STUDIES ON THE ECOLOGY, PHYSIOLOGY AND TAXONOMY OF THE HARVEST MOUSE, *MICROMYS MINUTUS* (PALLAS).

by

R. M. Cross

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Department of Zoology,
The University,
Southampton.

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CONTENTS

I INTRODUCTION

The aim of the work presented in this thesis is to provide information on the ecology, physiology and variation of the harvest mouse, Micromys minutus (Pallas), a member of the Family Muridae which, up to the present, has attracted little detailed research.

The first published description of the harvest mouse was given by P. S. Pallas in 1771 from animals found on the banks of the River Volga in Russia; he named it Mus minutus. The Reverend Gilbert White described the mouse in Britain in a letter dated 1767 but this was not published until 18 years after that of Pallas. The present generic name Micromys was first given by Dehne in 1841, and the name now used is Micromys minutus (Pallas), which includes all Old World harvest mice.

The species has a large range, extending over the central Palaearctic Region from Britain, across western Europe and central Asia, to Japan. Although 14 subspecies are recognised by Ellerman and Morrison-Scott (1951), many of these are of doubtful validity, being based on few individuals and often using only such a variable character as coat colour. The western European harvest mouse, including the one found in Britain, is M. m. soricinus Hermann.

The harvest mouse is a typical murid in structure but possesses a number of specialisations for life in the stalk-zone of tall grasses and reeds. Such a habitat demands small size and

good climbing ability. Weighing only about six grams and possessing a prehensile tail, Micromys is well-adapted for living in this habitat, an unusual one for a mammal. Other small mammals, notably Apodemus sp., are known to climb shrubs and small trees, but are prevented by their size and weight from climbing such slender plants as grasses and reeds. Micromys is one of the smallest rodents in the world, probably being equalled in weight only by Delanymys brooksi Hayman from Uganda.

The breeding biology of Micromys has been described by Kästle (1953), who found that the gestation period is 21 days and that the number of young in each litter varies between five and nine in M. m. soricinus. Frank (1957) has described the breeding behaviour of the other western European subspecies, M. m. subobscurus Fritsche. The building of the breeding nest, which is usually suspended about 18" - 24" from the ground, has been described on several occasions (e.g. Barrett-Hamilton and Hinton 1910-21, Frank 1957). The nest is woven from the growing leaves of the vegetation (usually grasses or reeds) in which it is built, and is sometimes approximately spherical but more often of irregular oval shape, about three inches in diameter. Considerable difficulty has been encountered in breeding the mouse in captivity, though this has been achieved on a few occasions (e.g. Pitt 1945, Frank 1957).

Harvest mice living on agricultural land often move to grain ricks in winter. Unlike house mice, Mus musculus (L.), which may

also occur in ricks, they have not been found to breed during winter. (Rowe 1958). In Poland breeding begins in late April (Kubik 1953) and in the Far East in late March or early April (Sleptzov 1947). Elsewhere the breeding season has not been defined.

Little information is available on the animal's ecology. No detailed studies have been made of its food, but casual information shows that it eats grain, seeds, berries, some green vegetable matter, and insects. Kubik (1953) suggests that the average life of the mouse in the wild is 16 - 18 months,but Sleptzov (1947) considers that, for the eastern subspecies M. m. ussuricus Barrett-Hamilton, it is not much longer than seven to eight months. Apart from these studies, no information exists concerning population dynamics.

The present studies on Micromys were initiated in Studland Heath National Nature Reserve in Dorset with the object of collecting detailed information on population dynamics, home range and other ecological aspects. Further ecological work was carried out on agricultural land in Hampshire. Complementary to these studies, the activity rhythm of the mouse was investigated in the laboratory. In addition, work on the comparative physiology of Micromys and other small mammals was undertaken. It was anticipated that the small size of the harvest mouse would be of particular physiological interest. Consequently, the energy requirements of Micromys were

compared with those of a larger species, Apodemus sylvaticus (L.), and a measure obtained of the effects of small body size in rodents. The habitat of Micromys also poses some interesting physiological problems, particularly when considered with those related to small body size. As a result, some work was also carried out on water balance.

As only one species of Micromys ranges over most of Europe and central Asia and also as many subspecies have been described, it was considered appropriate that a more detailed investigation might be made of the extent of variation between populations in different regions of the range. This was carried out in two ways: firstly, a number of measurements were taken on the skulls of mice from different localities and these were then subjected to a multiple-regression analysis; secondly, a series of non-linear characters were examined on each skull. These characters form a type of discontinuous variation known as epigenetic polymorphism which is developmental in origin and caused by both genetic and environmental factors, (Waddington 1953). These two independent methods were intended to provide measures of the variation between the different populations of Micromys and hence determine the validity of some of the subspecies.

II THE DISTRIBUTION OF MICROMYS IN BRITAIN

The British harvest mouse, together with that found over most of western Europe, belongs to the subspecies, Micromys minutus soricinus Hermann. Its status in Britain, as with most other mammals, has not been fully investigated. However, it has generally been thought that the harvest mouse has greatly decreased in numbers and range over the last fifty years, and it has been suggested that this is due to the introduction first of the mechanical reaper and later of the combine harvester (Matthews 1952). Presumably this suggestion was made because the machines cut the corn close to the ground and leave the mice little time to escape, but there is no definite information on this point.

A. Methods

The distribution of British mammals was recorded in the early years of this century by a number of authors, e.g. Millais (1904-06) and Barrett-Hamilton and Hinton (1910-21). The Victoria County Histories, also published near the turn of the century, give information concerning the occurrence of mammals in the counties of England. In order to investigate the status of the harvest mouse in Britain at the beginning of this century, these sources were consulted. It must be pointed out, however, that some of the records go right back to the time that the Reverend Gilbert White first described the mouse in this country in 1767 (published 1789) and

there is thus a possible span of 100-140 years between them. Nevertheless, most records in this survey date from the latter half of the 19th century.

The present distribution of the mouse was determined as follows. An arbitrary date of 1950 was fixed as the earliest for which records were to be included in the report, and letters were then sent to 72 Natural History Societies (all whose address could be found) enquiring whether or not harvest mice were present in that area. In addition, a substantial amount of information was gathered from a number of individual mammalogists and from museums. The mouse was recorded as present in an area if specimens were caught or found dead, and if their remains were recovered from owl pellets or milk-bottles (for details of this latter method, see Morris and Harper 1965). The occurrence of old breeding nests was also taken as evidence that the mouse was present, because these are distinctive and not easy to confuse with anything else. Sight records were not generally included unless they were made by an experienced observer, for it is possible to confuse harvest mice with young brightly-coloured field mice.

B. Results

The results of the surveys are shown in Figs. 1 - 3. Fig. 1 shows the counties from which the harvest mouse was recorded during

Fig. 1: The distribution of Micromys in Britain based on 19th. century records.

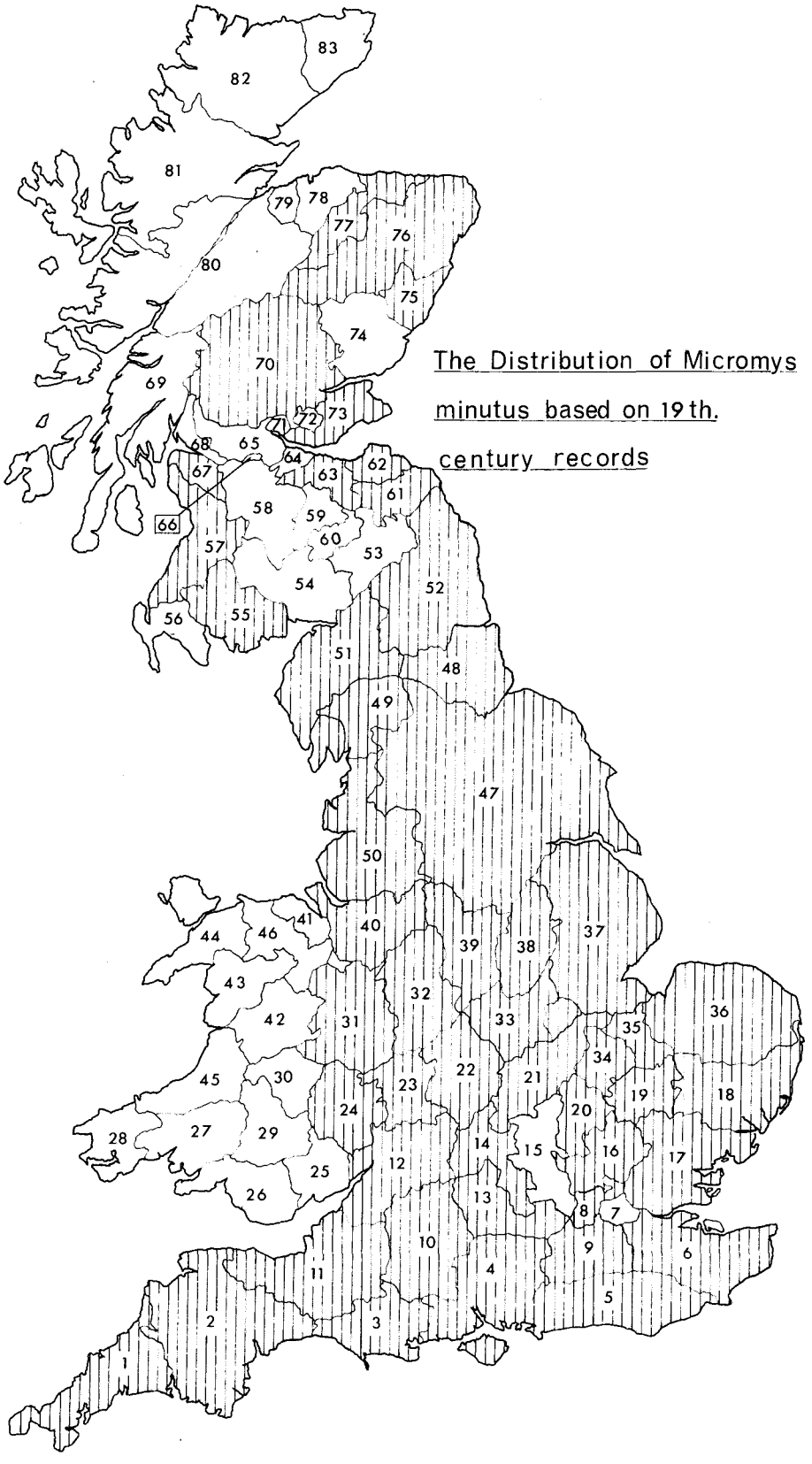
The Distribution of Micromys minutus based on 19th. century records

Fig. 2: The distribution of Micromys based on records since 1950.

