0	12.8	1	15.3
5	557	0.0	14.0	0.1	18.0
6	574	0.0	5.0	7.4	21.9
7	635	0.0	0.3	7.6	17.2
8	918	12.1	0.1	7.3	18.2
9	771	4.0	5.6	4.4	16.0
10	737	0.1	6.6	3.6	16.5

However it is worthwhile noting that all the correlations are positive, and that the minimum removal of peas by Clethrionomys and Apodemus occurred during a warm, dry and cloudless period, whereas maximum removal coincided with wet, cooler overcast conditions.

Results of trapping and the rates of pea removal by Apodemus and Clethrionomys.

Trapping on 20 and 21 June at all four sites, caught a total of 13 Clethrionomys, six males and seven females, all adults except one male juvenile from site 4, and eleven Apodemus, six males and five females, including three juveniles. No individual Clethrionomys was recorded at more than one site, whereas one adult male Apodemus was trapped at site 3 on 20 June, and following release at 04.00 hours, it was recaught at site 4 on 21 June, 24 hours later. The numbers caught at each feeding station are shown in Tables 2 and 3.

All Clethrionomys were trapped between 04.00 hours and 22.00 hours, whereas all Apodemus were caught between 22.00 hours and 04.00 hours, apart from one female juvenile caught on site 1 at 22.00 hours on 21 June.

It is seen from Tables 2 and 3 that those sites (2 and 3) in which the largest numbers of Clethrionomys individuals were trapped, were also those from which the greatest number of peas were removed, and each animal gives a higher value of removal/individual/day than at the other two sites. At site 1, with the lowest number of peas removed during the 10 day period, only two animals were trapped, and the removal rate/individual was only 31.9/day compared with a mean of 60.7/day for all four sites, and a maximum of 87.3/day. The differences in the mean number of peas taken/individual/day at each site are significant (X^2= 33, d.f.3, $p<0.001$).

Apodemus, on the other hand, showed a much less marked site preference. The largest number of peas taken by this species was from site 3, which was also visited by more individuals than any other site, as was the case with Clethrionomys. However the rate of removal/individual/day was lower than Clethrionomys at each site. The differences in the number of

Table 2. The number of individuals of *Clethrionomys* trapped at each site, and the rate of pea removal/individual/day.

	Individuals trapped.	Number of peas taken.	Mean number of peas taken/individual/day.
Site 1:	1 male 1 female	639	31.9
Site 2:	1 male 3 females	2016	50.4
Site 3:	2 males 3 females	4366	87.3
Site 4:	2 males	835	41.7
Total :	6 males 7 females	7890	60.7

Table 3. The number of individuals of *Apodemus* trapped at each site, and the rate of pea removal/individual/day.

	Individuals trapped.	Number of peas taken.	Mean number of peas taken/individual/day.
Site 1:	2 males 1 female	413	15
Site 2:	2 males	223	12
Site 3:	2 males 3 females	527	12
Site 4:	1 male x 1 female	443	25
Total :	6 males 5 females	1606	17

x Adult male caught at 04.00 hours on 21 June had been trapped previously at site 3.

peas taken/individual/day at each site are not significant (X^2=7.0, d.f. 3, p>.05).

Number of peas removed by both species and a consideration of energy budgets.

Of the 9496 peas taken during the 10 day period, it is estimated from the frequency of removal calculated from observation, that 83% were taken by Clethrionomys and 17% by Apodemus. The difference may be solely a function of the amount of time each species was spending active and above ground during the day. Clethrionomys was observed for approximately 18 hours/day, whereas Apodemus was recorded for only 6 hours/day. From the amount of time each species was active above ground and the total number of individuals trapped, the rate of pea removal/individual/hour was 3.4 for Clethrionomys and 2.8 for Apodemus.

The probable fate of the peas, and their contribution to the metabolism of the population, was determined by a consideration of the energy budgets of Clethrionomys and Apodemus. The calorific value of one dried pea is approximately 0.7 calories, of which 0.62 calories are metabolisable energy (Boulter, D. personal communication). Drożdż (1967) considered that in the order of 85% of the metabolisable energy intake of mice and voles feeding on seeds was assimilated, so that each pea if consumed could contribute 0.53 calories to the energy budget of an individual. According to Drożdż (1967), the average daily metabolic rate in summer of Clethrionomys corresponds to an energy expenditure of 0.55 cals./g. of body weight, and in Apodemus to 0.47 cals./g. of body weight.

Over the 10 day period Clethrionomys took an estimated 7882 peas, a rate of 788/day. An average sized Clethrionomys of 20g. requires a daily intake of 12 calories, approximately equivalent to 23 peas/day, although lactating females have an energy requirement nearly double the normal figure (Kaczmarski 1966, Migula 1969). The peas removed would supply 415 calories/ day of assimilatable energy. The number of peas removed by Clethrionomys could support a maximum population of 35 individuals over the period of the trials, if each individual had an energy requirement of 12 calories/day. However, if half the total number of peas taken were consumed by lactating females, then a population of 25 individuals would be the maximum number that could be maintained by the quantity of peas removed. These estimates compare with the total of 13 Clethrionomys caught when the sites were trapped.

Apodemus removed 1614 peas over the ten days at a rate of 161/day, supplying assimilatable energy of 85 calories/day. Although Apodemus requires a lower number of cals./g. of body weight than Clethrionomys, its slightly higher average body weight also means that it requires an estimated 12 calories/day. The peas taken would support a population feeding exclusively on this seed of seven individuals, compared with a trapped total of eleven animals.

Habitat preference.

Conclusions regarding habitat preferences are limited by the number of baited sites available. Nevertheless, from the quantity of peas removed, it is apparent that Clethrionomys was exhibiting greater activity where the ground cover was more abundant, in this case bramble at sites 2 and 3, and less activity and fewer individuals where the habitat was more open. The activity of Apodemus was more generally distributed and less influenced by the density of ground vegetation.

Section 2.

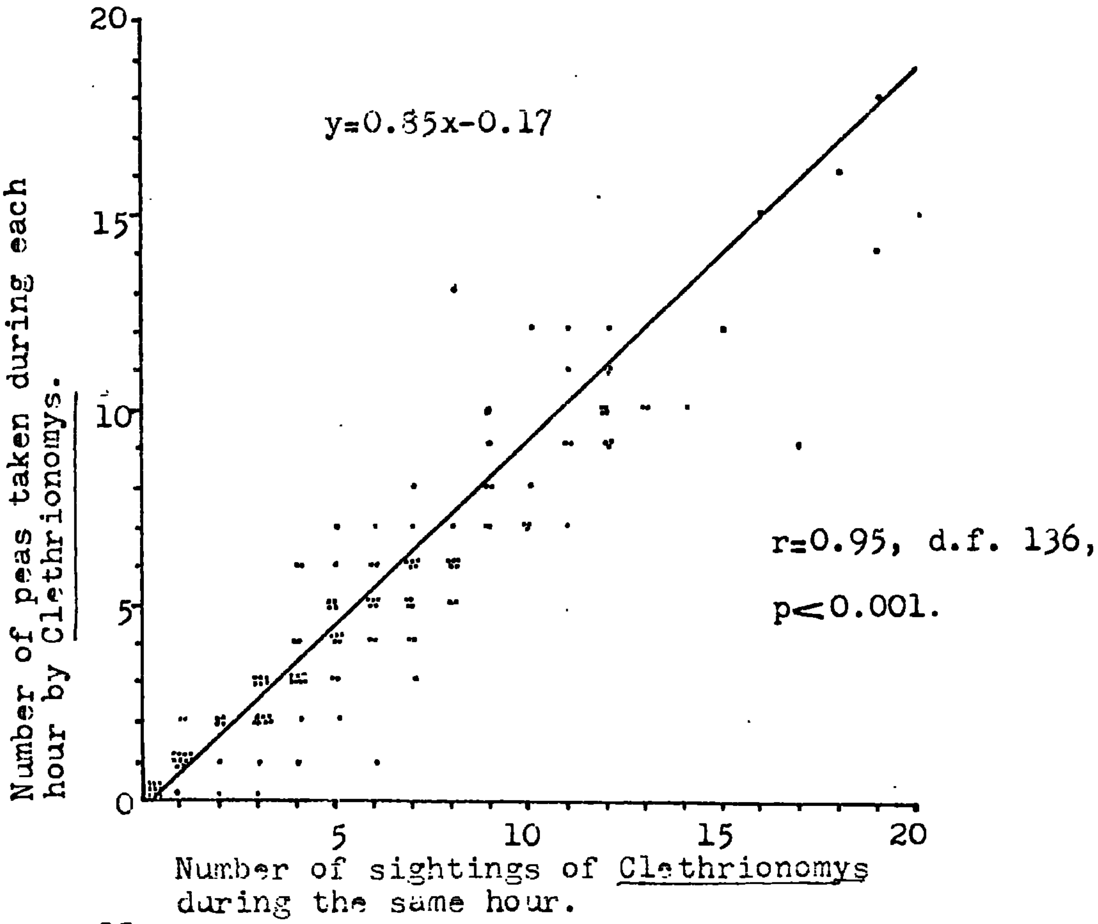
The results of observation at site 3, 27-May-9 July.

It has already been noted that fluctuations in the two hourly rate of pea removal occurred during the day, but that these were not necessarily correlated between sites and from day to day. The remainder of the study is concerned with actual observation of activity and the assessment of activity patterns from one hourly records.

Site 3 was watched from a distance of 5 metres. It was possible to observe during the day an area around the site of approximately 50 square metres. At night, using a torch emitting a narrow beam of red light, the area visible was decreased. All small mammals observed were recorded, but as far as possible an individual was not recorded a second time if it only temporarily disappeared from view, but remained above ground and then reappeared. All visits to the baited site were treated as separate records.

It can be seen from Figures 6 and 7 that the number of peas taken during each hour of observation is correlated with the number of *Clethrionomys* and *Apodemus* seen above ground. In both cases the correlation is very highly significant ($p < 0.001$). The correlation coefficients must be viewed with some caution and not regarded as giving an absolutely accurate estimate of probability of correlation, given that the data deviates somewhat from a bivariate normal distribution. However in both cases

Figures 6 and 7. The number of peas taken during each hour of observation compared with the number of sightings of *Clethrionomys* and *Apodemus*.



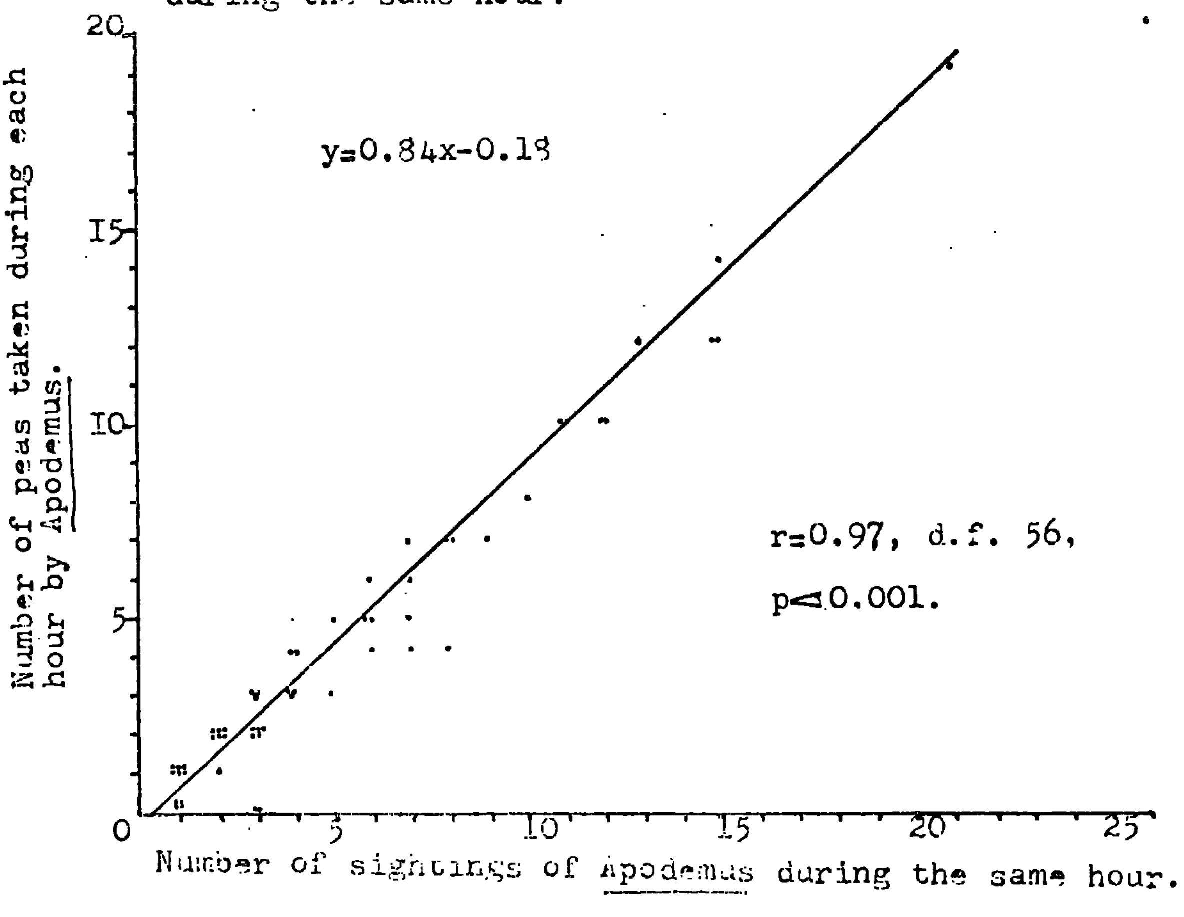
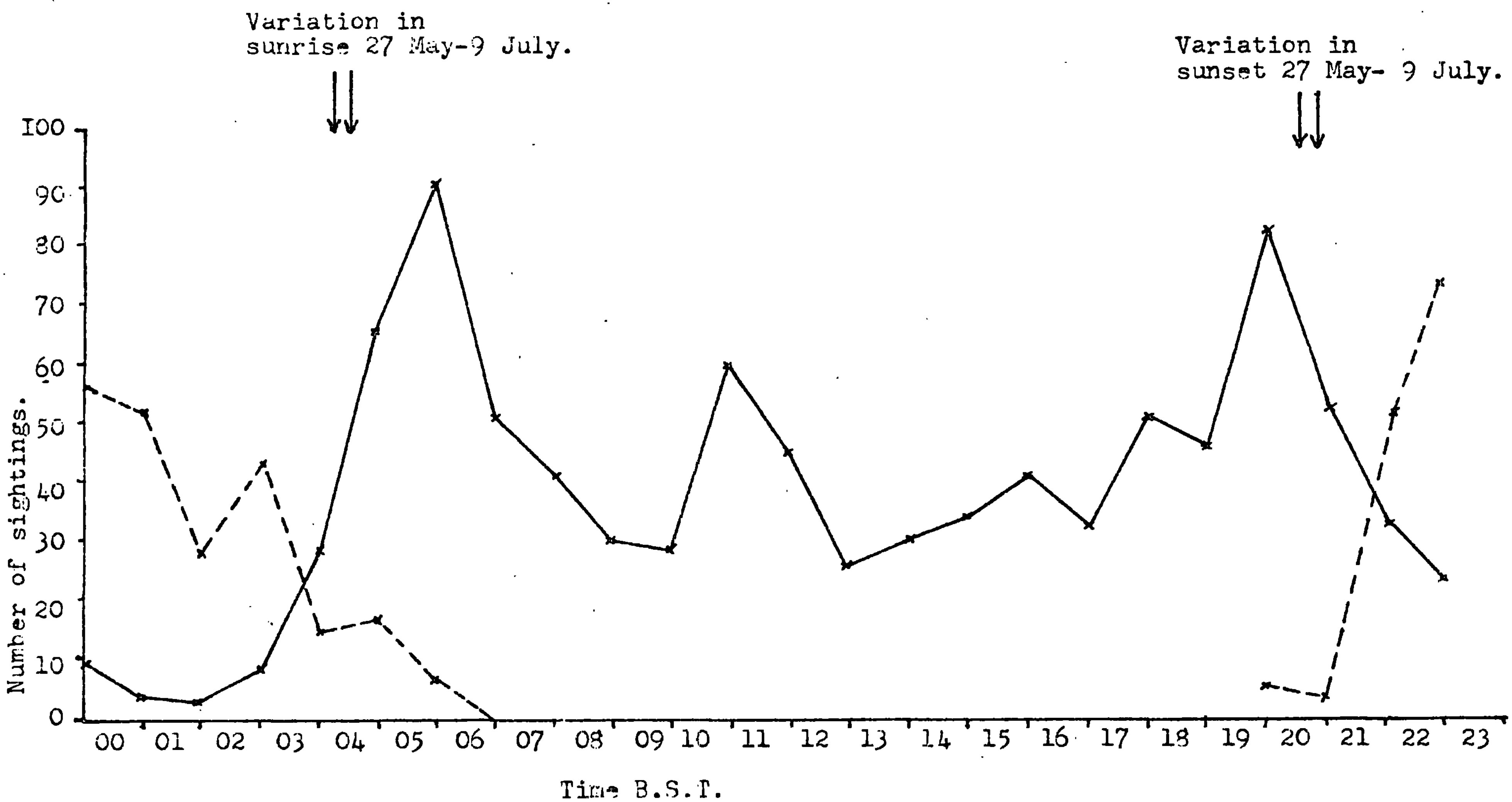