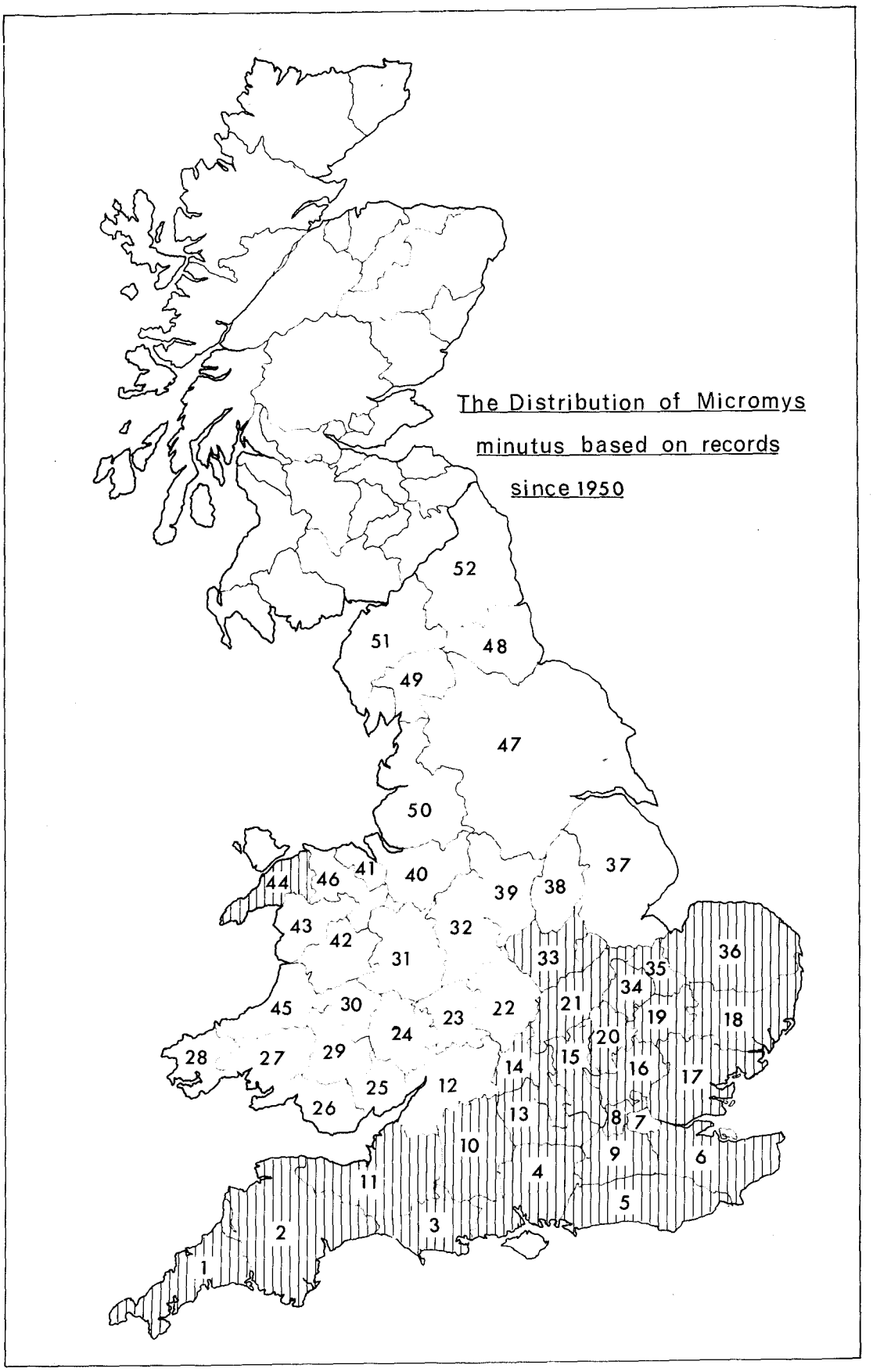
The Distribution of Micromys minutus based on records since 1950
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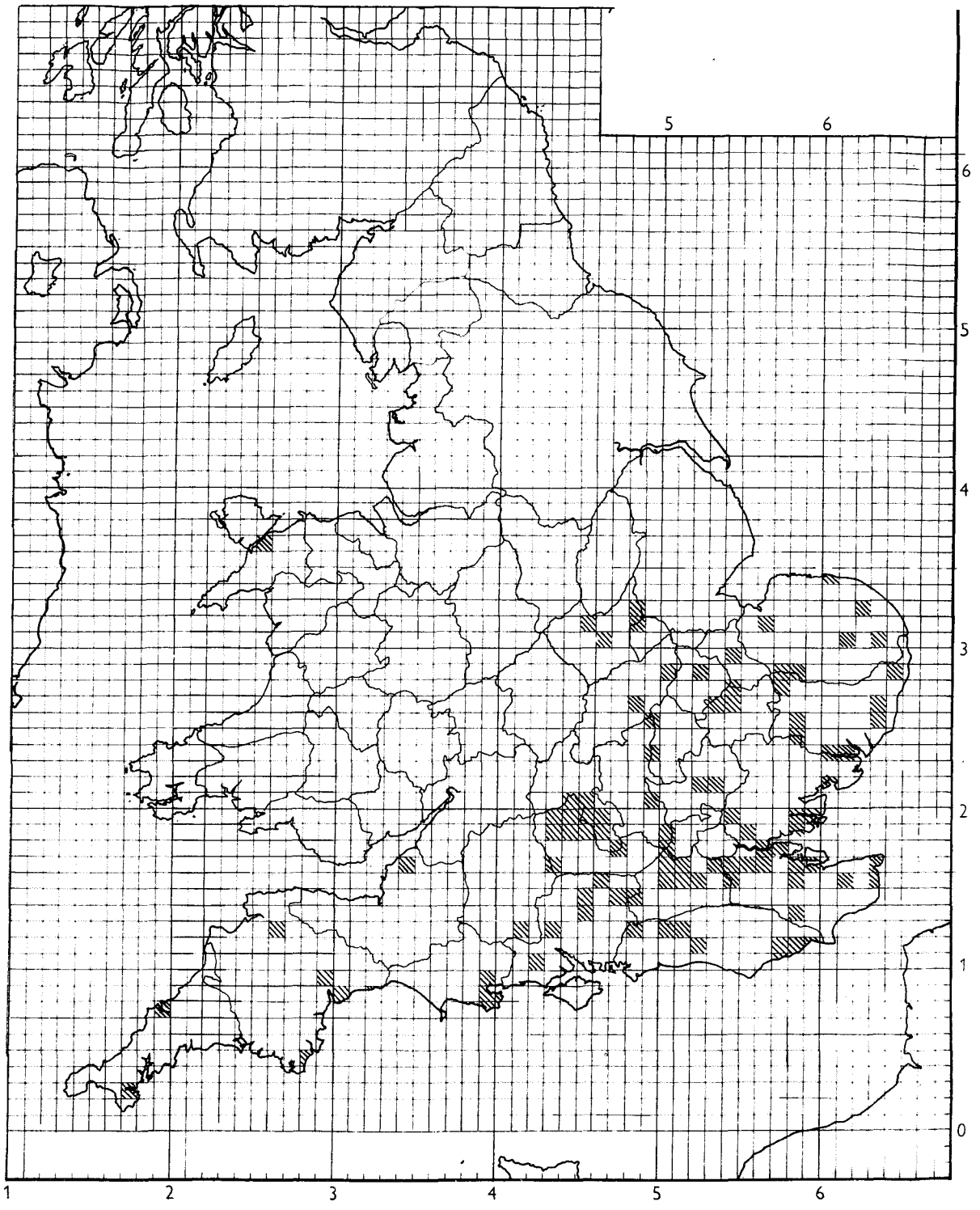
Fig. 3: Distribution of Micromys, based on records since 1950, plotted on 10km. grid squares.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the 19th century according to the sources mentioned above. It will be seen that it was thought not to be present in Wales, but occurred in some Scottish counties and all the English ones except Buckinghamshire and London. There were, however, a few unconfirmed reports from Wales, notably from Caernarvonshire and Brecon.

Fig. 2 shows the distribution by counties based on the records since 1950. Apart from Caernarvonshire, all the records were confined to the south and east of a line from the River Severn to the River Humber. Within this area, no records were received from Lincolnshire, Nottinghamshire, Warwickshire, Worcestershire or Gloucestershire.

Fig. 3 depicts the recent information in a more precise manner, by using the 10 km National Grid squares. A square was filled in even if only one record occurred in it. As a result of this presentation it will be seen that there are certain areas e.g. around London and Oxford, where a large number of records are available, whereas in other parts only a few widely scattered reports were received. This emphasises the point inherent in surveys of this sort that the distribution of observers is recorded as well as that of the animal. The harvest mouse appears to be quite widely distributed throughout East Anglia. Cranbrook (1953) and Payn (1956) consider that it is universally found in Suffolk but give only a few actual records. It has also been widely

recorded within a 20 mile radius of St. Paul's Cathedral, London, by members of the London Natural History Society (Teagle 1964). Southwick (1956) reported an unusual abundance of the species in corn ricks near Oxford. He found that the mice were common in ricks in Berkshire and south Oxfordshire but found none in north and north-west Oxfordshire. However, Jenkins (1957) found few mice in ricks in the Micheldever, Hampshire, area in the winter of 1955-56. Rowe (1958) found that they were present in ricks near Popham, Hampshire, and considered that an increase had occurred over the years 1955-57. Again, Rowe and Taylor (1964) recorded that during threshing at Odiham, Hampshire, in 1959-60, out of a total of 36 ricks 34 contained harvest mice, and the total catch from these ricks was 563 animals. It does seem, therefore, that in certain areas the harvest mouse may be quite abundant.

C. Discussion

It appears from consideration of Figs. 1-3 that there has in fact been a reduction in the range of the harvest mouse in this country since about 1900. However, it is difficult to assess the reliability of some of the older reports for a few of them are based on hearsay and the authors themselves admit that many of the Scottish records are somewhat dubious. Nevertheless Barrett-Hamilton and Hinton (1910-21) and Millais (1904-06) appear convinced that the mouse did occur in parts of Scotland and

northern England, even if it was not as widespread as Fig. 1 might suggest. The records for northern England and Scotland show that the mouse was certainly not as common there as it was in southern England. Millais (1904-06) summed up the situation: "The harvest mouse may be regarded as generally but locally distributed south of Aberdeenshire, though in Scotland it is much scarcer than in England".

In the survey of recent records the number of enquiries made throughout the Midlands and northern England was at least as many as those made in the south and south-east, and it is therefore significant that no positive records were forthcoming for areas north and west of Leicestershire. The only record for Wales comes from the remains of three specimens from barn owl, Tyto alba (Scopoli), pellets collected near Bangor, Caernarvonshire. In view of this record it is not unreasonable to suppose that more will be obtained in the area between Caernarvonshire and Leicestershire, especially in the west Midlands.

Other studies have shown that Micromys is almost certainly not uniformly distributed and its presence in one locality is by no means an indication that it is present over the whole of that area (see Ecology Section). In view of this, it is probable that the mouse does occur in a large number of places in which it has not hitherto been reported, for a thorough knowledge of the small mammal fauna of the district would be necessary before

it could be said with any certainty that the harvest mouse did not occur there.

This survey has also brought to light some interesting information about the animals' habitat. Harvest mice have not only been recorded from farmland. Many of the records from the London area are from sewage farms where there is usually plenty of tall herbage in which the mouse can build its breeding nest. Other habitats include rough common land, reed-beds, heathland, and, occasionally, woodland. This variety of habitats is most interesting from the distribution point of view, for it shows that the mouse may well be present in areas many miles from corn-fields and thus its presence in some places may not even be suspected. This undoubtedly means that it is to be found in many places not so far recorded.

In conclusion, it may be stated that the range of Micromys in Britain has decreased since 1900 and it now appears to be confined largely to the southern half of England, with one record from N. Wales. However, it has been revealed that the mouse is present in a wide variety of habitats and this fact, together with the sporadic nature of its distribution, indicates that it has a wider distribution than the present records suggest.

III ECOLOGY

A. Introduction

In 1789 the Reverend Gilbert White, in "The Natural History of Selbourne", recorded that the harvest mouse lived in cornfields at harvest time and in ricks or in the fields in burrows during winter. Since this time these three places have been regarded as the animal's chief habitats, at least in Great Britain.

Some additional information is available on the occurrence of the mouse in ricks. Southwick (1956) found harvest mice in 28 out of 65 corn ricks, the numbers in individual ricks varying from one to an estimated 110. The mice caught were not in breeding condition during the months of the survey (December to May). Rowe (1958) obtained the following numbers of mice from ricks at Popham, Hampshire : four mice from three ricks in June 1955; 20 mice from three ricks in April 1956; 119 mice from seven ricks in March 1957. Although 48% of the males were fecund in March 1957, the females were not. Rowe and Taylor (1964) collected 563 mice from ricks at Odiham, Hampshire, between October 1959 and June 1960. The ricks threshed in May and June contained an average of 6.7 mice per rick (20 ricks) compared with 26.7 per rick (16 ricks) in those destroyed earlier, but as observations before threshing showed comparable numbers of mice present, Rowe and Taylor concluded that the mice left the ricks for the fields and

hedgerows in the spring. Although these results provide some information concerning the numbers of Micromys present in certain areas, no information was collected on population changes during and after the breeding season. Very few farmers in the south of England still build ricks, so this habitat for Micromys has nearly disappeared.

Apart from these few studies, little quantitative information is available concerning populations of Micromys in the wild. Kubik (1953) studied mice living in open meadowland at Bialowieza, Poland, and his results will be discussed later. Bauer (1960) caught Micromys in a variety of vegetation in the Neusiedlersee district of Austria,but its principal habitats were areas of Carex, Salix, and Alnus swamp-woods. Sleptzov (1947) recorded that the Ussurican harvest mouse (M. m. ussuricus) is found in rice fields and cereal stacks and that its numbers can increase so that it becomes a serious pest.

The work of Kubik (1953) and Bauer (1960) has shown that Micromys may be found away from agricultural land and recently Teagle (1964) has questioned the view that cornfields and ricks are the animal's typical habitat in Britain. He records that in the London area alone Micromys has been found in the following places : a common, marsh, kale field, orchard, garden, marsh vegetation at four sewage farms, flooded clay and gravel pits,

and agricultural land. It has also been caught a few times in deciduous woodland in Britain and Poland, and has been found in fresh- and brackish - water reed-beds in Essex and Sussex as well as on the Continent. A factor common to all these habitats is the presence or proximity of tall grasses or reeds.

Although it occurs in such a variety of habitats, Micromys appears to be generally rare although it may be abundant locally at times, as in the rick populations mentioned above. The aim of the present work was to investigate population fluctuations, activity, home range, breeding period and relationships with other small mammals. The work was begun at Studland Heath Nature Reserve in the winter of 1963-64 and studies were also carried out in the "typical" habitats of agricultural land, chiefly at Odiham and Romsey in Hampshire.

B. Field Work.

1) Review of Methods for estimating Population size.

Since it is rarely possible to catch all the small mammals living in a particular area, it is necessary to estimate the total population from those animals that are sampled. Two major methods have been developed for estimating population size from trapping results. Firstly there is the removal method, in which animals are removed from the area as soon as they are caught, and

secondly the capture-recapture method, which involves releasing marked animals into the population and estimating its size from the proportions of marked to unmarked animals in subsequent catches.

The removal method was not used in the present study because activity and home range could not be investigated if the animals were removed. A method was required in which the population size could be estimated at the same time as the other information was collected. The removal method also has the disadvantage that, especially when dealing with small mammal populations, it is difficult to prevent animals from outside the area moving into it as the occupants are removed and thus a particular area may never be completely trapped out.

Many methods have been developed for estimating population size from capture-recapture data. All of them make a number of assumptions which, for most methods, are as follows:

1) The marking does not affect the normal life of the animal; for example, does not make it more conspicuous to predators and so more likely to be killed than unmarked animals.
2) The marked animals become thoroughly mixed in the population.
3) The probability of capturing a marked animal must be the same as that of capturing any member of the population i.e. once marked the animals do not become trap-shy or

trap-addicted.

4) The population is a closed one or, if not, immigration can be measured or calculated. Emigration will not affect the population estimate provided that marked and unmarked animals emigrate proportionately.

5) Allowance must be made for births occurring in the period between sampling. Death may be treated as emigration in 4) above.

Provided that all these conditions are satisfied, the Lincoln Index may be used in which the total population divided by the original number of animals marked is equal to the total number captured in the second sample divided by the number of recaptures of animals marked on the first occasion

or $N = \frac{ab}{r}$,

where N is the estimated population, a is the total number of animals marked, b is the total number of individuals in the second sample and r is the total number of recaptures.

The Lincoln Index is based on a single marking occasion; an extension of this method is the one proposed by Hayne (1949) in which the estimate of population size is based upon the increase in the proportion of recaptures which is observed in succeeding catches as more animals are marked in the course of the experiment. More sophisticated methods using data from a series of marking and

recapture occasions were later developed (e.g. Bailey 1951, Leslie 1952, Chapman 1954) in which allowances can be made for departures from some of the above assumptions. Leslie (1952) and Leslie and Chitty (1951) in particular devised a number of variations of their basic method which could be applied to situations where the birth and/or death rates were changing or constant over a series of multiple marking/recapture occasions. For an algebraic solution in most of the above methods it is necessary to assume that the survival rate over a period of time is an exact value and they are thus deterministic models. A more realistic approach is provided by a stochastic model in which the animal has a probability of surviving over the interval. Such an approach was used by Darroch (1958, 1959), and Jolly (1965) extended the method to allow for mortality (and emigration) and natality (and immigration) as well as for any animals killed after capture.

Apart from Bailey's (1951) triple-catch method, to which a correction factor can be applied to enable small samples to be used, these later methods were developed for use when large numbers of recaptures are made. In addition, it is necessary to have information from at least three consecutive marking/release periods since, in the estimation of the population size at a particular time, trapping results are used from the preceding and succeeding periods. These two points render these methods unsuitable for use in the present study in which, as will be seen from the results (Table 4), only small numbers of recaptures were

made and recaptures from one month to the next were only made on two occasions. Hence, if calculation of one month's results depended upon the preceding and succeeding months' captures, the population could have been estimated for only one of the four months in which the mice were caught. Since trapping was carried out for four days in each month, theoretically it would have been possible to apply these methods using one day as the trapping period. However, apart from the even smaller numbers involved in daily trapping, the numbers caught per day are liable to fluctuate with changing weather conditions and thus give variable and misleading estimates of population size.

Thus, a method was required in which the results of the four days trapping per month could be used to provide an estimate of the number of mice present during that month. Furthermore, as the mice were only caught during the non-breeding season (as verified by external examination of the genital organs) there was no dilution of the population by young animals, and corresponding complications, which the more complex methods of estimation could handle, were not introduced into the calculations. The results were therefore amenable to one of the simpler methods of population estimation and that of Hayne (1949) was considered suitable as the assumptions made by this particular method were fulfilled, as shown in detail below.

2) Population Studies at Studland Heath.

Studland Heath National Nature Reserve covers an area of 429 acres in the South Haven peninsular in Dorset. The central portion of the reserve is occupied by Little Sea, a fresh-water lake, and this is surrounded by extensive areas of marshland. The vegetation of the marshes includes Phragmites, Juncus, Molinia, Myrica, and Salix spp., and for the most part the area is impenetrable. The rest of the reserve contains Calluna moorland dotted with areas of Ulex and in places small areas of Pteridium and Rubus are to be found. On the sand dunes near the sea the dominant vegetation is Psamma. At the southern end of the reserve is a small area of deciduous woodland. Figure 4 is a map of Studland Heath showing the extent of the marshes and the trapping sites.

(i) Methods

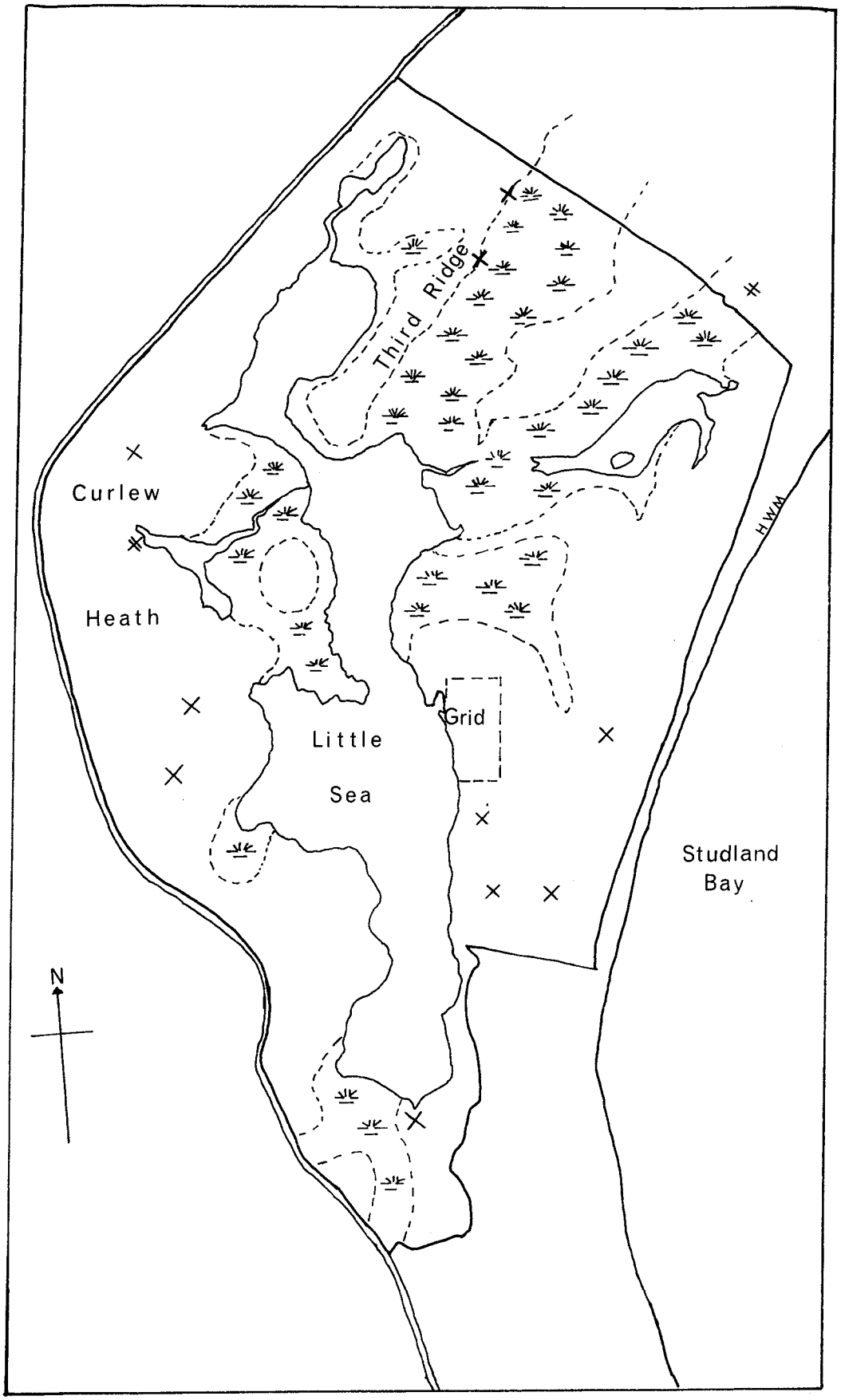
An area of approximately 2.2 acres on Studland Heath was selected for experimental purposes after extensive preliminary trapping had shown that this particular region contained more harvest mice than other parts of the reserve. Little Sea formed one side of this area. The vegetation next to the water consisted of a small zone of Phragmites and Juncus sp. and beyond this was a strip of dense Ulex which varied from 10 to 20 yards in width. This gave way to an area dominated by Calluna in which a few clumps of Ulex and Betula occurred, and finally the zone furthest away from Little Sea was composed solely of Calluna.

Fig. 4: Map of Studland Heath N.N.R., showing location of trapping grid, other points of capture of harvest mice, and nest sites.

× points where harvest mice were caught.

⋇ nest sites.

HWM = High Water Mark.


Third Ridge
Curlew
Heath
Little
Sea
Grid
Studland
Bay
HWM
N

The apparatus selected for catching the mice was the Longworth small mammal trap (Chitty and Kempson 1949) and this choice was determined by the following considerations. In the first place the trap is fairly easy to adjust to the sensitivity necessary for the capture of an animal as small as the harvest mouse (weight approximately 6 g). Other traps commonly used for catching small mammals alive, such as the Havahart and the Sherman, are not so easy to adjust and the Havahart in particular may be sprung by rain or vegetation falling on the release mechanism. Secondly, the Longworth trap allows for the provision of nest material, which helps to prevent the animals dying from exposure.

The traps were set in an area measuring 150 x 70 yards. This area was subdivided into small squares with 10 yard sides, and two traps were placed at one corner of each square for one night and then moved anticlockwise to the next corner, until after four nights the square had been completed. The traps were visited early in the morning and just before dark when they were moved. Trapping was carried out for four nights in every month from January until November 1964. The mice caught were identified, sexed, marked individually by toe-clipping, and released.

This method of working the grid was based on that used by Tullagar et al (1963) and was chosen because it helps to satisfy

some of the assumptions inherent in the recapture method of population estimation described above. Firstly, the placing of two traps at each point samples the area round that point more thoroughly than does a single trap, and, since it was rare for both traps to be occupied, it was judged that the two traps were sufficient. Secondly, moving the traps every twenty-four hours prevents the animals becoming accustomed to their presence in a particular place and thus may reduce the risk of trap-addiction. Also it ensures that the area as a whole is more thoroughly sampled.