Figure 8. The number of sightings of Clethrionomys and Apodemus during each hour recorded over six 24 hour cycles of observation between 27 May and 9 July.

00= 00.00-00.01 hours, 01= 00.01-00.02 hours etc.
----Apodemus, ——Clethrionomys.



the coefficient is so high that one is justified in regarding it as giving the order of probability of the observations occurring by chance.

The pattern of activity in Clethrionomys and Apodemus.

The observations show that Clethrionomys is mainly diurnal and Apodemus is predominantly nocturnal (see Figure 8). Of the total number of sightings of Clethrionomys recorded over the six day period, 87% occurred between the time of sunrise and sunset, whereas 88% of those of Apodemus were between sunset and sunrise. From 27 May-9 July sunrise varied from 04.26-04.39 hours B.S.T. and sunset from 21.29-21.49 hours B.S.T.. Full data tables are given in the Appendix (Tables 7-14).

Following a rapid increase, activity in Clethrionomys peaked two hours after dawn. It continued active throughout the day, peaking again at dusk. Various major or subsidiary peaks were recorded during the day, the most notable being between 11.00-12.00 hours, five hours after the first peak. Unlike Apodemus, Clethrionomys was observed during every hour of the day and night, though infrequently when dark.

The emergence of Apodemus coincided closely with sunset but its activity remained low for some time before rising rapidly to a peak between 23.00 and 24.00 hours, see Figure 8. Activity of the population then began to decline although a subsidiary peak is present between 03.00 hours and 04.00 hours. The association of cessation of activity with sunrise was less strict since animals were observed up to two hours after dawn.

The largest percentage of activity in any one hour is greater in Apodemus, since it is above ground for considerably less time than Clethrionomys. 21% of the total number of observations of Apodemus occurred between 23.00 and 24.00 hours, whereas no one hour recorded more than 10% of total activity in Clethrionomys.

Comparison of activity in adults and juveniles.

During the first two days of observation no juvenile Apodemus or Clethrionomys were recorded visiting the feeding station. Subsequent observation showed that juveniles gradually became more frequent visitors to site 3, see Table 4. It is probable that the influx of young individuals is an indication of an overall increase in the population as the period of study coincided with the middle of the breeding season.

Table 4.

The mean number of sightings/hour of juvenile and adult Clethrionomys and Apodemus recorded between 27 May and 9 July.

	Juv.Cleth.	Adult Cleth.	Juv. Apo.	Adult Apo.
27-29 May :	0	3.35	-	-
3-5 June :	0	4.58	0	1.8
21-23 June:	2.16	3.7	1.3	2.2
24-26 June:	2.33	3.91	1.5	2.0
4-6 July :	3.83	3.95	3.7	3.2
7-9 July :	3.62	4.08	4.8	4.7

Figure 9. The percentage distribution of the total number of observations of juvenile and adult Clethrionomys during each hour (00.00-24.00 hours).

00=00.00-00.01 hours, 01=00.01-00.02 hours etc.

——Adult Clethrionomys, - - - - Juvenile Clethrionomys.

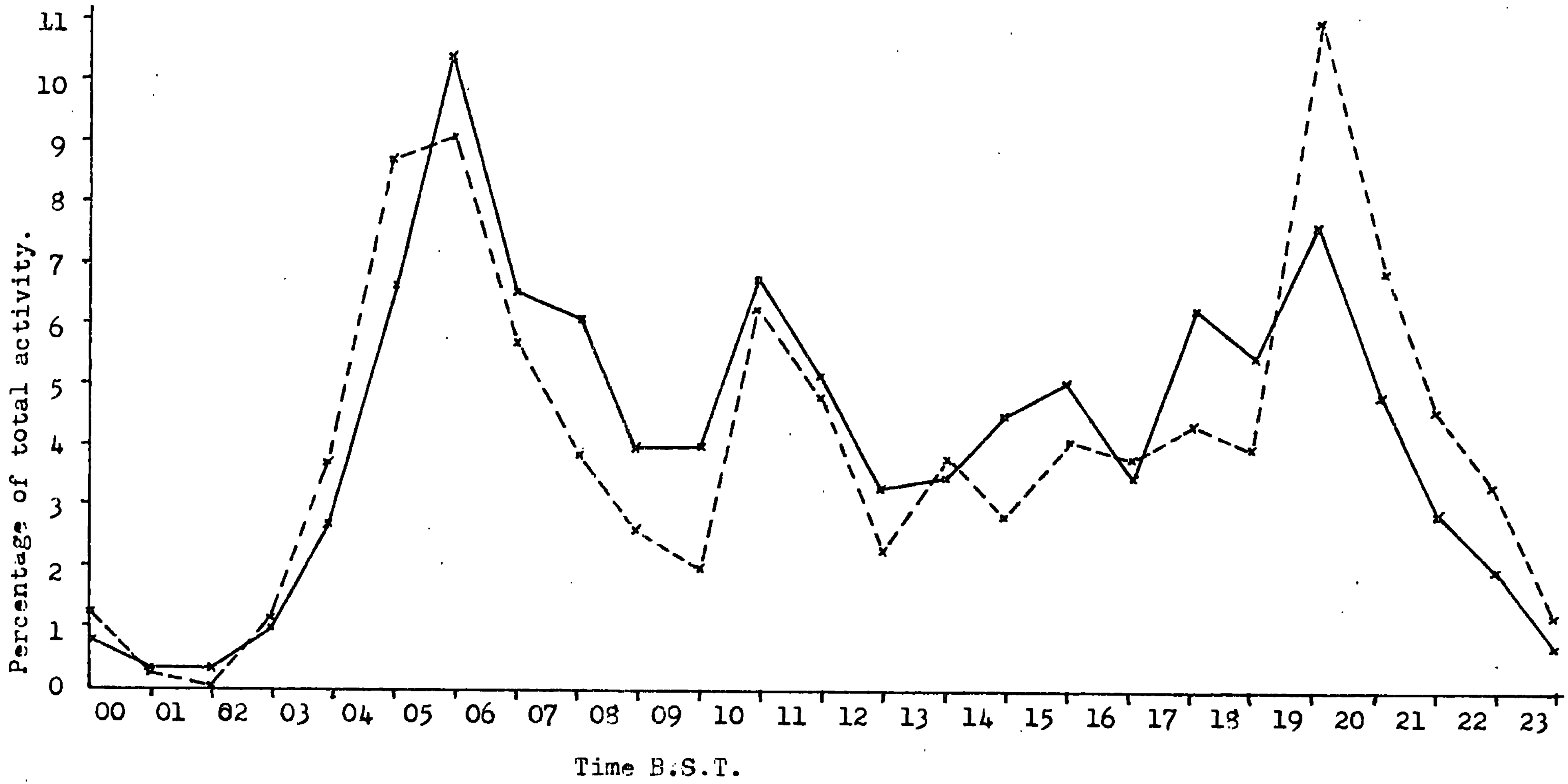
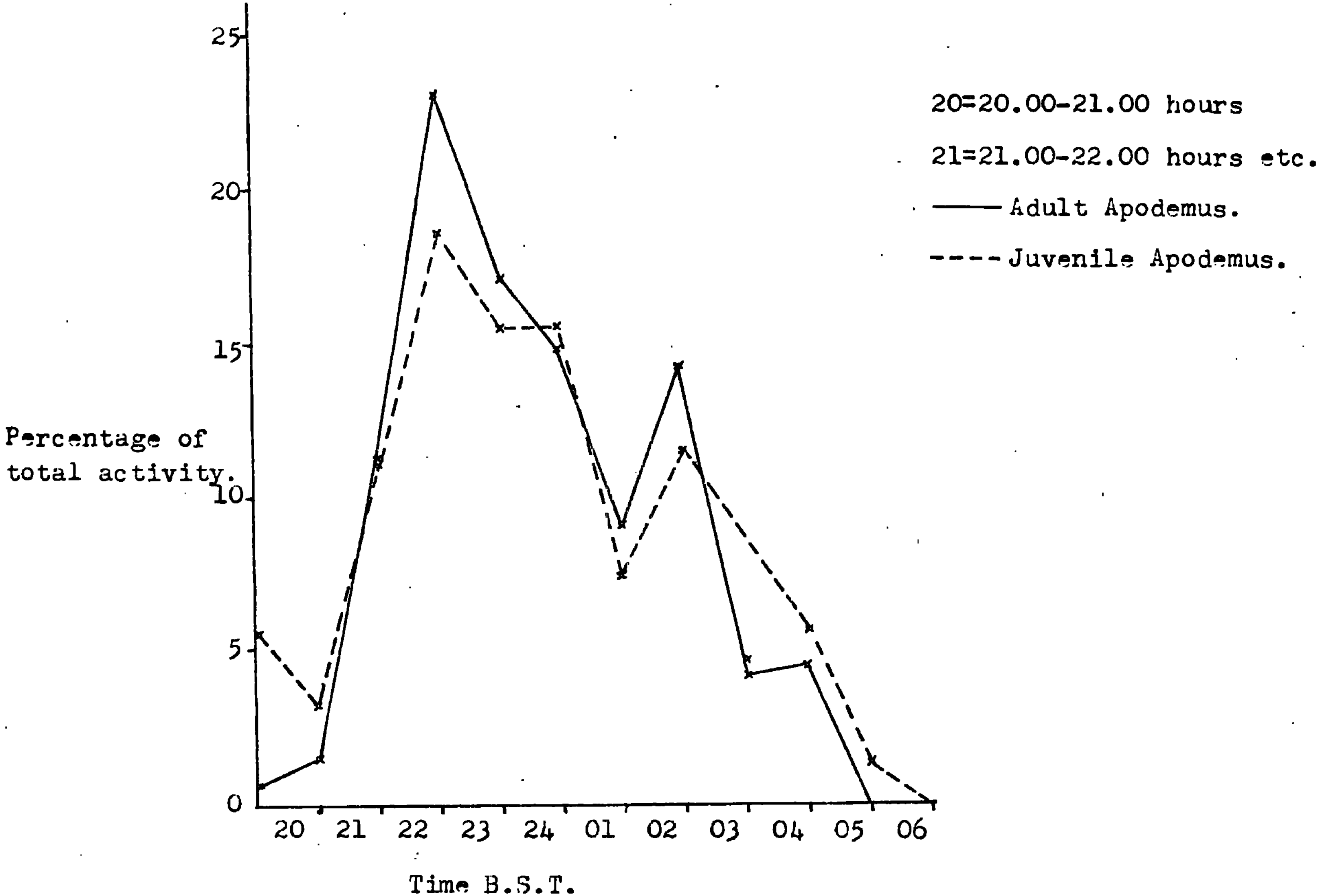


Figure 10. The percentage distribution of the total number of observations of juvenile and adult Apodemus during each hour (20.00-06.00 hours).