In practice the assumptions of the recapture method that are most difficult to fulfill are numbers 3 - 5 above. In the present case, the population was not being diluted by breeding during any trapping period as the mice were caught only in the non-breeding season. Thus, dilution of the population could only take place by immigration. The brevity of the trapping period (four nights) minimised the possibility of large-scale immigration and, in fact, as shown by the test described below, the immigration within any trapping period was negligible. Emigration and death do not introduce a systematic error into the method of calculation so long as they occur in equal proportion among marked and unmarked animals, and do not result in the replacement of lost animals by unmarked individuals from

outside the trapping area. Assumption 3, that there is random recapture of marked animals, may be a serious problem. For example, Leslie et al. (1953) showed that in a population of Microtus agrestis in N. Wales, marked individuals tended to be caught more frequently than expected and thus the assumption was not valid. It was necessary, therefore, to test the present data statistically to determine whether marked and unmarked animals were being caught with equal facility.

The method devised by Leslie et al. (1953) for testing this situation was followed here because it allows for the amalgamation of data which, in view of the small numbers involved, was necessary in the present case. The recaptures in each month's trapping were grouped according to the time they were first captured and marked. The data for March are given in Table 1. If there is an equal probability of catching a marked and an unmarked animal, the number of animals marked at a particular time should form a constant proportion of the total catch when recaptured in subsequent samples. Thus, the expected number of recaptures for each cell of the table may be calculated from the mean proportion captured in each row. For example, Table 1 shows that a total of 14 recaptures were made of the mice originally marked on the 24th March. The three samples in

Day when first marked	Day of capture 25th.	26th.	27th,	Total recaptures
24th.	5 (4.20)	6 (6.30)	3 (3.50)	14
25th.		1 (0.90)	1 (0.50)	2
26th.			1 (0.25)	1
Unmarked	1 (1.80)	2 (1.90)	0 (0.75)	
Total catch	6	9	5	20

Table 1: Distribution of Micromys recaptures at Studland from March 25th.-27th. according to the day when they were first marked and released. (Expected values in brackets below the observed values.)

Month	Marked	Unmarked	Total
January	4(3.00)	8(9.00)	12
March	17(15.65)	3(4.35)	20
April	7(7.01)	1(0.99)	8
November	11(9.09)	10(11.91)	21

Table 2: Observed and expected numbers of marked and unmarked Micromys caught at Studland in each month. (Expected values in brackets.)

which these recaptures were made consisted of a total of 20 animals and hence the recaptures formed a mean proportion of 0.70. The 'expected' number of this class caught on the 25th is therefore 0.70 x 6 = 4.20, compared with the observed number of 5. Similarly, the remaining 'expected' values were calculated and the expected values of the unmarked mice were obtained finally by subtraction. The departure from expectation can then be tested by calculating χ^2 in the usual way but this requires an expected value of five or more in each cell of the table. Since this condition is clearly not met in the present case the data in each month were combined and the totals for marked and unmarked mice were compared, as shown in Table 2. Since some of the expected values are still too small, January was amalgamated with March and November with April. Then, χ^2 = 1.070 and the probability that there is no departure from expectation lies between 0.1 and 0.9. Hence, the data have failed to indicate that more marked mice were being captured than expected on the assumption that marked and unmarked mice were being caught with equal facility. Furthermore, the test has failed to disclose any dilution of the population for, if there had been immigration of unmarked mice into the area during the trapping periods, a larger number of unmarked mice than expected would have been caught.

Thus, it appears that the sampling of the Micromys population was satisfactory and Hayne's (1949) method could accordingly be applied.

As mentioned earlier, Hayne's (1949) method is based on the Lincoln Index concept. When x animals have been marked and released into the population (N) from which they were trapped, the proportion of the population now marked (y) is given by the formula,

$$y = \frac{1}{N} x ,$$

This is the equation of a straight line passing through the origin and successive samples drawn from the population will give points on the line. The slope of the line may then be calculated and the reciprocal of this is the estimate of population size. However, the population may be estimated directly by inverting the usual expression for the slope of a regression line passing through the origin (Snedecor 1946), thus :

$$N = \frac{\sum wx^2}{\sum wxy} ,$$

where x and y are as defined above and w is the total number of animals caught in each sample. The results for each month are set out and calculated as exemplified by the month of November in Table 3.

Since the standard error of the slope of a line may be computed, Hayne (1949) suggests that the fiducial limits of the population estimate can be given by the reciprocals of the upper

and lower limits of the slope. The estimated standard deviation of the slope of a line (Mendenhall 1964) is given by the formula,

$$\text{estimated } \sigma_{\hat{\beta}} = \frac{s}{\sqrt{\sum_{i=1}^{n}(x_i - \bar{x})^2}} ,$$

$$\text{where } s^2 = \frac{1}{n-2}\left[\sum_{i=1}^{n}(y_i - \bar{y})^2 - \frac{\hat{\beta}}{n}\left(n.\sum_{i=1}^{n}x_i y_i - \sum_{i=1}^{n}x_i . \sum_{i=1}^{n}y_i\right)\right]$$

(n = number of samples, $\hat{\beta}$ is the estimate of the slope i.e. the reciprocal of the estimate of population size.)

The upper and lower limits of population size are computed from this as 95% confidence limits (see Table 3).

As Hayne (1949) points out, estimates of the density of the population may not be made from the estimate of population size because, although the trapping area is known, the total area inhabited by the estimated population is not known. So that comparison could be made with figures published for other small mammals, a minimum estimate of density was obtained by taking the actual number of mice caught per month as the minimum population size.

However, the home range of mice normally living outside the trapping area will extend on to part of the grid. Where this happens, the animals concerned may be caught on the grid and thus too high an estimate of population density will be obtained. Over a short trapping period (one night) this may be balanced to some extent because mice normally living on the grid, whose home range extends beyond it, may not be caught. When,

however, the trapping period extends over several nights, as in the present case, there is a greater chance of catching these mice whose home range is only partly on the grid. In order to estimate the area outside the grid from which mice may have been drawn, it is necessary to know their home range. Dice (1938) proposed that half the diameter of the average home range should be added to all sides of the grid to estimate the area covered effectively by the traps. This method assumes that any animal whose home range includes only one trapping station is as likely to be caught as one whose home range includes two or more stations. This assumption is difficult to test in practice but it would seem likely that the presence of two traps at each station and the movement of traps every night (provided that this took place within the animal's home range) would help to maximise the possibility of catching the animal.

In the present study the mice were not recaptured frequently enough for an accurate assessment of home range to be made. As an alternative, the movements of mice caught three or more times were plotted on graph paper and the distance between the furthest points of capture for each animal measured. To this distance is added half the distance to the next trap, as Stickel (1954) found that the estimates would be more accurate if this is done. This

distance is used as a substitute home range, following Miller (1958) and Fullager *et al.* (1965). Thus, half this average "range length" is added to three sides of the grid, it not being necessary to add it to the side formed by Little Sea. The estimates based on this "edge effect" tend to minimise the density, while if this is ignored, and a straight calculation made based on the area of the grid, a maximum figure is more likely to be obtained. The actual density may reasonably be expected to be within these limits, and both calculations are presented in the results.

While the grid was being worked, traps were also set in other parts of the reserve, sometimes in a grid or more often in lines, to determine the distribution of the mice on the reserve and to find a suitable area to set up another grid.

(ii) Results

The results are calculated for each month as shown for November in Table 3.

Table 4 gives the results month by month for the total period over which trapping was carried out. The average range length used in the calculation of density was 49.6 yards.

It will be seen from Table 4 that harvest mice were only caught on the grid in January, March, April, June, October, and November. The apparent absence of the mice during the February

Table 3: Results of trapping Micromys at Studland in November, 1964, showing method of calculation. (*includes one dead animal, not included in subsequent calculations.)

Date Nov.	No. caught(w) New	Previously handled	Proportion previously handled(y)	Total previously handled(x)	wxy	wx^2
23rd.	4	0	0.00	0	0	0
24th.	6	2*	0.25	4	8	128
25th.	3	6*	0.66	9	54	729
26th.	1	3	0.75	11	33	484
				Total	95	1341

Population $N = \frac{\Sigma wx^2}{\Sigma wxy} = \frac{1341}{95} = 14.1$ mice.

Confidence limits are calculated as follows:-

Estimated standard deviation of $(\frac{1}{N}) = \frac{s}{\sqrt{\Sigma(x-\bar{x})^2}}$ (for s, see text.)

$$\text{i.e. } S.D.(\tfrac{1}{N}) = \frac{0.002}{74.0} = 0.0052$$

$$\text{Then, slope}(\tfrac{1}{N}) = 0.0708 \pm 0.0052$$

The 95% confidence interval for $(\frac{1}{N})$ is $\pm t_{0.025}(S.D.)$.

With 2 degrees of freedom, t = 4.303, and thus the 95% confidence interval is $\pm$ 0.0223.

Upper limit of slope = 0.0708 + 0.0223 = 0.0931

Lower limit of slope = 0.0708 - 0.0223 = 0.0485

Then, upper limit of population is $\frac{1}{0.0485} = 20.6$,

lower limit of population is $\frac{1}{0.0931} = 10.7$

Month	No. caught	Recaptures from preceding months	Estimated population	Limits of popn. size	Uncorrected density (/acre)	Corrected density (/acre)
January	13	-	17.5	77.0-9.9	5.9	3.3
February	0	-	-	-	-	-
March	10	4(J)	9.93	9.97-9.89	4.6	2.6
April	4	2(M) 1(J)	3.5	see text	1.8	1.0
May	0	-	-	-	-	-
June	1	0	-	-	-	-
July-September	0	-	-	-	-	-
October	4*	0	-	-	-	-
November	14**	0	14.1	20.6-10.7	5.5	3.1

* denotes full grid not worked.

** includes two dead mice which were not included in subsequent calculations.

Table 4: Results of trapping Micromys at Studland during 1964.

trapping period deserves special mention because it is believed that they were in fact present at this time. The Longworth small mammal trap contains a built-in device for altering the sensitivity so that if it is desired to catch only large, heavy animals the trap can be made insensitive to lighter ones. In order to catch harvest mice the trap was naturally set on maximum sensitivity and until February 1964 no trouble had been experienced in catching the animals, even with some new traps. In February, however, a different batch of new traps was used on the grid which, although set on maximum sensitivity, failed to catch any Micromys and caught only three large Apodemus (13 Apodemus had been caught in January). Subsequently it was found that this batch of traps, even when set on maximum sensitivity, were so insensitive that only a heavy Apodemus would be caught.

However, there is evidence that Micromys visited the traps during this period. When eating a grain of corn, a harvest mouse holds it with one fore-foot at each end and chews round the middle, leaving a remnant shaped like an hour-glass. Such characteristic remains of the grain used to bait the traps were found during February.

Subsequently, all traps were specially adjusted to respond to a weight on the treadle of approximately three grams.

As Table 4 shows, with the exception of a single individual caught in June, harvest mice were evidently absent from the trapping area from the end of April until October 1964. No indirect evidence of their presence, such as was found in February, was observed during this time.

It has already been mentioned that trapping was also carried out on areas of the reserve away from the grid. During the months that mice were being caught on the grid, they were occasionally found elsewhere (see Fig. 4) but never as abundantly as on the grid. When the mice ceased to appear in the traps on the grid, efforts were increased to catch them on other parts of the reserve, both in the vicinity of the grid and away from it. 16 different sites including all types of vegetation were sampled with no success. In particular, efforts were centred on the edges of the marshes and, in the few places where this was possible, traps were set actually in the marshlands.

In September, three harvest mouse nests were discovered in clumps of Molinia in a marsh near the northern boundary and another in a similar habitat on the western arm of Little Sea (Fig. 4). 40 trap nights in each place failed to reveal any Micromys. However, one was captured in November at the northern boundary site.

Besides Micromys, the only other small mammal regularly trapped on the grid was Apodemus sylvaticus. In January, the same calculations as used for Micromys were carried out on the results for Apodemus. The estimated population was 14 mice and the 95% confidence limits were 8.5 and 32.7. The corrected and uncorrected estimates of density were 3.3 per acre and 5.9 per acre respectively, the average range length used in these calculations being 49.4 yards. It was found during January that Apodemus occupied a distinct area, being mainly confined to the Ulex zone bordering the Little Sea. Micromys occupied the central zone of Calluna with isolated patches of Ulex, and thus the two populations were for the most part separate from one another. For this reason, marking of Apodemus was discontinued, though records of their capture were kept and it was found that they continued to occupy the same area for the rest of the year, though one or two were found in the Calluna zone during the months that no Micromys were caught.

(iii) Discussion

The results of the grid trapping and that carried out concurrently elsewhere show the same trend - harvest mice are present in various places on the heather moorland in winter, but

disappear during the late spring and summer months. Additional evidence to support this picture was provided by the accidental catching of Micromys in spider traps. These were set by Dr. P. Merrett of Furzebrook Research station and consisted of jars containing preserving fluid sunk into the ground so that the rim was at ground level. Harvest mice apparently fell into these jars and could not get out. Dr. Merrett found Micromys in the jars during the autumn and winter, but never caught any during the summer.

It is suggested that the apparent absence of the mice from the heather in the spring and summer is due to the fact that the heather offers no suitable site for the harvest mouse to breed. The animal's breeding nest has been described several times (White 1789, Matthews 1952, Frank 1957) and requires tall grasses, reeds or similar vegetation for its construction. The only place where such material is to be found at Studland Heath is in the marshland areas, particularly in places such as the Molinia marsh where the four nests were found, and the discovery of these nests shows that breeding does take place in these areas. The onset of the breeding season in England is not known for certain, but in Poland it begins in late April (Kubik 1953) and from the scant

evidence available probably starts around that time in England as well. It continues through the summer months certainly until September (Southern 1964). These times coincide almost exactly with the observed absence of the mice from the grid at Studland Heath. The marshes on the reserve cover a considerable area, and, except in a few places, it is only possible to set traps along the landward edge. Such trapping was carried out in the summer of 1964 but was unsuccessful, as already recorded.

If as is suggested, the mice at Studland breed only in the marshes, it remains to be discovered whether the whole population moves out onto the heather in winter or whether the heathland population is an overspill. The single mouse caught in the marsh in November indicates that at least some of them remain in the marsh until then. It is of interest to note that Micromys have also been caught in marshes in other areas. Two were caught in a Molinia marsh in the New Forest, one in January and one in April 1964. This suggests that mice are to be found in marshes during the winter months as well as in the summer.

The confidence limits of the estimates of population size are wide in some months and this is a reflection of the small numbers of mice handled. When a maximum of five or six animals are being caught each night, there is a good chance that in a poor nights trapping when (say) only two animals are caught

that there will be no recaptures. This will, of course, affect the estimate slightly, but it will affect the variance much more, especially in view of the fact that there are only four samples. The method of calculation assumes that the samples fall on a straight line and if one out of the four samples is some distance from a straight line through the other three, then the limits of the slope of the line will be correspondingly large. In fact, as happened for the April sample, included in the 95% confidence limits may be a line which does not pass through the origin and hence may have a negative slope. This means that the upper limit of population size is infinity. The 90% confidence limits give an upper limit of the April population of 26.3 and a lower limit of 1.9 (95% limits give 1.1 - ∞).

The estimates of population size at Studland show a decline over the first four months of the year (Table 4). Four of the mice first caught in January were recaptured in March and one was also caught in April. Two of the mice first marked in March were recaptured in April. These results suggest that part at least of the population being sampled from January to April was a stable one, and that successive monthly samples were not drawn from different transient populations which might conceivably have

been the case in view of the later movement of the mice. Thus, it may be said that the population of the trapping area decreased towards the onset of the breeding season, as may be expected when mortality is not balanced by natality. The November estimate and its limits lie outside those of March (which is a more accurate estimate than that of April) and there is thus a distinct increase in numbers at this time compared with the earlier months. Since the November sample was taken only a few weeks after the probable end of the breeding season, this increase in numbers is only to be expected. However, there is no way of telling whether the November population was derived from that present in March and April (there were no recaptures of members of the earlier population). Neither can it be said that the numbers of mice caught on the grid in the first four months of the year represent the same proportion of the total population of the reserve as do those caught in November. Therefore, the increase in the numbers caught in November may or may not represent an increase of the whole population of the area, and the November sample should accordingly be regarded as a separate population from that present in the earlier months of the year.

Little trapping was carried out at Studland in 1965 and 1966. In November 1965 no harvest mice were caught on the old grid which

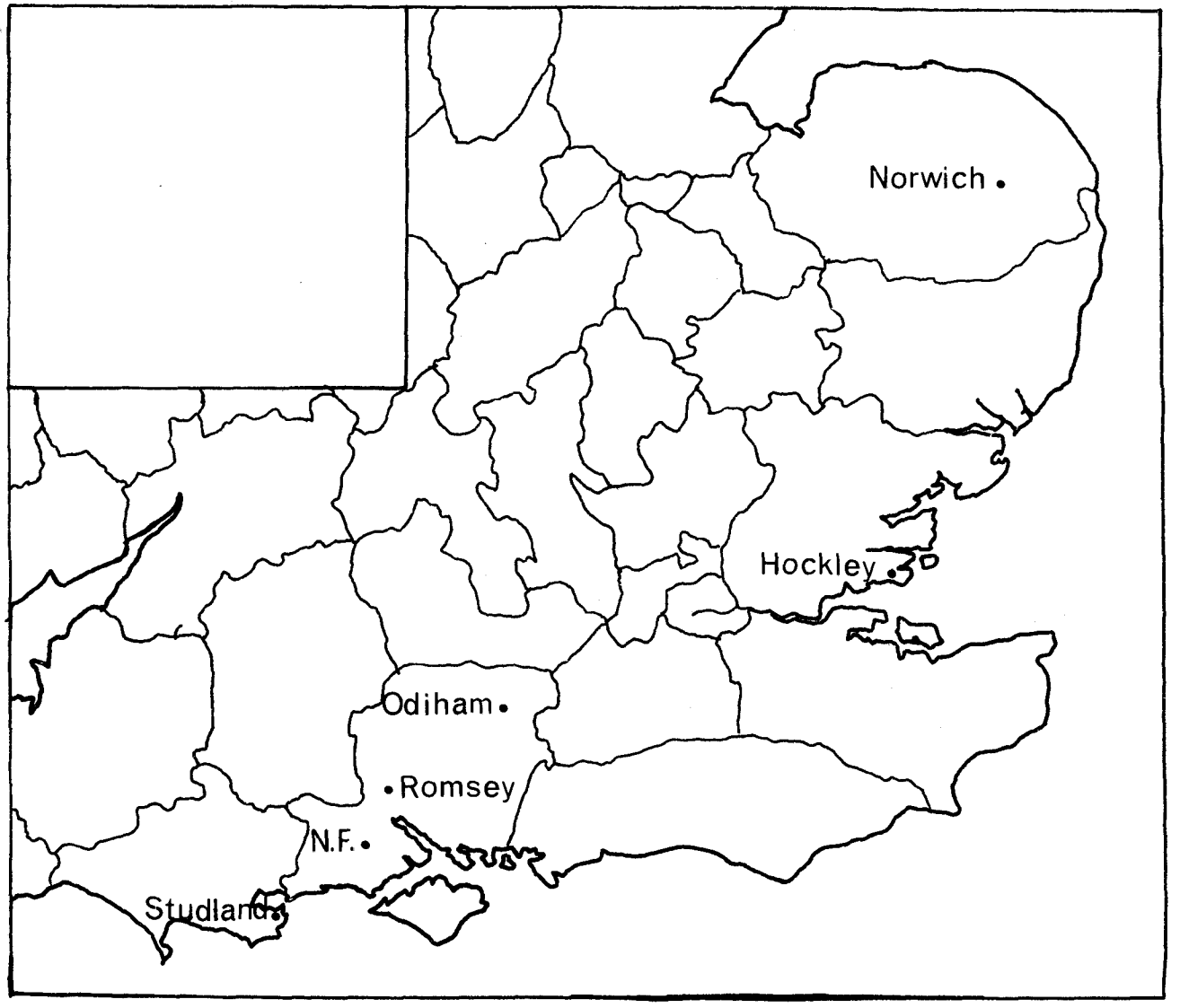
was worked as usual. In January 1966, two trap lines placed in this area caught three harvest mice on the first night and recaptured the same individuals but no new ones during the subsequent four nights. Two were caught on Curlew Heath (see Fig. 4) during this month and mice were also found in spider traps on Third Ridge. In general, it appeared that numbers were not as high as in 1964, though the mice may have been present in different areas.

3) Population Studies on Agricultural Land

When it became apparent that the population at Studland was relatively small and of only seasonal presence, the search for harvest mice was extended to farming areas. Trapping was carried out at Roke Farm, Odiham, Hampshire; Barton's Farm, Hockley, Essex; and at Warren and Spursholt Farms near Romsey, Hampshire. Although harvest mice and/or nests were found in each case, only at Spursholt Farm was it possible to carry out extensive work. A map showing the localities visited is provided in Fig. 5.

Fig. 5: Map showing the localities in south-east England where trapping was carried out.

N.F. = New Forest.


Norwich
Hockley
Odiham
Romsey
N.F.
Studland

(i) Methods

In each case the hedgerows of the farms were sampled by lines of Longworth traps set usually 10 yards apart but sometimes only five. The number of nights that the traps were left in one place varied from one to three. The large numbers of wood mice and voles caught in the hedgerows together with harvest mice made it advisable to have some means of excluding the larger animals from the traps in order to obtain a bigger catch of Micromys. Accordingly pieces of zinc sheet with a ½" square hole cut in one corner were fitted into the tunnels of the traps and these fairly effectively kept out the larger wood mice and voles, though the young of these animals were able to squeeze through. Owing to the small number of Micromys (three) present in the laboratory when these excluders were introduced, it was not possible to test comprehensively whether the mice entered traps fitted with them less readily than they did unmodified traps. However, experiments with these mice showed that though they would not (and probably could not) enter the traps when the hole in the excluder was less than ½", they would readily enter those with larger holes. No difference in the behaviour of the mice towards modified and unmodified traps was detected and all three animals readily squeezed through the hole in the excluder without hesitation.

(ii) Results at Spursholt Farm, Romsey.

In February, 1966, 15 harvest mouse nests were discovered in a hedgerow 150 yards long and 30 traps were set at five yard intervals along the hedge. After three nights, a single female harvest mouse was caught and, although the trap line was extended by 40 yards, no further harvest mice appeared. In a total of 191 trap nights in this hedgerow the following animals were caught:

Apodemus sylvaticus	14
Clethrionomys glareolus	7
Microtus agrestis	10
Sorex araneus	8
Sorex minutus	1
Micromys minutus	1

The figures for A. sylvaticus, C. glareolus and M. agrestis are minimum estimates of those present because some of the traps were fitted with excluders.

Trapping was also carried out for three weeks in a neighbouring hedgerow and five Micromys were caught, four of which were present during the first week and the fifth on the final day. 350 trap-nights were spent in this hedgerow and, as well as the five Micromys, the following animals were caught:

A. sylvaticus	7
C. glareolus	10
M. agrestis	12
S. araneus	8

Again, for the wood mice and voles these are certainly minimum values for those present because excluders were used in some traps.

Although 10 other hedgerows on this farm were investigated, harvest mice were caught in only one. The catch of animals in this particular hedge was as follows:

A. sylvaticus	13
M. agrestis	1
S. araneus	5
Micromys minutus	2

A summary of the trapping results at Spursholt Farm is shown in Fig. 6. Altogether 739 trap-nights were spent at this farm in February and March 1966, and eight Micromys were caught, representing a trapping success for this animal of just over 1%. Out of the 2,790 yards of hedgerow trapped, Micromys were found in 150 yards.

It is possible that the eight mice caught represent only a

fraction of the population present as the climbing habits of *Micromys* may make it less liable to capture in traps set on the ground. While this may be true during the summer months, it is not thought that any significant proportion of the population lived off the ground in February and March. The reasons for this are as follows. Firstly, there is much less vegetation for the mice to climb during the winter. Secondly, there is no evidence that the mice build nests off the ground in the vegetation as they do in the summer; in fact there is definite evidence to the contrary (see later section). Thirdly, in one place four mice were caught soon after the traps were first set and only these four were captured for the next three weeks. It seems unlikely that a large number of mice lived so completely off the ground that at least one or two would not have been caught during these three weeks. The fact that the traps were baited and that corn was scattered around them adds to this point as presumably food is scarcer at this time of year and the animals are forced to search for it thoroughly. It seems reasonable to assume, therefore, that the mice caught represented a large proportion of those present, though a few extra animals were probably not captured owing to trap-shyness.