The number of records during each hour for adults and juveniles of both species were compared (see Figures 9 and 10, and Tables 9, 10, 13 and 14 in the Appendix). Distributions were ranked in order of abundance, and in both species adult and juvenile activity patterns were very highly significantly correlated (Clethrionomys rs 0.83, d.f. 22, $p < 0.001$, Apodemus rs 0.96, d.f. 9, $p < 0.001$).

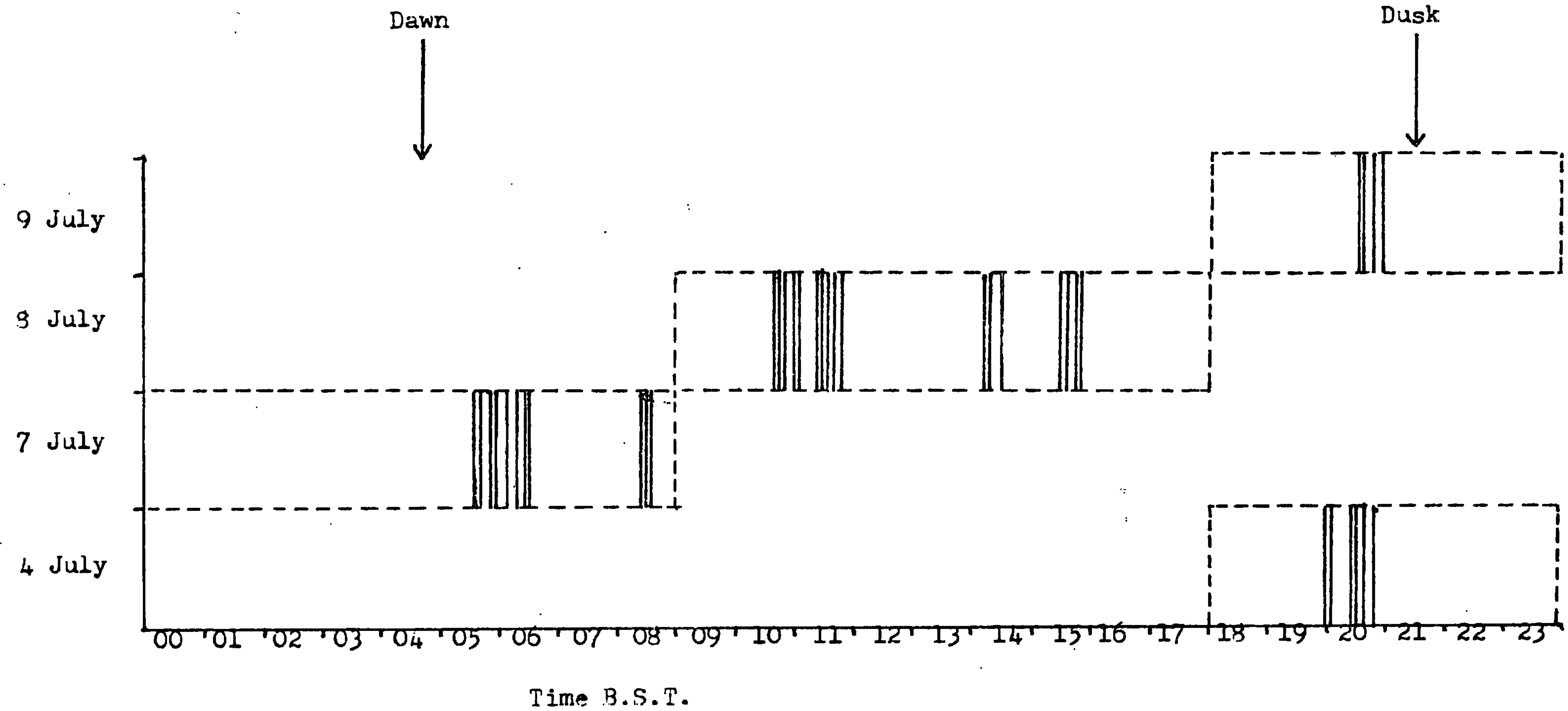
Notwithstanding the similarities between adult and juvenile records, it was noticeable that juvenile Apodemus were invariably observed first between 20.00 and 21.00 hours, prior to any general increase in activity by adults, and that proportionately the number of sightings was greater during this period for juveniles than adults. Following the decrease in activity before dawn, young animals tended to remain active above ground for up to two hours after sunrise, and for a longer time than adults, though they were not necessarily visiting the baited site for food.

Activity of an adult female Clethrionomys.

One of the problems of drawing conclusions about the activity patterns of species from observation is that, especially with small mammals, it is difficult to identify individuals, particularly when they are infrequently seen together. Thus the activity recorded is that exhibited by a section of the population as a whole. An attempt was made to overcome this problem by bleaching the fur of several individuals, released on 25 May.

Figure 11. The timing of visits to site 3 by a marked female *Clethrionomys*.

----Period of observation.



From 27 May until 3 July none of the marked animals visited site 3, or was trapped at any of the other sites. However between 4-9 July one marked adult female Clethrionomys made regular visits to site 3, taking 1-3 peas on each visit. Figure 11 shows the time of all visits that this animal made. Conclusions are limited by the small number of observations. Activity began one hour after dawn and continued throughout the day until just before dusk. Altogether 38 visits were made but they were not evenly distributed in time. Instead bursts of activity were recorded followed by prolonged periods of absence. The intervals of time between bursts of activity observed on the same day were one hour 45 minutes on 7 July, and two hours and one hour on 8 July.

Behaviour of Clethrionomys and Apodemus.

Clethrionomys invariably approached the baited site through areas with dense undergrowth. Movement was smooth and regular, only occasionally would the animal stop, put its head upwards and sniff the air. Those individuals not concerned with removing peas were often seen moving through the leaf litter, sometimes scratching at the surface and less frequently feeding on live vegetation, which in this area was either bramble or leaves of grasses. Movement was particularly rapid if an animal had to cross a section of wood devoid of ground vegetation.

There were a total of 575 records of visits to the site by Clethrionomys in which the approach and withdrawal paths of the animal were visible over a distance greater than two metres from the site. On 220 occasions (38%), withdrawal was along the path of approach, whereas on 355 occasions (62%), the path of withdrawal was different to that of approach. The fact that in the majority of cases animals do not use a similar pathway of approach and retreat may be of selective advantage in the avoidance of predators, in that it does not establish predictable lines of movement.

It was also evident that during bursts of activity of specific individuals that peas removed, if not immediately consumed, were not all taken away and deposited in the same place, since the modes of approach and withdrawal were not consistent from visit to visit. On one occasion an adult Clethrionomys recovered a pea buried in the leaf litter about four metres from the site and transported it another six metres before again depositing it in the ground.

The length of time that any Clethrionomys spent at the bait was short and never longer than 30 seconds. Generally approach was from the side or behind the site. Usually only one pea was taken. This was invariably the case with juveniles, limited by their size of mouth, but adults often took two peas and occasionally three. The first pea was normally picked up directly into the mouth without aid of the front feet, while the securing of second and third peas was assisted by the front legs as the animal sat upright. If three peas were taken, two were positioned in the cheek pouches while the third was held between the front teeth. This method of food gathering was also used in the selection of leaves. The animal would sit upright on its haunches and use mouth and fore legs to secure a piece of vegetation, grasp it between the front legs and bite sections off with its teeth.

The movement of Apodemus close to the site was more jerky than Clethrionomys and more readily interrupted by stoppages and deviations from a direct mode of approach. The direction of approach was usually from the side of the site, and from areas not frequently used by Clethrionomys. Apodemus on the whole spent longer at the feeding station and would wander over the petri-dish before selecting a pea and moving off, often swiftly with a jump. Only one pea was taken at each visit.

As they were active at night when the use of a red light restricted the area visible, it was not possible to determine to what extent individual Apodemus used different directions of approach and withdrawal. Furthermore, the ability to identify individuals was severely limited, particularly as no marked ones were recorded. Animals were separated only into adults and juveniles by size. It was apparent though that in the transition between dusk and night, Apodemus would more readily move into areas devoid of ground cover and often approached in the open within one metre of the observer.

Both Apodemus and Clethrionomys used the petri-dishes and the surrounding areas as places for the deposition of faeces and urine.

Intraspecific and Interspecific encounters.

Although 150 hours were spent in observation at site 3, the number of encounters between animals was few. Aggressive behaviour was seen once between the marked female Clethrionomys and a juvenile, in which the adult threatened the juvenile behind the feeding site. The young individual rapidly retreated; in the act of running away it jumped 30 cms. in the air.

The usual situation encountered if more than one animal was involved in visiting the feeding station was that, particularly when a juvenile was in the process of removing a pea, it would often retreat without completing the operation, to be followed shortly afterwards by an adult, which would take a pea and depart, after which the displaced juvenile would return. Although it is not demonstrated conclusively that the displacement of individuals was a direct result of the presence of another animal nearby, the observer was able to anticipate on many occasions the occurrence of such behaviour, before another individual came into sight, either by the noise of movement within the undergrowth or by squeaks from the approaching animal.

On six occasions Apodemus came into contact with Clethrionomys. Neither seemed to tolerate the presence of the other, but whether one species was dominant over the other was not apparent from so few encounters. The outcome of any meeting was that both animals bolted. On four occasions Apodemus was present at the site when Clethrionomys approached, for the other two the reverse was the case. Once an adult *Apodemus* and juvenile *Clethrionomys* moved towards each other, ending up nose to nose without touching and without displaying any visible agonistic behaviour or emitting any audible sound, before both animals ran off. It may be significant that of the six encounters, on five occasions it was *Apodemus* which returned to the site first to remove a pea, often as rapidly as less than ten seconds after the encounter.

Section 3.

The six day unobserved 24 hour study and a comparison with the observed.

The effect of disturbance on the level of activity.

It was obvious that during the study there was a significant reduction between the number of peas taken when the site was being watched, compared with the number removed when the site was undisturbed. During the six days of observation there were 920 separate records of *Clethrionomys* and 348 of *Apodemus*, compared with totals for the six day undisturbed period in July of an estimated 5352 peas taken by *Clethrionomys* and 1405 by *Apodemus*. The number of sightings of *Clethrionomys* is only 17% of the number of peas taken when the site was not watched, and 20% in the case of *Apodemus*. However the observed period began before the influx of juveniles into the population at the end of June and beginning of July, consequently the level of activity should be lower. The effect of an observer being present was probably less than the percentages indicate, although some degree of disturbance was apparent.

Despite affecting the intensity of activity, it was essential that observation was not inflencing the periodicity. It was therefore necessary to determine whether the use of a red light was having a differential effect on the level of activity in the two species. *Apodemus* was active during all the period of illumination and appeared unconcerned. The activity of *Clethrionomys* during the same period was considerably reduced, although some recordings were made during all the hours when the red light was used.

There are several points which suggest that Clethrionomys was tolerant of red light and not adversely affected by it. Firstly, the amount of activity had already reached a low level, 21.00-22.00 hours, before the red light was switched on, usually 22.00-22.30 hours. Secondly, the increase in activity leading to the morning peak began before the red light had been switched off, 04.00-04.30 hours.

Table 5.

The percentage of peas taken by each species during the hours when both species were visiting site 3, calculated from observation on 21-23, 24-26 June, 4-6, 7-9, 26-27 July. (20 equals 20.00-21.00 hours, 21 equals 21.00-22.00 hours etc.).

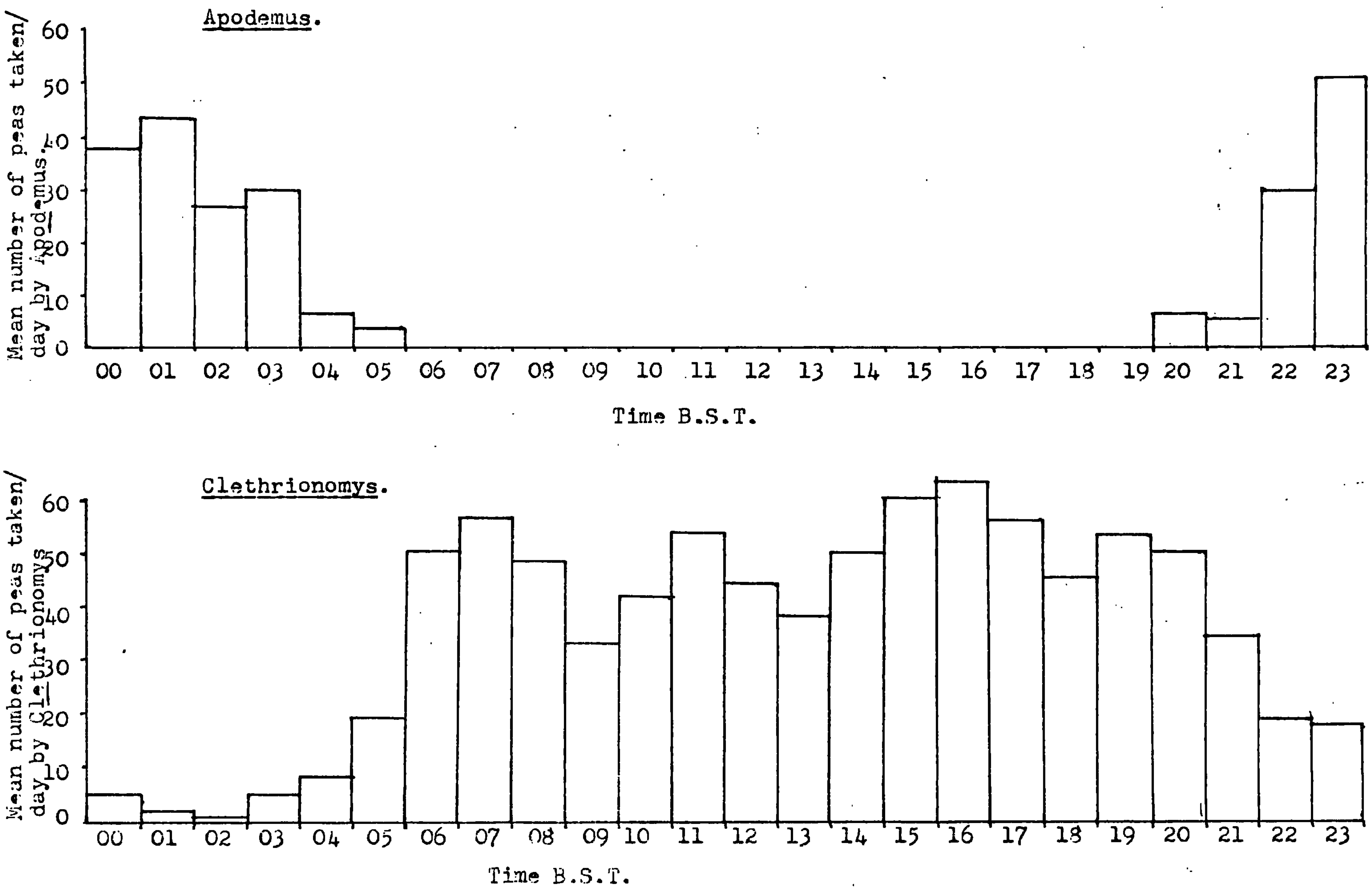
Time, hours	20	21	22	23	24	01	02	03	04	05	06
Total peas taken	66	39	56	76	51	46	23	43	32	61	68
Peas taken by Cleth.	59	34	23	20	7	2	1	6	21	52	68
Peas taken by Apo.	7	5	33	56	44	44	22	37	11	9	0
% peas taken by Cleth.	89	87	41	26	16	4	4	16	66	85	100
% peas taken by Apo.	11	13	59	74	84	96	96	84	34	15	0

Thirdly, from the overlap period of observed activity of Clethrionomys and Apodemus in June and July, the percentage of the total number of peas taken during each hour by the two species was calculated (see Table 5). These percentages were used to calculate the number of peas removed by both Clethrionomys and *Apodemus* when their activity coincided during the six day unobserved period. If the activity of *Clethrionomys* at night increased to a level approaching its daytime intensity then the number of peas taken during the unobserved period would reflect any increase in activity. A disparity between the observed and unobserved distribution of activity would then exist. During June and July, of the 757 records of *Clethrionomys*, 690 were between 04.00 hours and 22.00 hours, and 67 between 22.00 and 04.00 hours, the approximate period when the red light was being used. For the six day unobserved trial it is calculated that 5046 peas were taken by *Clethrionomys* from 04.00-22.00 hours, and 306 from 22.00-04.00 hours. The use of a 2X2 contingency table shows that there is no evidence to lead to the rejection of the hypothesis that the reduction in activity recorded when the red light was switched on, was similar to the reduction in activity during the unobserved period, and that the distribution of activity in both cases was similar (X^2 1.3, $p > 0.2$). Finally, there was no significant difference between the proportionate distribution of the total number of sightings of both species combined, during the six observed days, 22.00-04.00 : 04.00-22.00, 351 : 905, and the distribution of peas taken during the six unobserved days, 22.00-04.00 : 04.00-22.00, 1682 : 5084, (X^2 1.08, $p > 0.2$).

The results of the six day unobserved study.

The number of peas taken during each one hour is shown in the Appendix, Tables 15-17. The distribution of the number removed

Figure 12. Estimated mean number of peas taken/day during each hour by Apodemus and Clethrionomys recorded over six 24 hour periods between 10 and 25 July.

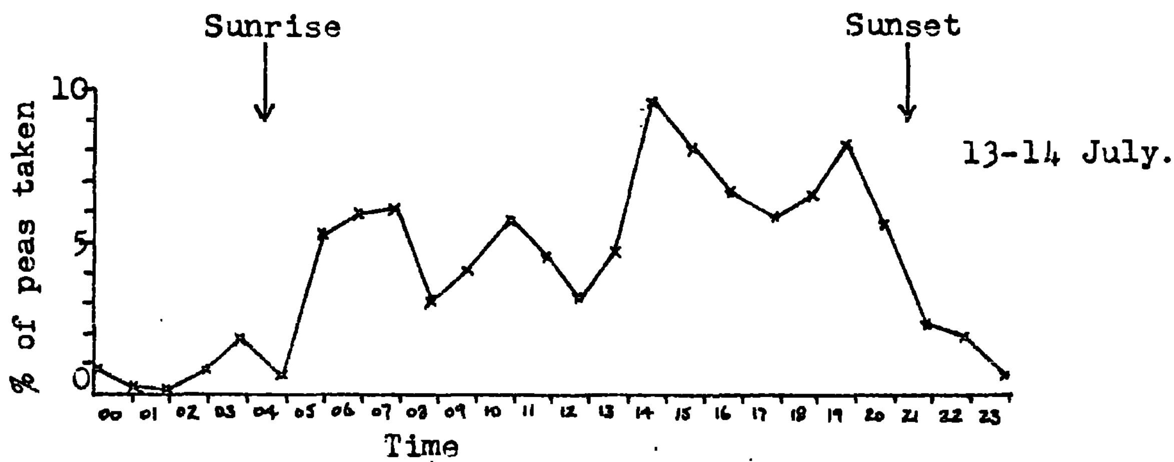


by the two species was estimated from the observed overlap period (see Table 5). The percentage taken by each species during each hour when both species were observed active was used to calculate the number of peas taken by the two species from the total number of peas removed in each unobserved hour during the six days (see Tables 16 and 17 in the Appendix). Figure 12 shows the mean number of peas taken and the estimated rate of removal/hour by Clethrionomys and Apodemus.

The mean rate of removal/hour by both species was ranked and compared to the ranked totals for the observed six days. There is a very highly significant correlation between the distribution of activity throughout the observed and unobserved six days, (Clethrionomys rs 0.64, d.f. 22, $p < 0.001$: Apodemus rs 0.93, d.f. 9, $p < 0.001$).

Figures 13 and 14 show the percentage of peas taken during each hour for the six days by Clethrionomys, and Figures 15 and 16, the same for Apodemus. In both species the populations were exhibiting a daily polyphasic rhythm of irregularly spaced peaks. To discover whether the overall patterns were correlated from day to day, hourly records were ranked and correlations calculated for all pairings of days (see Tables 18 and 19 in the Appendix). The rank correlations demonstrate in each species an overall resemblance in activity. They are affected mainly by the day/night differences in activity of Clethrionomys and Apodemus, and do not necessarily indicate that the lesser fluctuations in activity are synchronised over the period of the trial.

<u>Figures 13 and 14</u>. Estimated percentage of peas taken during each hour by *Clethrionomys* recorded over six 24 hour periods between 10 and 25 July.



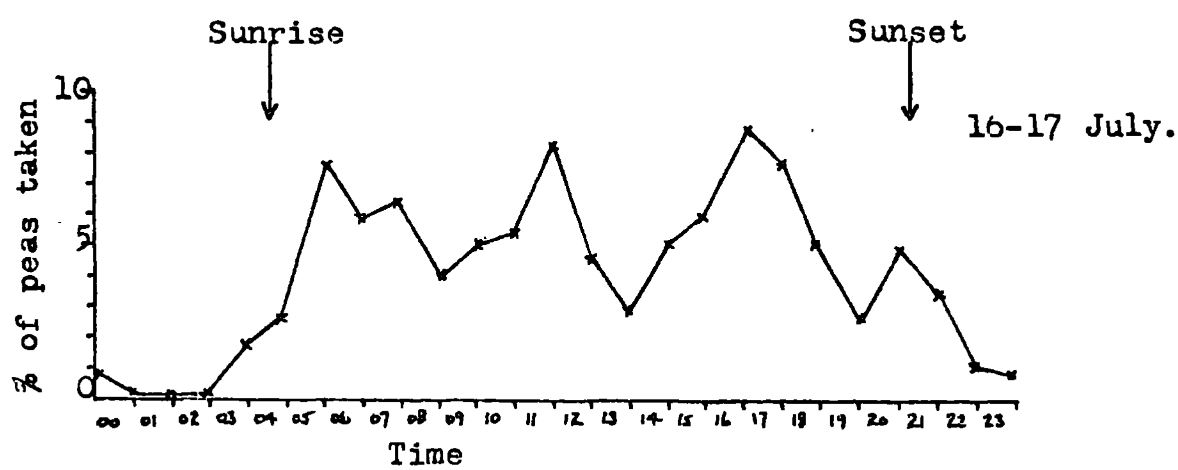
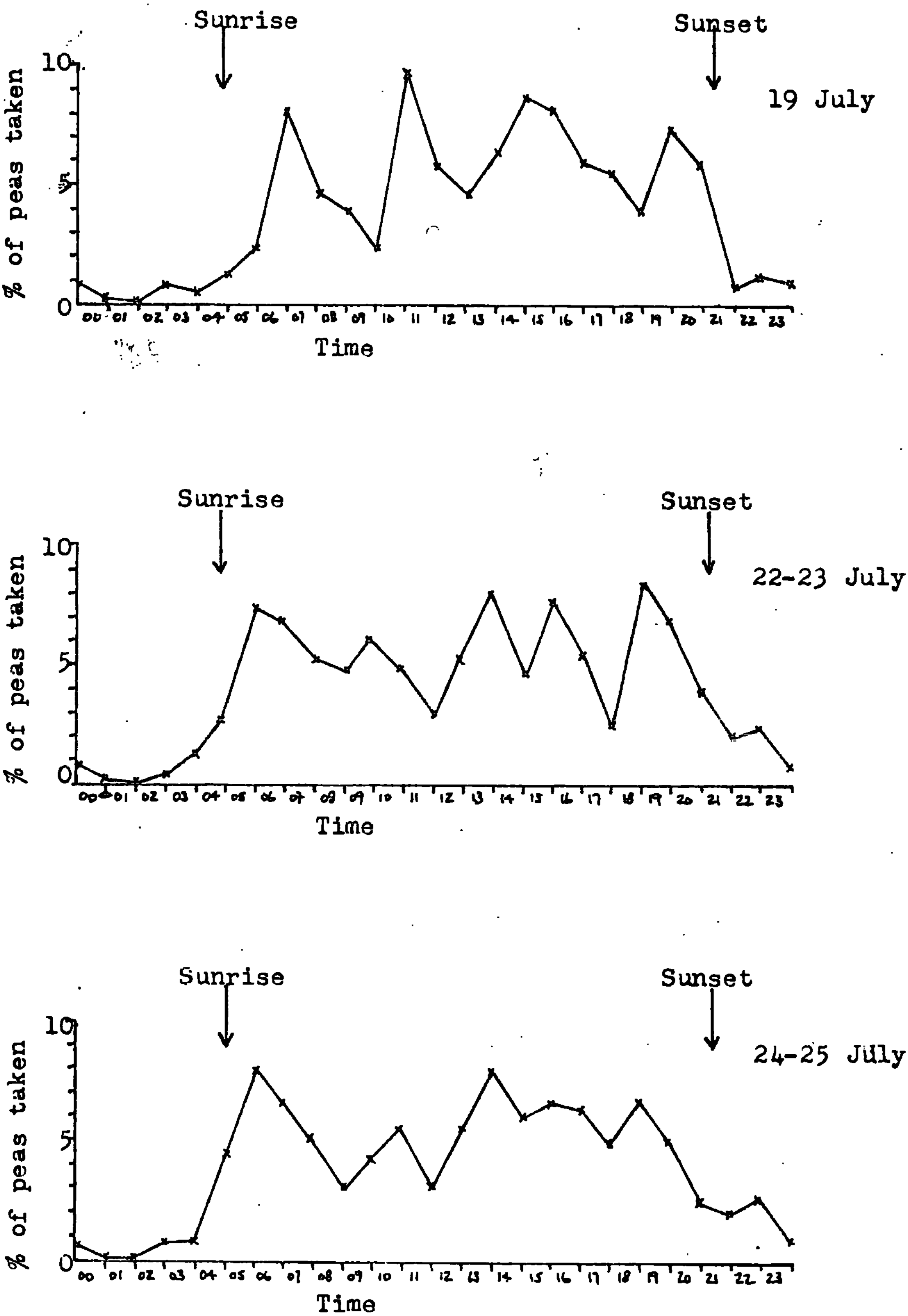


Figure 14.


Sunrise
Sunset
19 July
% of peas taken
10
5
0
00 01 02 03 04 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time
Sunrise
Sunset
22-23 July
% of peas taken
10
5
0
00 01 02 03 04 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time
Sunrise
Sunset
24-25 July
% of peas taken
10
5
0
00 01 02 03 04 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time

Figures 15 and 16. Estimated percentage of peas taken during each hour by *Apodemus* recorded over six 24 hour periods between 10 and 25 July.