Old nests were found in most hedgerows visited, although they showed a tendency to be aggregated in those parts of the hedges where there was tall grass. Owing to the presence of these old breeding nests it is possible to obtain a minimum estimate of the numbers of harvest mice produced during the previous summer. Certainly not all the nests built during the summer survived until March and some would have been built in the corn and thus destroyed at harvest time, although various authors have observed that usually far fewer nests are actually built in the corn than in the bordering hedge. It is also probable that not all the nests that did survive were found. However, 37 nests were found in the 2,790 yards of hedgerow trapped in March. The litter size of harvest mice is between five and nine (Southern 1964) so if seven is taken as an average there were at least 37 x 7 = 259 harvest mice born in the hedgerows during the summer of 1965. Obviously this is a minimum figure as many more would have been born in the nests subsequently destroyed or not found. As discussed above, the eight animals that were caught in March probably represent a reasonable estimate of the number actually present. Comparison of the two figures represents either a high mortality rate, all the more so considering the estimate of those born as the absolute minimum, or implies migration of some animals elsewhere. However, on this almost exclusively arable farm, the only alternative habitat to the hedgerows in winter was the open ploughed field. It is possible that the mice had migrated to hedgerows that

were not trapped, but all the hedgerows within three or four hundred yards of the main site were trapped and the reason for any such move would be obscure.

(iii) Results at Roke Farm, Odiham.

In May and June 1964 large scale trapping was carried out at Roke Farm. At the beginning of May, eight harvest mice were caught in 225 trap nights, but when the lines were extended in June no Micromys were seen at all in over 1,100 trap nights. The fauna of other small mammals in the hedgerows of this farm was rich and a 40 - 50% catch was the rule, and it often reached 70 - 80% in certain places. In August, both before and after the corn was cut, no harvest mice were caught in 200 trap nights and it was not until late September that one appeared in the traps. Some results of the Odiham trapping are shown in Fig. 7.

(iv) Results at other farms.

Following the discovery of a breeding nest of Micromys, 497 trap nights were spent at Barton's Farm, Hockley, Essex, in December 1965-January 1966. Although over two miles of hedgerow were investigated by traps at 10 yard intervals, no Micromys were caught.

Nine Micromys were caught during the threshing of an oats rick at Colney, near Norwich, Norfolk, in February 1965.

Warren Farm, Romsey, Hampshire, was visited in February 1966, but although a breeding nest was discovered, no Micromys were caught in 210 trap nights.

Fig. 6: Relative abundance of the small mammals caught in the hedgerows at Spursholt Farm, Romsey, in February and March 1966. Only those hedgerows in which Micromys were caught are included.

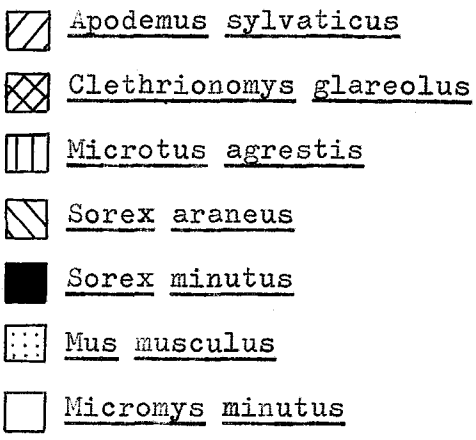


Fig. 7: Relative abundance of the small mammals caught in the hedgerows at Roke Farm, Odiham, in May and September 1964. Only those hedgerows in which Micromys were caught are included.

Fig.6

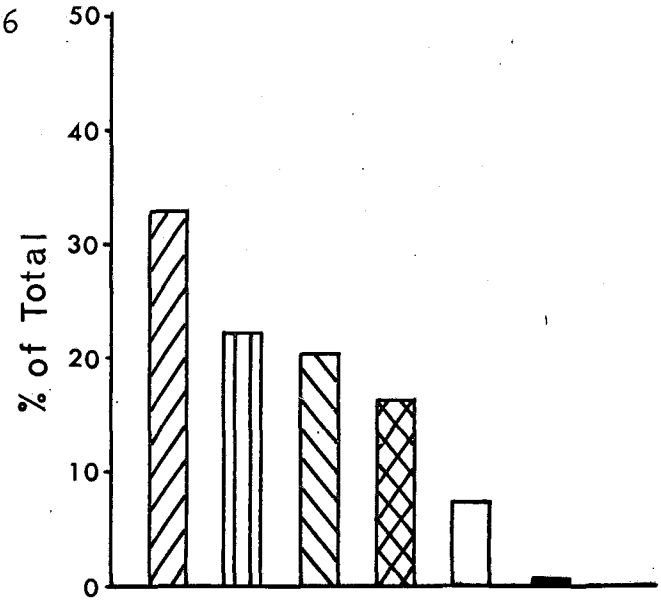
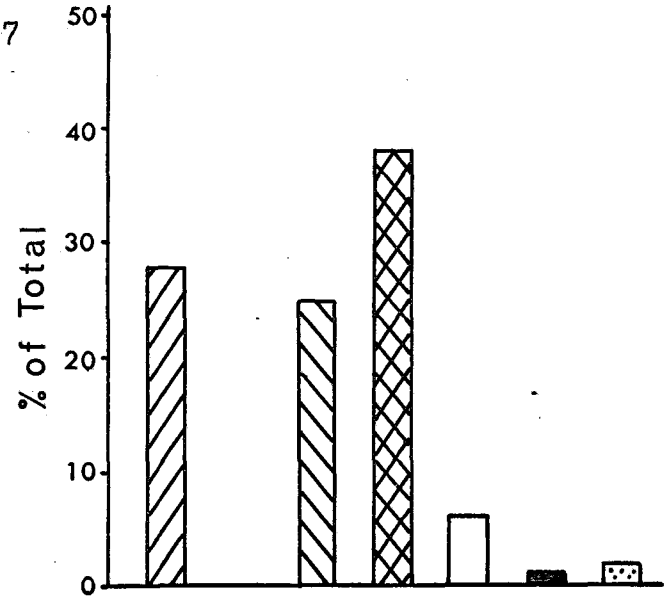


Fig.7



4. Discussion of Population Results

Little published data are available on populations of Micromys. Kubik (1953) studied a population living in open meadowland at Bialowieza, Poland, from 1946-50. In 1949, when he had most trapping success, one animal was caught in January, none at all from February to April inclusive, two in May and the population then rose to a peak of 23 in October and subsided to one in December. Kubik considers that the low number of harvest mice caught in the winter and spring was due to normal processes of predation and mortality rather than emigration, though he did find that some mice emigrated to nearby woodland.

The results of the present study at Studland show that the mice are rather more numerous than in Kubik's study area. The greatest density of harvest mice estimated on the grid at Studland was 3.3 per acre (corrected) in January 1964 while that of Apodemus at the same time was also 3.3 per acre (corrected). It is interesting to compare these figures with the densities obtained for other small mammals. The mean density of Apodemus in woodland varies between c. 5-40 per acre according to season and year (Southern 1964), while the density of both Clethrionomys and Microtus can be anything between zero and hundreds per acre. Shillito (1960) found a minimum density for Sorex araneus of nine

per acre in a small wood. It would seem therefore that the population of Micromys on the grid was rather small compared with the normal densities of other small mammals.

It is not really meaningful to translate the numbers of Micromys found in hedgerows into density per acre because of the discontinuity of the habitat. Also, trapping results show that the mice live in some hedges and not in others of apparently similar nature, and that they may even live in one part of one hedgerow and not in another. The percentage catch of harvest mice compared with other small mammals in regions where they co-exist is shown in Figs. 6 and 7 for Spursholt and Roke Farms. As already discussed, the numbers of Micromys caught at Spursholt Farm are considered to be reasonable estimates of the numbers actually present. The same is not necessarily true of the mice caught at Roke Farm since, in May and September, they could have been breeding in which case, as discussed below, they would spend much more time off the ground and be less liable to capture.

Considering only the Spursholt results, Micromys has a discontinuous distribution and, compared with the numbers of other small mammals found in the hedgerows, it was in the minority. This state of affairs may also extend to other

habitats, for Bauer (1960) found that Micromys formed only 12% of the small mammal catch in areas of Carex, Phragmites and Alnus swamp in Austria. Other workers have had varying success in trapping. Giban (1957) recorded that the winter catch of Micromys using live-traps varied from 3.3 - 22.4% in one trap-line and from 0.9 - 16.3% in another. Kulicke (1956) trapping all the year round had an average catch of Micromys of 1% of the total in 1953, 0.8% in 1954 and 2.1% in 1955.

The highest percentage of Micromys in any catch was 14.5 in one of the hedgerows at Odiham in May. However in considering this figure it must be remembered that the mice may have started breeding and, as suggested below, this may make them less liable to capture. If this was the case, then the eight animals caught would represent an unknown proportion of the total number present. Because they were needed for experiments in the laboratory all the mice caught were not killed and thus their reproductive condition could not be verified by internal examination. All four females caught were imperforate, though the four males showed a slight enlargement of the testes. Two of the males were killed and the size of the testes (6.5mm and 7mm in length) and the visibility of tubules in the cauda epididymidis confirmed that the animals were in breeding condition (Rowe 1958).

The disappearance of harvest mice from the traps in the summer months at Odiham in spite of the intensive trapping programme in many parts of the farm could be explained by one or

more of the following interpretations:-

1) The mice are local and occur perhaps in just one part of a hedgerow and the line of traps happens to miss this part. There is support for this view from the results at Spursholt and at other times of the year at Odiham, but the fact that they were caught at other times makes it improbable that this could be the only reason.

2) The mice are not on the ground for much of the time during the summer months and thus do not come into contact with the traps. This second view is supported by the fact that their nests are built off the ground and most of their food could be collected without coming to the ground. Observations in the laboratory (see Activity section) show that they spend over 60% of their time off the ground when conditions as natural as possible are provided. Under such conditions, they visit the ground mainly for food and to rest in their nest-boxes. During the breeding season in the wild, both food and nest would be off the ground and thus much more than 60% of their time could easily be spent away from ground level.

3) Tanton (1965) in a two year study of Apodemus caught few animals during the summer months. He suggests that the animals showed little interest in the traps as there was an

abundant supply of food, and that as a result only a small proportion of the population was being sampled. It is possible that Micromys could show such a change in their behaviour towards traps. Tanton (1965) did catch a few animals in the summer whereas in the present study there was a complete absence from the traps and it does seem unlikely that a whole population would ignore food-baited traps if they encountered them.

In the absence of further information, it is suggested that all these factors play some part in accounting for the lack of trapped animals in summer. Some light might well be shed on this problem by fastening radioactive rings to the animals' legs in April. A check could then be kept on the hedgerows during the summer with the aid of a Geiger-Muller or scintillation counter (Godfrey 1954; Linn and Shillito 1960).

Leaving aside the inability to catch the mice during the summer, when their presence at other times showed that they were in the area, the general conclusion of this study is that Micromys is a rare animal. Although it may occasionally be locally abundant, as shown by the numbers in corn ricks, the results indicate that it is usually less common than most other small mammals.

5. Movement and Home Range

(i) Introduction

Small mammals usually have a definite area over which they move in the normal activities of food-gathering, mating, and caring for the young. This area is known as the home range (Burt 1943). It has been suggested that this definition should be modified to allow for the animal changing its home range at different times (Shillito 1963). The home range is usually determined by trapping the animal a number of times in different places. There has been much discussion on the estimation of home range from trapping results, (for review, see Brown 1962), and on the best pattern of setting the traps. The greater number of times the animal is caught the more reliable the estimate that can be made of its home range, but usually the trap-revealed range size increases rapidly for the first few captures and then levels off until a size approximating to the true home range is reached. The number of records necessary for an accurate estimation of home range seems to vary with different species and individual workers have different opinions on the subject. The number of captures used by various authors has varied from six to 19 (Brown 1962).

In some cases, however, it is not possible to capture the

same individual a large number of times - where the species has a high death rate or avoids recapture, for example. In such cases, Davis (1953) has discussed reasons for using the frequency distribution of distances between captures in the analysis of the ranges of small mammals. This method allows some assessment of the normal extent of the animals' movements where recaptures are too few to give an accurate area of home range. It has the additional advantage that records may be used from all animals captured more than once. Disadvantages include the fact that the animals do not travel in straight lines between captures, and that movements within the home range cannot be distinguished from dispersal movements. However, these disadvantages are common to all methods attempting to analyse data of these types and this method does give an index of movement for the species that can be used for comparative purposes.

With the aid of a synthetic trapping model, Davis (1953) showed that the chance of capture is not equal at all distances, there being fewer chances at short and long distances. Thus, a more accurate result will be obtained if the observed frequencies of capture at different distances are adjusted according to the probability of capture at these distances.