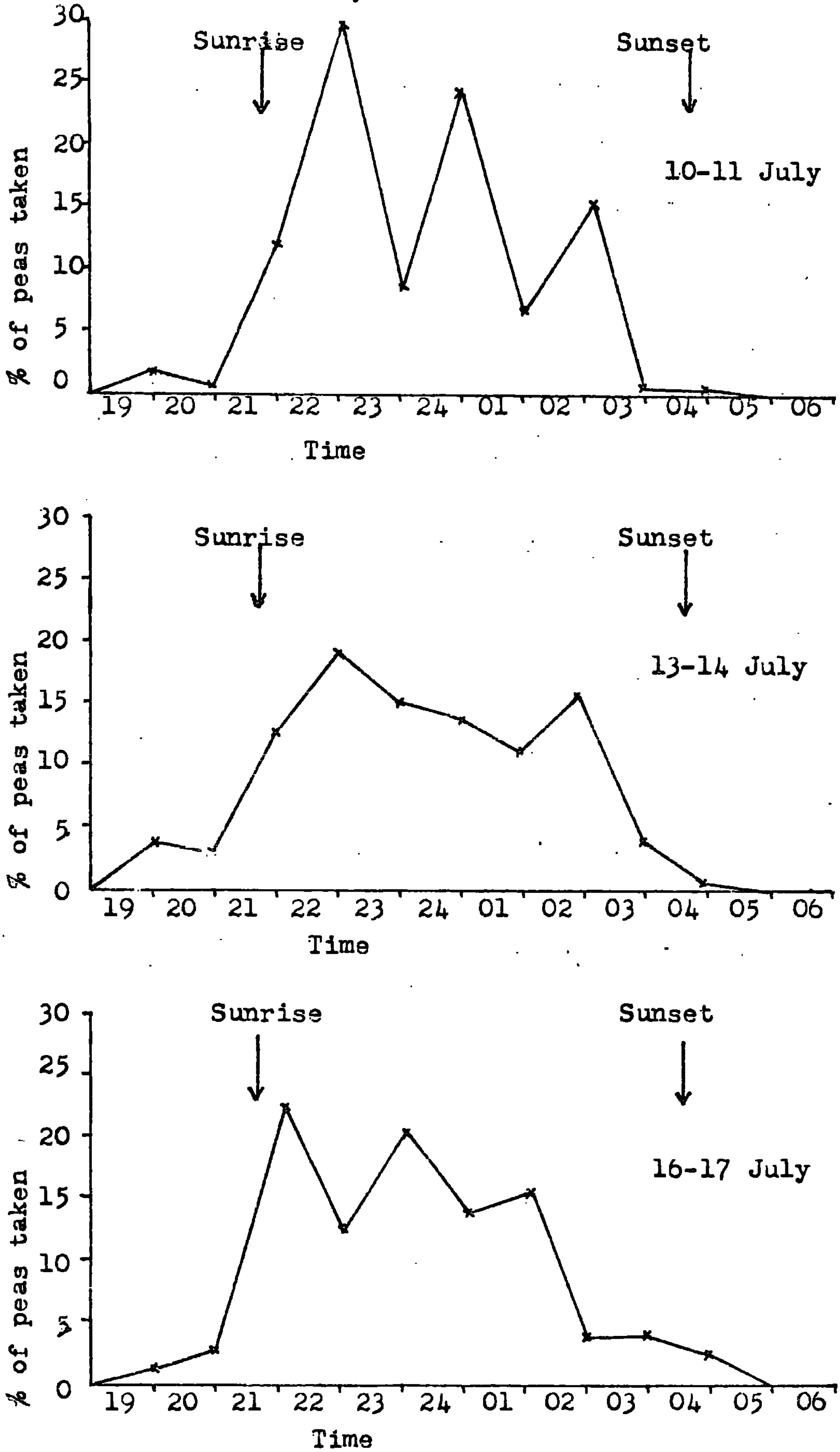
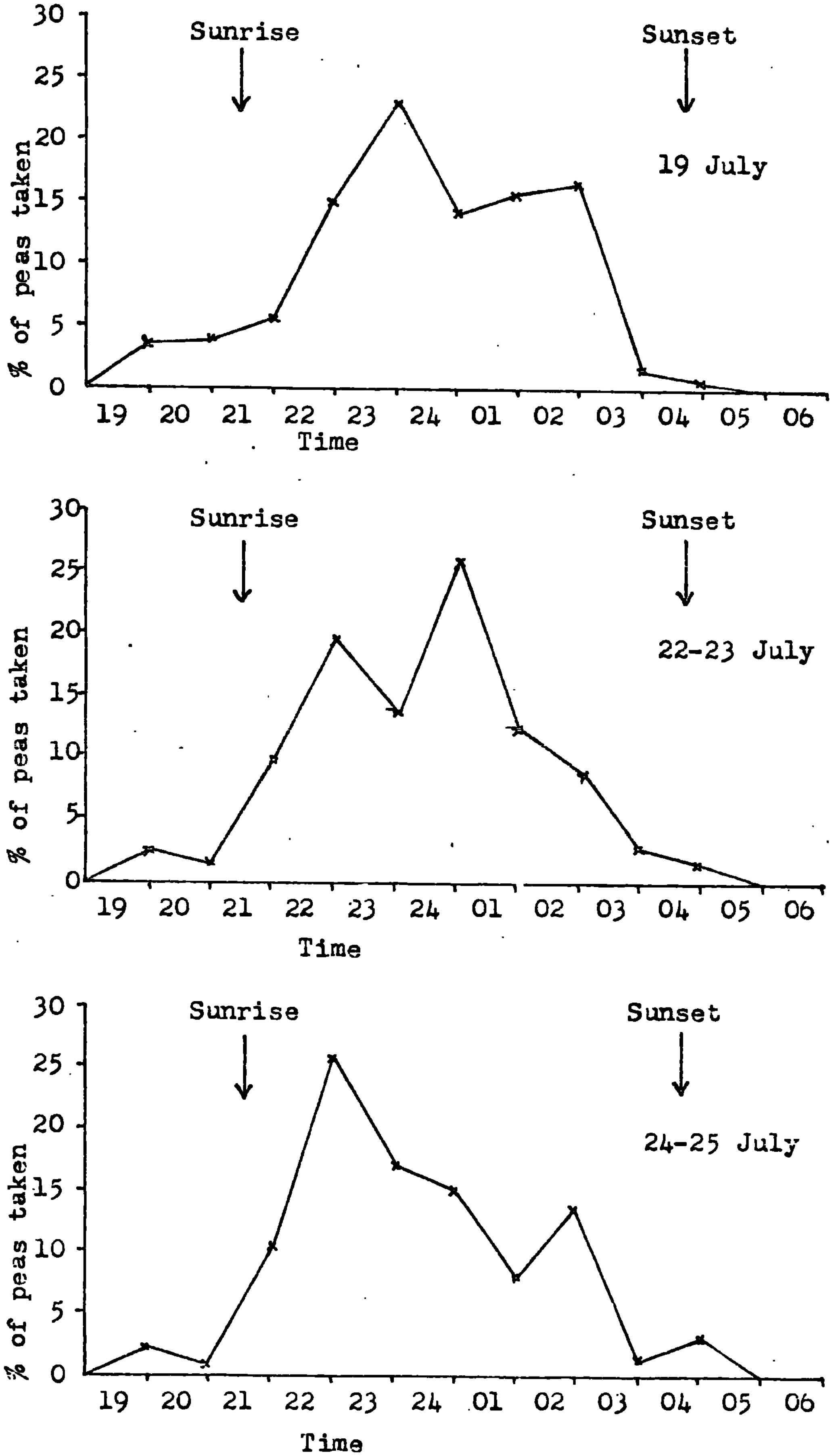


Figure 16.


30
25
20
15
10
5
0
% of peas taken
Sunrise
Sunset
19 July
19
20
21
22
23
24
01
02
03
04
05
06
Time
Sunrise
Sunset
22-23 July
Time
Sunrise
Sunset
24-25 July
Time

Of the 15 correlations for Clethrionomys, 14 are highly significant (rs 0.65-0.89, p<0.001), Day 3 is correlated with Day 5, (rs 0.54, p<0.01). Ten correlations for Apodemus are significant to levels varying from p<0.02 to p<0.001, (rs 0.72-0.92). Day 3 accounts for the five correlations which are not significant (p>0.1 to p<0.05, rs 0.52-0.69).

During the periods of observation it eventually became possible to distinguish various individuals that were visiting the site, by colour or size, although to conclusively distinguish them was difficult since only one was marked and readily identifiable. During July, at least seven Clethrionomys (three adults and four juveniles) were regularly visiting the site. From the mean summated data shown in Figure 12, it would appear that these individuals were exhibiting four main peaks periods of activity at four hourly intervals during the day.

The first peak occurred about two hours after dawn at 07.00 hours, the second at 11.00 hours, the third in mid afternoon, 15.00-16.00 hours, and finally one at dusk, 19.00-20.00 hours. This fluctuating pattern of activity is similar to the observed pulses of activity of the marked individual (see Figure 11), in that the timing of activity in the single animal occurred during the four peak periods shown by the population as a whole.

The peaks at dawn and dusk during the unobserved six day study were less marked than those recorded from observation, and the distribution of total activity was more evenly spread throughout the daylight hours (see Figures 8 and 12). Overall 92% of peas taken were removed between dawn and dusk, and 8% between dusk and dawn.

The pattern of activity of Apodemus, with inconsistent peaks and troughs from day to day, was very variable. However, the overall picture that emerged (see Figure 12) was one of a rapid increase in activity peaking between 23.00 and 24.00 hours, about two hours after dusk. Then followed a slow decline with possibly a subsidiary peak between 03.00 and 04.00 hours, but the general trend was one of a unimodal distribution of activity. Immediately preceding sunrise the decline in visits to the feeding station was rapid, although some animals were still active after dawn. Over the six days 6% of the peas taken by Apodemus were removed between dawn and dusk, and 94% between dusk and dawn.

DISCUSSION

The problem of interpreting laboratory results in terms of their ecological implications is nowhere more prominent than when studying activity patterns of small mammals. Kavanau (1966), using sophisticated 22-channel recorders, has provided much useful information on the various physical factors to which activity rhythms are geared, but these environmental factors may bear little relation to those ecological components most significant to the animal (Cloudsley-Thompson 1960), particularly when selection pressure favours those organisms capable of adapting their functions to the periodicity and influences of their surroundings.

It is evident that considerable knowledge has accumulated about periodicity in individual species (Cloudsley-Thompson 1961, Harker 1964, Brown 1965) but that the study of the community aspect has seriously lagged behind. As Ashby (1972) pointed out, there is still a great need for actual field observations of mammal activity particularly of those small mammals normally considered to be secretive and previously thought of as being unsuitable for observational techniques.

It will suffice to point out a few of the problems with which laboratory studies are beset, and the anomalies which uninvestigated extrapolation to the field could produce. Kavanau (1962) studied the drinking behaviour of confined small mammals. He found that <u>Peromyscus maniculatus</u> spent on average only $1\frac{1}{2}$ hours/day out of the nest in apparatus supplied only with food and water, but on adding an activity wheel it stayed out for up to 10 hours/day. One of the problems then in laboratory experiments is actually simulating the variety of conditions found in nature. Furthermore the periodicity of an activity pattern may bear little resemblance to that recorded in the field. Kavanau (1969) found that the least weasel was 98% nocturnal in light conditions simulating those in the wild, but pointed out that this animal showed little diel preference in the field. Graham (personal communication in Kavanau 1969) found that the meadow vole, Microtus pennsylvanicus was active mostly at night in the laboratory but mostly by day in the wild. Notwithstanding that mammals can adopt habits far removed from conditions to which their visual systems would seem best suited, the results presented in this study stress the importance of investigating activity rhythms in the field before making generalisations from those recorded under abnormal and uniform laboratory conditions.

The use of bait as an index of activity and a comparison with other methods.

Hamilton (1937), who placed food at points in the runways of the field mouse, Microtus pennsylvanicus, was probably the first to use bait in a study of activity and home range. However he made limited use of the technique; his hourly measurements were not recorded for periods of longer than 24 hours at a time, and over few days in total. Chitty and Shorten (1946) baited

Norway Rats, but were more concerned with ways of attracting and controlling the rats than with any periodicity that emerged from the removal of bait. Kikkawa (1964) made observations of Clethrionomys glareolus and Apodemus sylvaticus at baited traps but in this paper he merely said that daytime visits of voles were long and frequent, while at night they were brief and comparitively infrequent, and that mice appeared only at night. Investigation of activity using feeding stations and observation of small mammals has thus been a technique infrequently used.

The use of feeding stations does have limitations in a study of activity, even during periods when the site is being watched. It assumes that feeding and storing behaviour is an accurate index of activity. However Crowcroft (1954) and Kavanau (1969) considered that measures of feeding activity are reliable indices of total activity in the laboratory, and Blair (1951), who tracked individuals of Peromyscus polionotus in the field, found that movements were principally associated with feeding and food gathering. These results are supported by a very close correlation in this study between the number of animals observed above ground and the total number of peas taken during each hour. It suggests that the removal of bait is a reliable index of the total above ground activity of both Apodemus and Clethrionomys.

Where more than one individual is making repeated trips to a baited site, the index of activity over the diel cycle must be accepted as being an average one for that particular species. Never less than four individuals of both Apodemus and Clethrionomys were recorded during any period of observation, so that the activity pattern resulting is one of a section of the population. Any periodicity that emerges must be interpreted with care as the nature of any rhythm and its lability may not be consistent between individuals. This method does however provide an insight into the diel periodicity of the community at the point of observation, as is the case with automatic photographic recordings (Dodge and Snyder 1960), and it allows broad conclusions to be drawn about those periods of the day when activity is either intensive or subdued and provides information about times of day when animals are inactive for long periods. One of the more important features of observation at baited sites is that it has been shown feasible to observe marked individuals. This is one aspect of the study which could be greatly extended.

Like the use of baited live traps, baited feeding stations might have the effect of stimulating activity in small mammals. Pearson (1960a), using a combination of photographic apparatus and traps in a study of harvest mice, *Reithrodontomys megalotis*, and meadow mice, *Microtus californicus*, showed that on nights when trapping was carried out, there was a great increase in the amount of recorded activity; it did, in fact more than double in the case of the harvest mice. If bait does influence the amount of activity it should not however distort the diel periodicity. Unlike trapping though, open baited sites do not restrain the animals and present fewer problems of dealing with the apparent heterogeneity in reaction to traps (Crowcroft and Jeffers I96I). Even of those individuals actually visiting traps, on many occasions the animals are not caught. Sheppe (I967) showed that in 84% of the occasions when a Peromyscus leucopus left tracks at a station it left without being trapped. At best trapping gives an average indication of the number of individuals above ground, not an index of activity, since there is no measure of actual intensity of activity that can be recorded from an animal which is periodically immobilised.