In the present study the data from Studland have been analysed in this way because of the low number of recaptures

involved. The observed frequencies were adjusted according to the probability of capture by dividing the frequency by the probability and expressing the quotient as a percentage of the total,

$$\text{adjusted frequency} = \frac{100x}{\Sigma x},$$

$$\text{where } x = \frac{\text{observed frequency}}{\text{probability of capture}}$$

The probability of capture was calculated by determining the number of traps available to the animal at different distances from the point of capture. Davis (1953) has shown that usually the probability of capture follows a normal curve but in this case, owing to the shape of the grid, it does not. This method was used so that comparison could be made with the figures for Apodemus given by Miller (1958).

(ii) Results at Studland

The movements of each mouse on the grid at Studland from one point of capture to that on the following day were measured and the frequency of movements of different distances are shown in Table 5 and Fig. 8. The table shows that, although more movements occurred in the 21-40 yard range than in any other single class, this was due mainly to the fact that there were more traps, and thus a higher probability of capture, in this range. When the adjusted frequency distribution of movements

Distance (yards)	Observed frequency		Probability of capture	Adjusted frequency
	No.	%	%	%
0-20	11	31.4	6.4	62.7
21-40	17	48.6	27.4	22.9
41-60	5	14.3	24.6	7.4
61-80	1	2.8	18.8	1.9
81-100	0	-	12.3	-
101-120	1	2.8	6.9	5.1
121-140	0	-	3.1	-
141-160	0	-	0.8	-
161+	0	-	0.0	-

Table 5: Frequency of capture at different distances for Micromys at Studland.

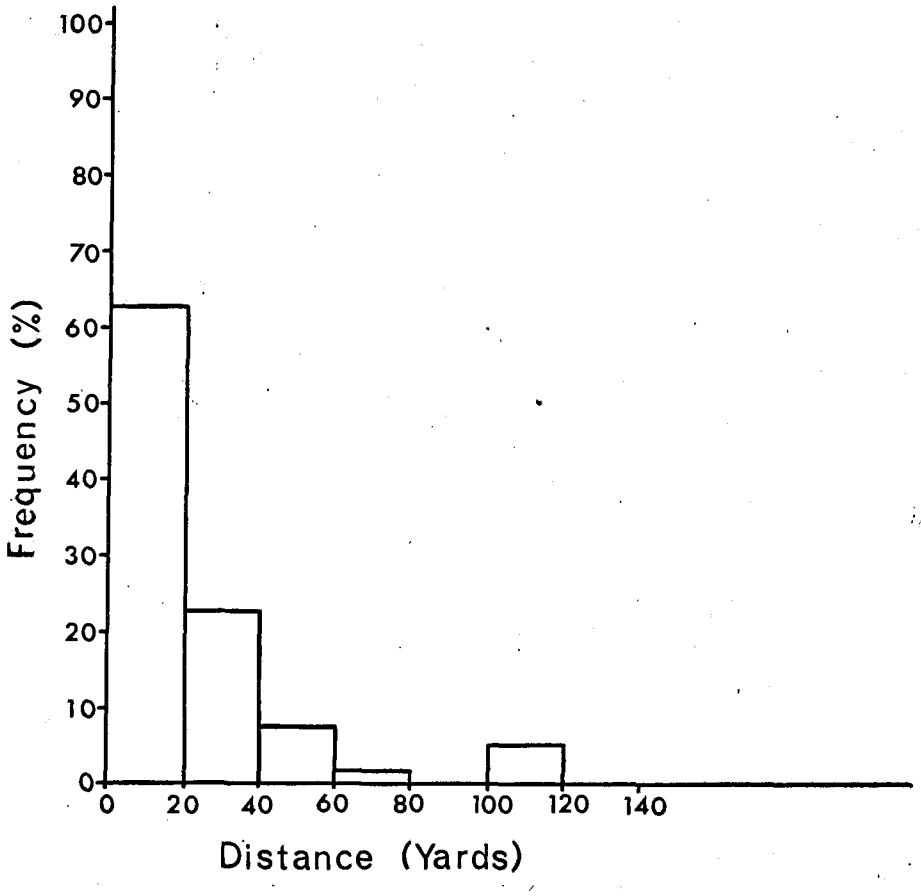
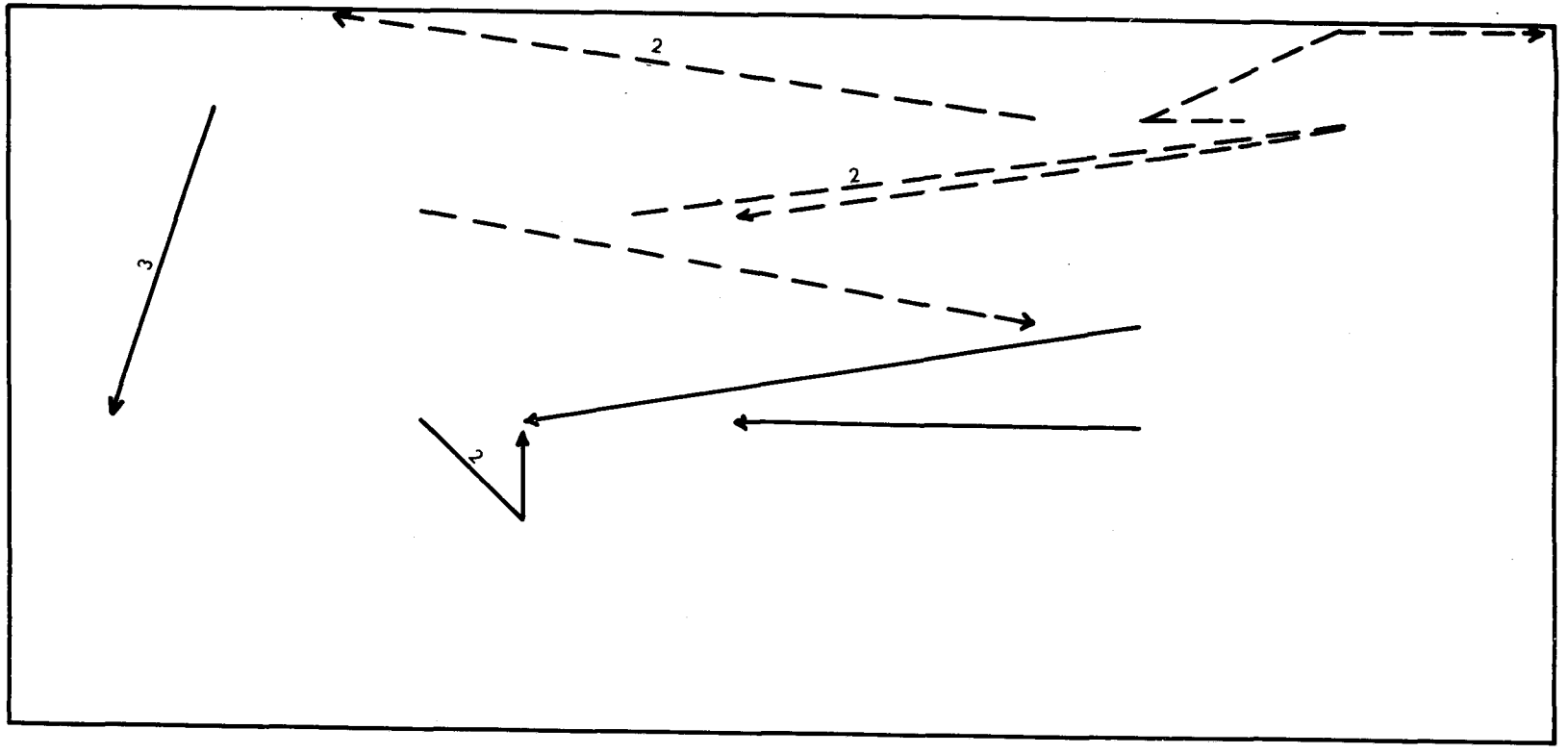


Fig.8: Adjusted frequency distribution of number of movements at each interval of distance shown for animals at Studland.

Fig. 9: Movements and points of capture of those Micromys and Apodemus caught more than once on the grid at Studland in January, 1964.

In Figs. 9-13 the time between each point of capture is one day (24hrs) unless otherwise stated.

Scale:- ½" = 10 yards.



Apodemus sylvaticus

Micromys minutus

Fig. 10: Movements and points of capture of some Micromys caught more than once on the grid at Studland in March, 1964. Some mice have been omitted for the sake of clarity.

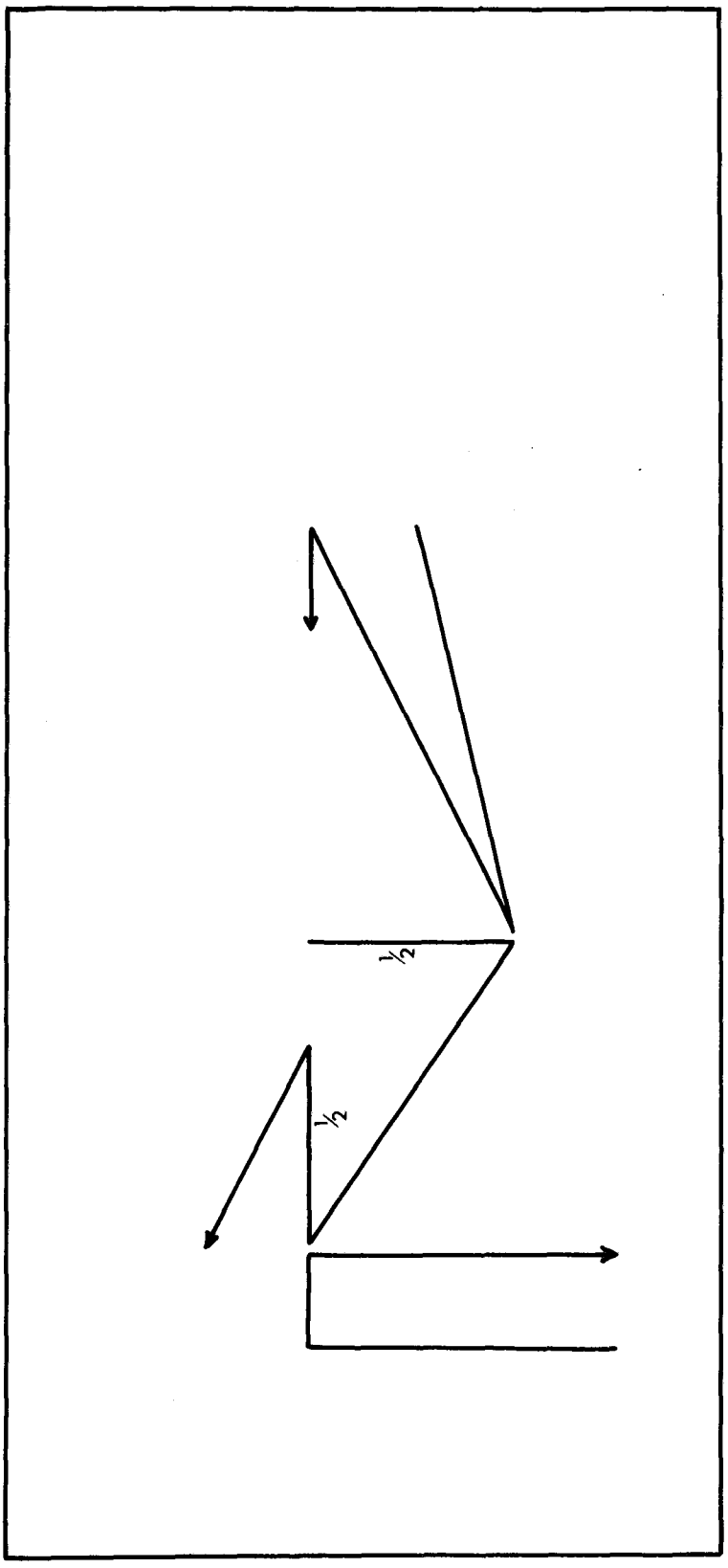

½
½

Fig. 11: Movements and points of capture of Micromys caught more than once on the grid at Studland in April, 1964.