Of the studies of activity which have been done using traps, both Elton et al. (I93I) and Brown (I956) used trapping intervals of two hours. This study indicates that two hours is too long to discern accurately any short term changes in the level of activity, which anyway it would be difficult for trapping data to show. Kikkawa (I964) used only four trapping periods during the day, (I) Afternoon to 20.00 hours; (2) 20.00-23.00 hours; (3) 23.00-02.00 hours; (4) 02.00 to morning. Not only were the intervals irregularly spaced but two periods, (I) and (4), were exceptionally long and inexact. Even more surprising is that Stoddart (I969) claimed that the water vole (Arvicola terrestris) shows a daytime maximum of activity from only two visits to traps/day, at 09.00 hours and the other at 17.00 hours. He compared the number of animals caught during the day with the halved total of night captures, since the overnight period was 16 hours long and twice the length of the daytime period. This is a comparison and analysis of highly dubious validity.

Of the more sophisticated modern techniques of studying activity in the field, automatic photography has the advantage over observation at feeding stations only in that it releases the observer from round the clock watching. The use of telemetry (Le Munyan *et al.* 1959, Cochran and Lord 1963) and radioactive isotopes (Bailey *et al.* 1974) are becoming important tools in tracking animals but are expensive to operate and often limited by the number of individuals that can be traced at any one time. They do however involve minimal manipulation of the animal's habitat. On the other hand actual observation and the use of feeding stations does allow the behaviour of small mammals to be recorded, and gives a satisfactory diel index of the intensity of activity of a species, and has the added advantage of being an inexpensive technique.

The activity of *Clethrionomys* and *Apodemus*.

The results of this study indicate that *Clethrionomys* is diurnal during the summer when *Apodemus* is present. This disagrees with Grodziński (1963), and the data referred to by him, (Miller 1955, Ostermann 1956, Saint-Girons 1960, 1961, and Pearson 1962), who suggested that *Clethrionomys* was mainly nocturnal in the summer. All these publications concerned the results of laboratory investigations using individual animals in isolation, there being no intraspecific or interspecific studies.

The results of two field studies have suggested that Clethrionomys is mainly diurnal in the summer. Kikkawa (1964) noted that visits to baited sites were infrequent between dusk and dawn. Brown (1956) found that Clethrionomys was not trapped overnight when Apodemus was active. She reported competition for traps between the two species. Using a two hour trapping interval it could not be discounted that Clethrionomys might still be active. These works have largely been ignored in subsequent research on the activity of Clethrionomys and ecological generalisations have invariably been drawn from the more numerous laboratory studies, perhaps because the field investigations have been of a limited and inexact nature.

Important papers relevant to this study have been published on the interspecific behaviour of mice and voles, in the wild by Andrzejewski and Olszewski (1963) and in outdoor enclosures by Bergstedt (1965). The former showed that Apodemus flavicollis was dominant over Clethrionomys glareolus in free-living populations. This was confirmed by Bergstedt, who in addition found that the activity of Clethrionomys outside its nest tended to decrease in the presence of A. flavicollis. Furthermore there was a tendency for the nocturnal rhythm of the vole to give way to a diurnal one.

Evidence is given in this study showing that Clethrionomys glareolus is intolerant of the presence of Apodemus sylvaticus, and suggesting that the timing of activity of the latter is the major determinant of the onset and decline in activity of Clethrionomys over the diel period. It is further believed that the disparity between activity rhythms of Clethrionomys revealed in laboratory studies and those that exist in the field, is a product of the interspecific relationships within the community, and not solely the result of responses to physical factors or the manifestation of an endogenous rhythm.

If the timing of the beginning and cessation of activity in Clethrionomys is a direct response to the strict nocturnalism of Apodemus then the peaks of activity of Clethrionomys observed at dawn and dusk may be determined by interspecific hostility and not entrained by physical factors. This could be tested by a study of activity in the field with no Apodemus present. The association between marked changes in light intensity, so often assumed to be important factors in the diel activity of mammals, and peaks in activity may be purely coincidental since recent laboratory studies have shown little association between the activity rhythm and dawn and dusk in Clethrionomys, (Sewell 1973). If, during the night, the bank vole is remaining underground then for a peak of above ground activity to occur at dawn, as that of Apodemus is reduced, is not unexpected, nor is the occurrence of one at dusk, prior to the emergence of Apodemus.

This study does not undermine the importance of those experiments which have been done under laboratory conditions, but stresses the importance of relating any results to factors operating at the community level, and the interspecific aspects of exogenous behavioural interactions of ecological significance. It may well be that the activity rhythms exhibited by *Clethrionomys* in some experiments (e.g. Pearson I962) are those operative in the field, and that in the absence of *Apodemus sylvaticus* or related species, the basic biological rhythm is influenced and phased by other environmental factors, photoperiodism perhaps being the important Zeitgeber.

Competition between Apodemus and Clethrionomys.

Miller (I955), from a comparison of the activity rhythms of *Clethrionomys* and *Apodemus* in the laboratory, found that for a regime of I6 hours light, 8 hours dark, the activity of isolated individuals of both species occurred over much of the same time in the daily cycle. Furthermore, from a study of their diets (Miller I954), he concluded that activity brought the species together in the habitat where they competed directly in time for space and food. Watts (I968) considered that Miller had overestimated the overlap in diet between the two species, and that competition could be avoided by *Clethrionomys* eating leaves and seeds with a soft testa, with *Apodemus* consuming largely insects in early summer and seeds with a hard testa during the remaining seasons. In addition, the small degree of overlap in their above ground activity cycles shown in this study indicates that they are also separated in time, thereby reducing still further any direct competition. Whether this separation is a response to competition for resources, mediated via an avoidance of mutual interference at the social level, has not been shown.

The effect of predation on the periodicity of small mammals is also operating at the community level. The evolution of Apodemus and other nocturnal species, well adapted to a nocturnal way of life, could be viewed as an adaptation partly brought about by the selection pressure of predation. It may be that predators can bring about changes in the activity pattern of a small mammal population, although the prey periodicity is more likely to determine the activity of the predator. Competition between animals occupying similar roles within the community has probably more influence in determining periodicity, because of their more immediate association in space, and it may well be that population increases enhance any interspecific differences that occur in activity rhythms. In the absence of potential competitors, or where population levels are low and interspecific encounters infrequent, the activity rhythm of an animal may return to that which it is best suited, in terms of its evolutionary adaptations, either physiological or environmental. This may be of particular importance to those species (e.g. Clethrionomys) whose herbivorous diet make regular feeding throughout the day obligatory.

Activity rhythms and the environment.

It is now necessary to examine the extent to which the physical environment modifies the degree of activity, within the confines of the overall activity pattern, and to point out that interspecific intolerance is in no way responsible for much of the variability which was recorded. It must also be borne in mind that the standard approach in ecological field investigation of making concurrent measurements of biological events and attempting to correlate these with environmental factors may not necessarily indicate that the exogenous stimuli are those to which activity rhythms are geared, but rather that an internal rhythmicity may represent the substrate on which environmental stimuli act (Enright 1970). However much of the variability in the overall level of activity can be attributed to changing physical conditions.

Calhoun (1945) showed that the lability in the activity rhythms of Sigmodon hispidus and Microtus ochrogaster was in part due to various environmental changes, including light intensity, intraspecific social relations and food. Gentry and Odum (1957) recorded larger catches of Peromyscus polionotus on warm cloudy nights than on clear cold nights. Pearson (1960b) considered that the dawn peak of activity in Microtus californicus in California was not controlled by light, temperature or evaporation but probably by the availability of dew early in the morning, while Grodzinski (1963) referred to the nature of the diet as being an important influence on activity patterns. It is therefore apparent that numerous interacting environmental factors are affecting activity.

There was some indication in this study, though the individual correlations were not significant, that the above ground activity of Clethrionomys and Apodemus was reduced on cloudless, dry days and nights and increased when it was cloudy and wet. It is possible, too, that the use of a highly concentrated food was influencing the amount of activity. Grodzinski (1963) found with Apodemus agrarius that a bulky diet caused an increase in activity and produced a series of three peaks during a nine or ten hour night, in contrast to a single peak resulting from a high protein diet. In this study, the summated data from both observation and unobserved removal of bait showed a unimodal distribution of activity in Apodemus. This is considered to be a more accurate reflection of the overall pattern than the series of peaks and troughs recorded on individual days. The fact that Apodemus tends to wander to a greater extent than Clethrionomys may have produced an anomalous amount of daily variation at a fixed feeding station. This wandering, coupled with the normal diet of Apodemus, which in the summer contains a large proportion of insects, could have resulted in the absence of several individuals from the baited site for concurrent periods.

Although a great deal of information has accumulated on the 24 hour rhythms of small mammals and speculation continues on exogenous and endogenous biological rhythms (Aschoff 1966), much of the variation recorded goes unexplained. For instance Stebbins (1968), in an outdoor enclosure study of Clethrionomys gapperi, found that this species was predominantly nocturnal at Heart Lake (62°N), whereas individuals transferred to Edmonton, Alberta (53°N) exhibited an essentially diurnal rhythm. Marked seasonal changes also occur; Erkinaro (1961) recorded a reversal of diel activity patterns from winter to summer in Microtus agrestis. Lability is then a key component of many activity patterns, but the factors to which the animals are responding need much more investigation, and the effect which specific biotic and abiotic factors are having on activity needs further elucidation particularly, as this study points out, within the community.

Short term activity rhythms.

Notwithstanding that mammals may not necessarily show a 24 hour periodicity entrained to environmental factors, particularly light intensity, many of them do, it is reported, exhibit a short term activity rhythm. Davis (1933) showed that Microtus has a two to four hour rhythm of feeding activity, which agrees with the seven to nine feeding periods in 24 hours recorded for M. californicus (Calhoun 1945). Other short term feeding rhythms have been identified in laboratory experiments in Sorex araneus and S. minutus (Crowcroft 1954), Clethrionomys glareolus (Miller 1955), Mus musculus and Rattus sp. (Southern 1954). However Marten (1973), who studied Peromyscus and observed periodic short pulses of activity, considered that short term rhythms had only infrequently been demonstrated in the field.

One of the problems of identifying short term rhythms from observation and bait removal is that the individuals in the population may not be showing synchronous activity rhythms. Saint-Girons (1960, 1961), on the basis of laboratory studies, has claimed that male and female *Clethrionomys* may have asynchronous activity rhythms. She found that under a light regime of 16 hours light, 8 hours dark, 40.5% of total female activity but only 26% of male activity was during the day. However, evidence from other species would suggest that in the field the activity of the two sexes is more uniform. Orr (1959) found no difference in activity patterns of individual *Peromyscus leucopus*, and Pearson (1960b) showed that voles (*Microtus californicus*) of both sexes and all ages showed the same activity patterns. In this study there was a close correlation between the activity rhythms of adults and juveniles in both *Clethrionomys* and *Apodemus*, and very close correlations between the periodicity of activity and all pairings of days from the hourly records taken in July.

As *Clethrionomys* was exhibiting a 24 hour periodicity in activity, it is likely that the onset of activity of the population after dawn is well synchronised. The periodicity that was exhibited in the increase in the intensity of activity at intervals throughout the six day trial in July may be manifestations of a short term feeding rhythm. This was confirmed by the activity of the marked female *Clethrionomys* which, in visiting the site, did so in short bursts. These bursts of activity coincided closely in time with the main peaks of activity recorded for the population as a whole.

Comparison with other recent work (Sewell I973) indicates that the short term rhythm exhibited in the field is manifested to a greater extent under laboratory conditions. Sewell found that under an abnormally uniform and limited laboratory environment there was a marked four hour short term periodicity throughout the day and night. The amplitude of the peaks and troughs was reduced when repetitive disturbance was introduced as an attempt to simulate some degree of environmental variability, but a daily short term rhythm was still apparent despite the levelling out of activity, although as a synchronous phenomenom of successive days it virtually disappeared. When the additional factors operating in the field are taken into account, plus the fact that the activity recorded was that exhibited by the population as a whole, it is not surprising that the short term rhythm recorded is not as regular as that usually shown under uniform conditions. However it is worth noting that Clethrionomys was exhibiting a short term rhythm in the field comparable to Sewell's disturbed laboratory environment.

The ecological implications of pea removal.

Results of this study on the quantity of peas removed by mice and voles are similar to those recorded by Ashby (I967), in his study of population trends in Houghall Wood, and the effect of rodents on natural forest regeneration. For instance, both his study, and that reported here, showed evidence of social facilitation. It was apparent that the presence of other

Clethrionomys in the neighbourhood was sufficient to increase not only the number of peas removed, but also the rate at which individuals were removing them. Perhaps proximity to areas where nests were situated was an important factor in this stimulation of activity.

It is clear from a consideration of the energy budgets of both Clethrionomys and Apodemus, and the fact that both species continued to take peas at a high rate throughout the study, that the majority of peas were probably subsequently eaten. Furthermore in a field experiment on the removal by Clethrionomys and Apodemus of peas made radioactive with colloidal gold, Cleminson (unpublished) found that the majority of those removed and taken into store had been eaten within 48 hours of removal. In this investigation satiation was not a major problem, though the influx of juveniles into the population aided in keeping pea removal at a high rate during the course of the experiments.

Cleminson found a close correlation between the rate of removal of wheat used as bait and the trapped revealed population density in both Clethrionomys and Apodemus. One of the possible problems with this type of study is that the preference for artificial seed may not be constant throughout the year. It is clear that the population of Clethrionomys within the area of investigation, could have survived exclusively on the quantity of peas removed. Apodemus, on the other hand, would have needed to supplement its diet with food other than that removed from the feeding stations. This may be a reflection of an abundant natural food supply under favourable summer conditions, but the possibility cannot be discounted that *Apodemus* was consuming peas that had been removed and stored by *Clethrionomys*. The removal rates/individuals of both species would not necessarily be similar throughout the year, and would be expected to increase in the winter. Ashby (1967) found that the rate of removal of bait approximately doubled in winter in both species. Furthermore, the number of peas removed in this study varied from day to day in both species and was probably related to the environmental conditions prevailing. Both dietary and changing physical factors would have to be taken into account before an accurate index of population fluctuations could be determined from the removal of bait.

It is probable that rodents are important agents in determining the amount of natural forest regeneration (Ashby 1967) although this was disputed by Tanton (1965). This study, although concerned entirely with an artificial seed supply, would tend to confirm the likelihood, from the quantity of peas removed, that the consumption of natural seed, and consequently forest regeneration, is in a large part effected by the feeding activity of small rodents. As natural seed is in seasonal and limited supply, the number which germinated could be seriously affected by *Clethrionomys* and *Apodemus*.

ACKNOWLEDGEMENTS.

I am grateful to Dr K.R. Ashby, who supervised this work, for helpful criticism and encouragement. I would also like to thank Mr R. Terry and Ms S. Wayne for assistance in the field, Mr D. Knight for many useful discussions, and Dr V. and M. Standen for their hospitality during the writing up of this dissertation.

SUMMARY

Studies of activity patterns in small mammals have mostly been carried out under uniform laboratory conditions because of the difficulties of investigation in the field. In this study a description is given of field experiments to determine the activity of *Clethrionomys glareolus* and *Apodemus sylvaticus* in mixed woodland.

It is concluded that both the removal of a standard bait and observation at a fixed feeding station give satisfactory indices of above ground activity in both species, and that these means of assessment are preferable to many other field techniques, particularly trapping.

Both species took dried peas at a high rate throughout the summer, *Clethrionomys* apparently in excess of the daily feeding requirements of the individuals involved in their removal, *Apodemus* slightly below their feeding requirements.

Apodemus and *Clethrionomys* showed a 24 hour rhythm of activity, the former emerging after dusk and remaining active until dawn, while the latter was predominantly diurnal, activity starting after dawn and continuing until dusk.

Apodemus had overall a unimodal distribution of activity, although daily fluctuations distorted this pattern. *Clethrionomys* had a series of peaks of activity throughout the day and the population appeared to be exhibiting a synchronised short term rhythm of moderate amplitude of approximately four hours in

length. Observations of a single marked vole indicated that activity occurred in short bursts.

Attention is drawn to the differences between results recorded in laboratory experiments and those shown in the field. An attempt is made to explain the discrepancy between these results. The importance of interspecific relationships as being determinants of the onset and decline of activity in Clethrionomys is stressed. It is emphasised that caution must be taken in extrapolating activity rhythms recorded under artificial conditions to the field, and in correlating patterns of activity to physical factors when the interspecific aspects of the community have not been investigated.

BIBLIOGRAPHY

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

Aschoff, J. (1966) Circadian activity pattern with 2 peaks. Ecology 47: 657-662.

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

Ashby, K.R. (1972) Patterns of daily activity in mammals. Mammal 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. J. Zool., Lond. 158: 209-214.

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

Barrett-Hamilton, G.E.H. and Hinton, M.A.C. (1910-1921) A History of British Mammals. London, Guerney and Jackson.

Bergstedt, B. (1965) Distribution, reproduction, growth and dynamics of the rodent species Clethrionomys glareolus (Schreber), Apodemus flavicollis (Melchior) and Apodemus sylvaticus (Linné) 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. 43: 1-47.

Brown, F.A. Jr. (1965) A united theory for biological rhythm. 231-261. In: Aschoff, J. (Ed.). Circadian Clocks. Amsterdam, North-Holland Publishing Co..

Brown, L.E. (1956) Field experiments on the 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 rhythms 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. J. Mammal. 27: 63-78.

Cloudsley-Thompson, J.L. (1960) Adaptive functions of circadian rhythms. Cold Spring Harbor Symp. Quant. Biol. 25: 345-355.

Cloudsley-Thompson, J.L. (1961) Rhythmic Activity in Animal Physiology and Behaviour. New York and London: Academic Press.

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

Crawley, M.C. (1965) Studies on the movements, population dynamics and food of Apodemus sylvaticus and Clethrionomys glareolus. Ph.D. Thesis, Fac. Sci., Univ. Durham.

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

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: 573-582.

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

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

Drożdż, A. (1966) Food habits and food supply of rodents in the beech forest. Acta. theriol. 15: 363-384.

Drożdż, A. (1967) Food preference, food digestibility and natural food supply for small rodents. 323-330. In: Petrusewicz, K. (Ed.). Secondary productivity of terrestrial ecosystems. Polish Scientific Publishers. Warszawa-Krakow.

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.

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

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

Evans, F.C. (1942) Studies of a small mammal population in Bagley Wood, Berkshire. J. Anim. Ecol. 11: 182-197.

Falls, J.B. (1968) Activity. 543-570 (Chapter 14). In: King, J.A. (Ed.). Biology of Peromyscus (Rodentia). Special publication No. 2, The American Society of Mammalogists.

Finley, R.B. (1959) Observations of nocturnal animals by red light. J. Mammal. 40: 591-594.

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

Fullager, P.J., Jewell, A.A., Lockley, R.M. and Rowlands, T.W. (1960) The Skomer vole (*Clethrionomys glareolus skomerensis*) and Long-tailed Field mouse (*Apodemus sylvaticus*) on Skomer Island Pembrokeshire in 1960. Proc. zool. Soc. Lond. 140: 295-314.

Gentry, J.B. and Odum, E.P. (1957) The effects 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 europaea* L.). *Ecology* *36*: 678-685.

Gorecki, A. (1968) Metabolic rate and energy budget in the bank vole. *Acta theriol.* *23*: 341-365.

Grodziński, W. (1962) Influence of food upon the diurnal activity of small rodents. *Symp. Theriol.* 134-140. Publ. house Gech. Ac. Sci. Praha.

Grodziński, W. (1963) Seasonal changes in the circadian activity of small rodents. *Ekol. Pol. B* *9*: 3-17.

Grodziński, W. and Górecki, A. (1967) Daily energy budgets of small rodents. 295-314. In: Petrusewicz, K. (Ed.). *Secondary productivity of terrestrial ecosystems*. Polish Scientific Publishers. Warszawa-Krakow.

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

Harker, J.E. (1964) *The Physiology of Diurnal Rhythms*. Cambridge, Cambridge University Press.

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

Kaczmarski, F. (1966) Bioenergetics of pregnancy and lactation in the bank vole. *Acta theriol.* *11*: 409-417.

Kavanau, J.L. (1962) Precise monitoring of drinking behaviour in small mammals. *J. Mammal.* *43*: 345-351.

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.

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

Le Munyan, C.D., White, W., Nyberg, E. and Christian, J.J. (1959) Design of a miniature radio transmitter for use in animal studies. J. Wildl. Mgmt. 23: 107-110.

Marten, G.G. (1973) Time patterns of Peromyscus activity and their correlations with weather. J. Mammal. 54: 169-188.

Meese, G.B. and Cheeseman, C.L. (1969) Radioactive tracking of the mole (Talpa europaea) over a 24 hour period. J. Zool., Lond. 158: 197-203.

Migula, P. (1969) Bioenergetics of pregnancy and lactation in European common vole. Acta theriol. 14: 167-179.

Miller, R.S. (1954) Food habits of the wood mouse, Apodemus sylvaticus (Linné, 1758) and the bank vole, Clethrionomys glareolus (Schreber, 1780) in Wytham Woods, Berkshire. Säugetierk. Mitt. 2: 109-114.

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.

Miller, R.S. (1958) A study of a wood mouse population in Whytham Woods, Berkshire. *J. Mammal.* 39: 447-493.

Newson, R. (1963) Differences in numbers, reproduction and survival between two neighbouring populations of bank vole (*Clethrionomys glareolus*). *Ecology* 44: 110-120.

Orr, H.D. (1959) Activity of white-footed mice in relation to their environment. *J. Mammal.* 40: 213-221.

Ostermann, K. (1956) Zur Aktivität heimischer Müriden und Gliriden. *Zool. Jb.* 66: 355-388.

Pearson, O.P. (1960a) Habits of harvest mice revealed by automatic photographic recorders. *J. Mammal.* 41: 58-74.

Pearson, O.P. (1960b) Habits of *Microtus californicus* revealed by automatic photographic methods. *Ecol. Monogr.* 30: 231-249.

Pearson, A.M. (1962) Activity patterns, energy metabolism and growth rate of the voles *Clethrionomys rufocanus* and *C. glareolus* in Finland. *Ann. zool. Soc. 'Vanamo'* 24; 1-58.

Saint-Girons, M.C. (1959) Les characteristiques du rhythme nycthéméral d'activité chez quelques petits mammiferes. *Mammalia* 23: 245-276.

Saint-Girons, M.C. (I960) Le rhythme nychthéméral d'activité du campagnol roux, Clethrionomys glareolus (Schreber) I780. I-Les males. Mammalia 24: 5I6-532.

Saint-Girons, M.C. (I96I) Le rhythme nychthéméral d'activité du campagnol roux, Clethrionomys glareolus (Schreber) I780. 2-Les femelles. Mammalia 25: 342-357.

Sewell, P.I.V. (I973) Activity patterns and behaviour of Clethrionomys glareolus. M.Sc. Thesis, Fac. Sci., Univ. Durham.

Sheppe, W. (I967) The effect of live trapping on the movements of Peromyscus. Amer. Midl. Natur. 47I-480.

Southern, H.N. (I954) Control of Rats and Mice 3. House Mice. Oxford, Oxford University Press.

Southern, H.N. (I955) Nocturnal Animals. Sci. Amer. I93(4); 88-98.

(I) Southern, H.N. (I964) The Handbook of British Mammals. Oxford. Blackwell.

(2) Stebbins, L.L. (I968) Seasonal and latitudinal variations in the circadian rhythms of three species of small rodents in Northern Canada. Ph.D. Thesis, University of Alberta, Edmonton.

(I) not referred to in text.

(2) as quoted in Ashby (I972).

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

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

Tanton, M.T. (1969) The estimation and biology of populations of the bank vole (*Clethrionomys glareolus* (Schr.)) and wood mouse (*Apodemus sylvaticus* (L.)). *J. Anim. Ecol.* *38*: 511-529.

Watts, C.H.S. (1968) The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *J. Anim. Ecol.* *37*: 25-41.

Zollhauser, M. (1958) Versuche über Ruhe-und Aktivität speriodem bei verschiedenen Mäusearten. *Z. vergl. Physiol.* *40*: 642-663.

APPENDIX

TABLE I. Number of peas taken from all sites during each two hour period from 04.00-22.00 hours, for ten days commencing 10 June.

	04-06:	06-08:	08-10:	10-12:	12-14:	14-16:	16-18:	18-20:	20-22:	Total
10 June 1974:	118	130	123	130	86	73	93	163	116	1082
11 June :	126	179	137	200	104	65	68	78	77	1034
12 June :	102	143	117	123	88	96	79	153	46	947
13 June :	67	46	116	65	55	42	60	124	60	635
14 June :	47	63	84	56	57	72	57	87	34	557
15 June :	68	83	81	62	50	46	51	89	44	574
16 June :	107	93	64	64	59	59	60	66	63	635
17 June :	94	129	35	93	86	132	119	138	92	918
18 June :	89	81	113	61	70	93	120	87	57	771
19 June :	83	95	93	60	59	93	78	117	59	737
Total :	901	1092	963	914	714	771	785	1102	648	7890

TABLE 2. Number of peas taken from site 1 during each two hour period from 04.00-22.00 hours.

	04-06:	06-08:	08-10:	10-12:	12-14:	14-16:	16-18:	18-20:	20-22:	Total.
10 June 1974:	5	12	4	6	1	2	3	20	5	58
11 June :	6	13	1	7	6	7	20	4	5	69
12 June :	5	10	3	4	23	15	16	29	7	112
13 June :	8	0	19	5	0	3	1	7	7	50
14 June :	5	9	1	0	4	6	2	4	2	33
15 June :	5	7	5	2	7	0	3	0	1	30
16 June :	0	8	1	5	0	6	5	1	5	31
17 June :	7	10	1	6	3	21	22	8	8	86
18 June :	10	16	5	13	10	10	10	9	6	94
19 June :	6	9	7	12	7	16	12	4	3	76
Total :	57	94	47	65	61	86	94	86	49	639

TABLE 3. Number of peas taken from site 2 during each two hour period from 04.00-22.00 hours.

	04-06:	06-08:	08-10:	10-12:	12-14:	14-16:	16-18:	18-20:	20-22:	Total.
10 June 1974:	29	42	17	31	25	19	20	41	29	253
11 June :	36	47	12	63	30	17	4	18	27	254
12 June :	29	42	21	18	0	17	16	37	13	193
13 June :	5	26	18	6	7	5	9	10	24	110
14 June :	12	21	8	23	12	17	5	14	9	121
15 June :	21	31	25	22	17	18	10	18	16	178
16 June :	43	38	18	16	22	16	9	12	11	185
17 June :	30	33	23	15	40	42	38	27	25	273
18 June :	21	18	31	17	23	25	60	31	24	250
19 June :	25	20	21	12	18	28	21	38	16	199
Total	251	318	194	223	194	204	192	246	194	2016

TABLE 4. Number of peas taken from site 3 during each two hour period from 04.00-22.00 hours.

	04-06:	06-08:	08-10:	10-12:	12-14:	14-16:	16-18:	18-20:	20-22;	Total.
10 June 1974:	48	119	87	92	60	52	70	92	41	661
11 June :	54	110	98	113	65	39	42	51	30	602
12 June :	48	87	78	96	59	50	43	76	16	553
13 June :	13	21	81	53	55	35	43	79	25	405
14 June :	15	34	50	33	37	49	44	60	9	331
15 June :	33	46	53	29	18	25	29	55	17	305
16 June :	51	49	34	33	18	13	44	35	27	304
17 June :	51	80	8	66	34	65	54	90	46	494
18 June :	28	47	60	16	33	49	41	40	19	333
19 June :	42	61	48	33	29	38	43	63	21	378
Total :	383	654	597	564	408	415	453	641	251	4366

TABLE 5. Number of peas taken from site 4 during each two hour period from 04.00-22.00 hours.

		04-06:	06-08:	08-10:	10-12:	12-14:	14-16:	16-18:	18-20:	20-22:	Total.
10 June 1974	:	26	7	15	1	0	0	0	10	21	80
11 June	:	30	9	26	10	3	2	2	5	15	102
12 June	:	20	4	15	5	6	3	5	11	10	79
13 June	:	17	7	10	0	3	5	9	14	25	90
14 June	:	3	2	25	0	4	0	6	9	14	63
15 June	:	8	3	2	9	8	3	9	16	10	68
16 June	:	6	1	11	10	19	24	2	18	20	111
17 June	:	7	2	3	6	9	5	4	13	13	62
18 June	:	24	8	17	10	4	9	9	10	5	96
19 June	:	10	5	17	3	5	11	2	12	19	84
Total	:	151	48	141	54	61	62	48	118	152	835

TABLE 6. Number of peas removed/day from all sites between 22.00-04.00 hours for nine days commencing 10-11 June.

	Site 1:	Site 2:	Site 3:	Site 4:	Total
10-11 June:	69	1	69	74	213
11-12 June:	65	61	59	55	240
12-13 June:	68	5	40	30	143
13-14 June:	33	17	35	40	125
14-15 June:	35	17	21	41	114
15-16 June:	16	30	32	40	118
16-17 June:	22	31	68	78	199
17-18 June:	57	34	107	45	243
18-19 June:	48	27	96	40	211
Total :	413	223	527	443	1606

TABLE 7. The number of sightings of Apodemus during each hour from 20.00-06.00 hours (20 equals 20.00-21.00 hours etc.)

	20	21	22	23	24	01	02	03	04	05	06	Total.
27-29 May :	0	0	2	-	-	-	-	-	-	1	0	3
3-5 June :	0	0	1	3	4	4	2	3	1	0	0	18
21-23 June:	0	1	6	11	3	7	2	4	1	0	0	35
24-26 June:	0	1	6	3	8	2	7	5	2	1	0	35
4-6 July :	3	1	8	15	7	12	6	9	3	3	1	68
7-9 July :	3	3	7	26	12	15	8	11	3	6	1	95
26-27 July:	4	2	10	15	22	12	4	13	5	7	0	94
Total :	10	8	40	73	56	52	29	45	15	18	2	348

TABLE 8. The number of peas taken by Apodemus during each hour of observation from 20.00-06.00 hours.

	20	21	22	23	24	01	02	03	04	05	06	Total.
27-29 May :	0	0	2	-	-	-	-	-	-	0	0	2
3-5 June :	0	0	1	2	4	4	2	3	1	0	0	17
21-23 June:	0	0	5	10	3	6	2	3	1	0	0	30
24-26 June:	0	0	6	2	4	2	5	5	2	1	0	27
4-6 July :	2	1	7	12	6	12	5	7	2	0	0	54
7-9 July :	2	3	7	20	10	14	7	10	3	4	0	80
26-27 July:	3	1	8	12	18	10	3	12	3	4	0	74
Total :	7	5	36	58	45	48	24	40	12	9	0	284

TABLE 9. The number of sightings of adult Apodemus during each hour from 20.00-06.00 hours.

	20	21	22	23	24	01	02	03	04	05	06	Total.
27-29 May :	0	0	2	-	-	-	-	-	-	1	0	3
3-5 June :	0	0	1	3	4	4	2	3	1	0	0	18
21-23 June:	0	0	4	7	2	4	1	3	1	0	0	22
24-26 June:	0	1	3	3	4	1	4	3	1	0	0	20
4-6 July :	0	0	4	7	4	6	4	4	2	1	0	32
7-9 July :	0	1	4	14	6	7	4	6	1	4	0	47
26-27 July:	1	1	4	10	12	6	2	8	2	3	0	49
Total :	1	3	22	44	32	28	17	27	8	9	0	191

TABLE 10. The number of sightings of juvenile Apodemus during each hour from 20.00-06.00 hours.

	20	21	22	23	24	01	02	03	04	05	06	Total.
27-29 May :	0	0	0	-	-	-	-	-	-	0	0	0
3-5 June :	0	0	0	0	0	0	0	0	0	0	0	0
21-23 June:	0	1	2	4	1	3	1	1	0	0	0	13
24-26 June:	0	0	3	0	4	1	3	2	1	1	0	15
4-6 July :	3	1	4	8	3	6	2	5	1	2	1	37
7-9 July :	3	2	3	12	6	8	4	5	2	2	1	48
26-27 July:	3	1	6	5	10	6	2	5	3	4	0	45
Total :	9	5	18	29	24	24	12	18	7	9	2	157

TABLE 11. The number of sightings of *Clethrionomys* during each hour from 00.00-24.00 hours. (00 equals 00.00-01.00 hours, 01 equals 01.00-02.00 hours etc.).

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
27-29 May :	-	-	-	-	3	3	7	4	4	3	4	1	7	2	3	1	3	3	13	7	3	5	2	-	78
3-5 June :	1	0	1	2	0	4	4	9	11	8	4	7	5	7	1	8	7	3	4	7	12	3	1	1	110
21-23 June:	0	3	0	2	6	11	15	9	5	4	6	9	4	1	7	8	4	5	11	6	12	5	5	3	141
24-26 June:	2	0	0	2	1	10	12	10	6	3	6	12	5	3	10	6	4	3	9	12	13	7	8	6	150
4-6 July :	1	0	1	1	8	12	19	8	9	5	5	13	12	6	7	5	14	10	9	7	15	12	5	3	187
7-9 July :	2	0	0	2	8	12	18	11	8	7	4	18	11	7	4	7	10	9	5	6	12	12	6	6	185
Total :	6	3	2	9	26	52	75	51	43	30	29	60	44	26	32	35	42	33	51	45	67	44	27	19	851

TABLE 12. The number of peas taken by *Clethrionomys* during each hour from 00.00-24.00 hours.

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
27-29 May :	-	-	-	-	1	2	5	3	2	3	3	1	4	0	2	1	0	2	10	6	3	4	2	-	54
3-5 June :	1	0	1	2	0	3	4	8	9	6	4	7	3	4	1	5	6	2	3	5	9	3	1	1	88
21-23 June:	0	2	0	1	5	9	12	9	2	3	6	8	3	0	5	6	1	4	7	5	10	4	5	2	109
24-26 June:	2	0	0	2	1	8	9	7	5	2	6	10	4	3	7	5	3	3	6	8	10	3	6	5	115
4-6 July :	1	0	1	1	5	10	15	6	7	3	5	10	10	4	6	5	10	8	7	6	16	12	5	3	156
7-9 July :	2	0	0	1	6	12	17	11	7	5	6	19	11	6	6	8	7	10	4	7	11	9	4	6	175
Total :	6	2	2	7	18	44	62	44	32	22	30	55	35	17	27	30	27	29	37	37	71	41	26	21	697

TABLE 13. The number of sightings of adult *Clethrionomys* during each hour from 00.00-24.00 hours.

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
27-29 May :	-	-	-	-	3	3	7	4	4	3	4	1	7	2	3	1	3	3	13	7	3	5	2	-	78
3-5 June :	1	0	1	2	0	4	4	9	11	8	4	7	5	7	1	8	7	3	4	7	12	3	1	1	110
21-23 June:	0	2	0	1	4	7	10	5	4	2	4	5	3	1	4	5	3	2	8	4	7	3	3	2	89
24-26 June:	2	0	0	1	1	6	8	7	4	2	4	8	3	2	6	4	2	2	5	8	7	4	4	4	94
4-6 July :	0	0	1	0	3	6	11	5	4	3	3	7	6	4	3	3	8	4	5	3	6	5	3	2	95
7-9 July :	0	0	0	1	4	7	13	3	3	4	4	12	5	3	3	5	6	7	2	3	5	4	2	2	98
Total :	3	2	2	5	15	33	53	33	30	22	23	40	29	19	20	26	29	21	37	32	46	28	17	12	564

TABLE 14. The number of sightings of juvenile *Clethrionomys* during each hour from 00.00-24.00 hours.

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
27-29 May :	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0
3-5 June :	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21-23 June:	0	1	0	1	2	4	5	4	1	2	2	4	1	0	3	3	1	3	3	2	5	2	2	1	52
24-26 June:	0	0	0	1	0	4	4	3	2	1	2	4	2	1	4	2	2	1	4	4	6	3	4	2	56
4-6 July :	1	0	0	1	5	6	8	3	5	2	2	6	6	2	4	2	6	6	4	4	9	7	2	1	92
7-9 July :	2	0	0	1	4	5	5	8	5	3	0	6	6	4	1	2	4	2	3	3	7	8	4	4	87
Total :	3	1	0	4	11	19	22	18	13	8	6	20	15	7	12	9	13	12	14	13	27	20	12	8	287

TABLE 15. Number of peas removed from site 3 during each one hour period from 00.00-24.00 hours, 10-25 July. (00 equals 00.00-00.01 hours, 01 equals 00.01-00.02 hours etc.).

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
10-11 July:	29	71	20	49	6	16	48	64	62	48	61	74	56	30	65	89	71	85	72	73	52	17	57	110	1325
13-14 July:	44	34	28	45	26	5	45	52	55	28	36	51	41	28	42	87	73	57	52	61	82	58	51	62	1144
16-17 July:	40	25	27	7	21	26	61	46	52	31	38	42	65	41	22	38	48	68	59	36	24	42	64	28	951
19 July :	56	31	34	42	8	13	23	73	42	36	22	83	52	41	56	76	71	52	48	34	73	60	20	44	1090
22-23 July:	41	70	31	26	18	30	62	57	43	38	51	36	23	46	68	37	63	45	20	70	65	34	42	69	1085
24-25 July:	51	41	22	43	12	52	74	60	45	28	41	52	30	51	73	56	61	58	47	61	51	26	45	92	1172
Total :	261	272	162	212	91	142	313	352	299	209	249	338	267	237	326	383	387	365	298	335	347	237	279	405	6767

TABLE 16. Estimated number of peas removed by *Clethrionomys* from site 3, 10-25 July.

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
10-11 July:	5	3	1	8	4	14	48	64	62	48	61	74	56	30	65	89	71	85	72	73	46	15	23	29	1046
13-14 July:	7	1	1	7	17	4	45	52	55	28	36	51	41	23	42	87	73	57	52	61	73	50	21	16	905
16-17 July:	6	1	1	1	14	22	61	46	52	31	38	42	65	41	22	38	48	68	59	36	21	37	26	7	783
19 July :	8	1	1	7	5	11	23	73	42	36	22	83	52	41	56	76	71	52	48	34	65	52	8	11	878
22-23 July:	6	3	1	4	12	26	62	57	43	38	51	36	23	46	68	37	63	45	20	70	58	30	17	18	834
24-25 July:	7	2	1	7	8	44	74	60	45	28	41	52	30	51	73	56	61	58	47	61	45	23	18	24	916
Total :	36	11	6	34	60	121	313	352	299	209	249	338	267	237	326	383	387	365	298	335	309	206	114	105	5352

TABLE 17. Estimated number of peas removed by *Apodemus* from site 3, 10-25 July.

	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total.
10-11 July:	24	68	19	41	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	34	81	279
13-14 July:	37	33	27	38	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	8	31	46	239
16-17 July:	34	24	26	6	7	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	5	38	21	168
19 July :	48	30	33	35	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	8	12	33	212
22-23 July:	35	67	30	22	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	4	35	51	251
24-25 July:	44	39	21	36	4	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	3	27	68	256
Total :	225	261	156	178	31	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	31	165	300	1405

TABLE 18.

Spearman Rank correlations between all days for the estimated hourly number of peas removed by *Apodemus* from site 3 during six 24 hour periods recorded 10-25 July.

	10-11 July:	13-14 July:	16-17 July:	19 July:	22-23 July:	24-25 July:
10-11 July:		rs 0.92 $p<0.001$	rs 0.53 $p>0.1$	rs 0.74 $p<0.02$	rs 0.87 $p<0.01$	rs 0.91 $p<0.001$
13-14 July:			rs 0.52 $p>0.1$	rs 0.84 $p<0.01$	rs 0.82 $p<0.01$	rs 0.93 $p<0.001$
16-17 July:				rs 0.57 $p>0.05$	rs 0.69 $p<0.05$	rs 0.57 $p>0.05$
19 July :					rs 0.74 $p<0.02$	rs 0.87 $p<0.01$
22-23 July:						rs 0.89 $p<0.001$
24-25 July:						

Degrees of freedom in all correlations, eight.

TABLE 19.

Spearman Rank correlations between all days for the estimated hourly number of peas removed by *Clethrionomys* from site 3 during six, 24 hour periods recorded 10-25 July.

	10-11 July	13-14 July	16-17 July	19 July	22-23 July	24-25 July
10-11 July:		rs 0.86 $p<0.001$	rs 0.74 $p<0.001$	rs 0.81 $p<0.001$	rs 0.68 $p<0.001$	rs 0.82 $p<0.001$
13-14 July:			rs 0.67 $p<0.001$	rs 0.84 $p<0.001$	rs 0.73 $p<0.001$	rs 0.76 $p<0.001$
16-17 July:				rs 0.65 $p<0.001$	rs 0.54 $p<0.01$	rs 0.68 $p<0.001$
19 July:					rs 0.65 $p<0.001$	rs 0.72 $p<0.001$
22-23 July:						rs 0.89 $p<0.001$

Degrees of freedom in all correlations, 22.