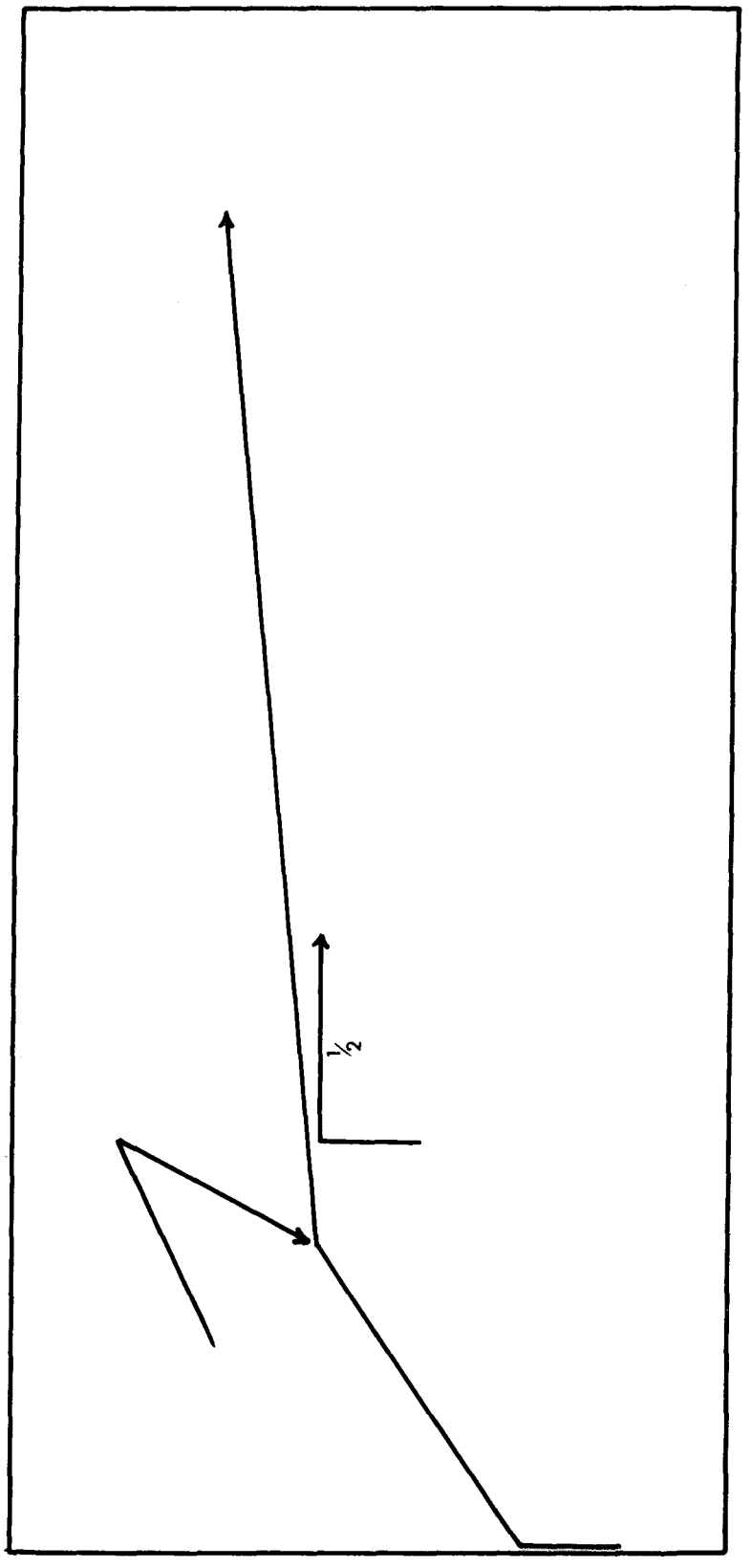

½

Fig. 12: Movements and points of capture of Micromys caught more than once on the grid at Studland in November 1964,

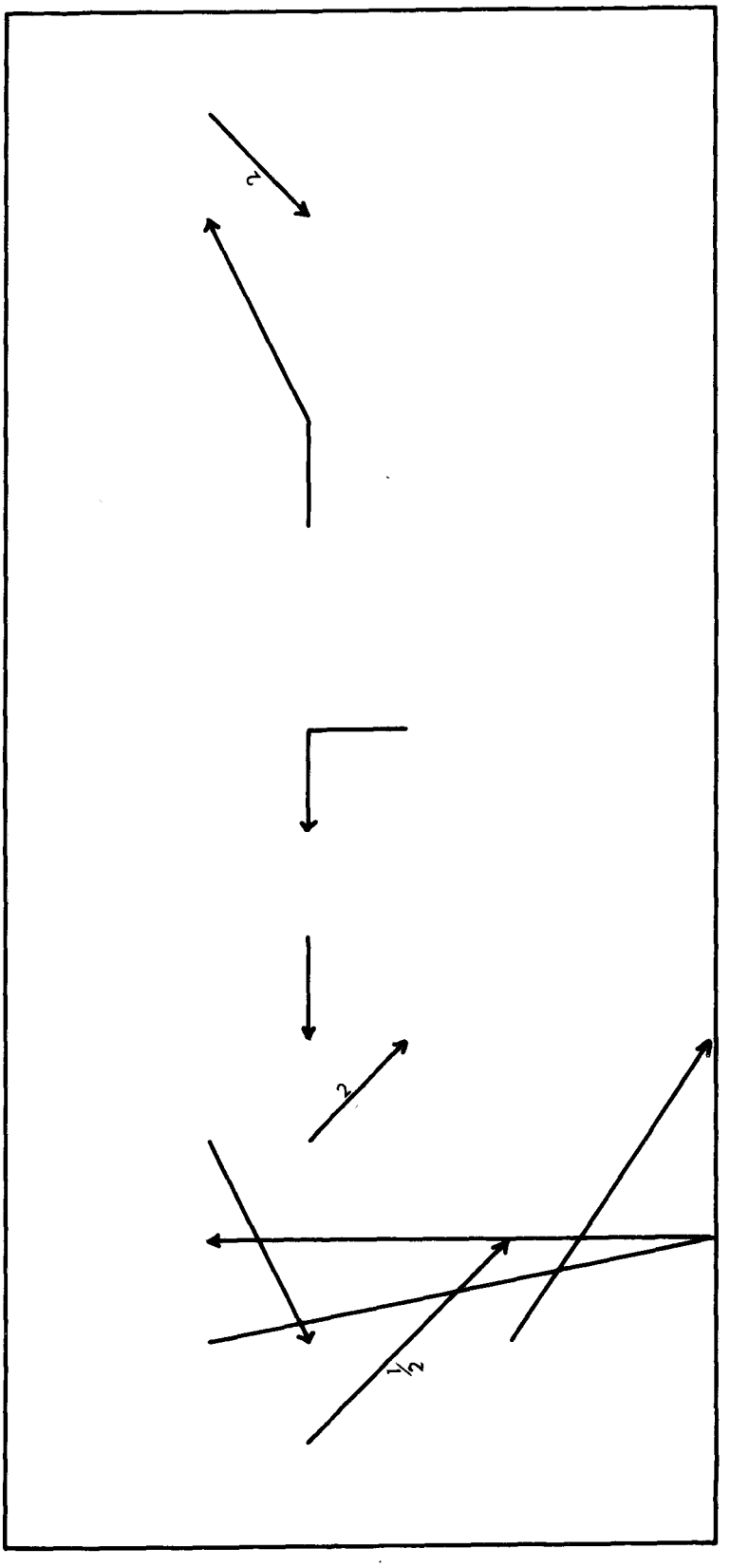
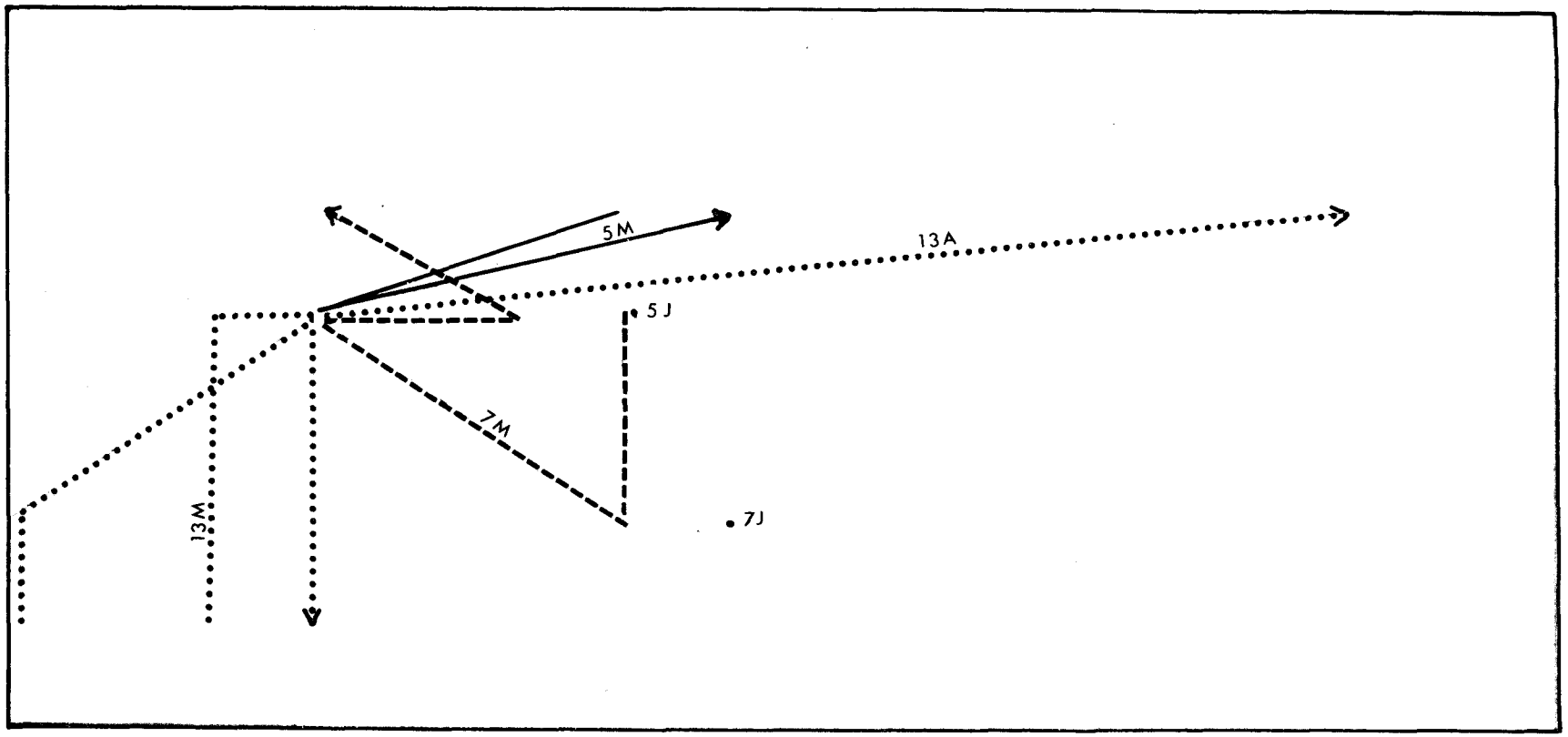

2
2
½

Fig. 13: Movements and points of capture of those Micromys caught during two month's trapping. The figures refer to the individual mice, and the letters stand for the different months, i.e. J = January, M = March, A = April.


5M
13A
5J
7M
13M
7J

is considered, it will be seen that 93.0% of the movements of Micromys at Studland were less than 60 yards.

Figs. 9-12 show the extent of the movements of the mice caught more than once in each month at Studland. Although it would be unreliable and misleading to attempt a calculation of home range from the small number of recaptures obtained, consideration of Figs. 9-12 suggests that the home ranges of different mice may overlap. On a few occasions, both traps set at one position were occupied at the same time, and lines joining successive points of capture for one mouse sometimes cross those joining such points for another.

Fig. 13 shows the points of capture and range of movements for each mouse caught in more than one month. Broadly speaking, the mice inhabited the same area of the grid from one month to the next, indicating that their home range had changed little if at all.

(iii) Results at Romsey

Individual harvest mice were caught more frequently at Spursholt Farm than they were at Studland and it is more reliable to use these data for calculation of home range. However, the environment at Spursholt Farm was rather different from that generally described in home range studies in that it was closely bounded on two sides. The mice were caught in a hedgerow bordered

on one side by a very busy main road and on the other by an open ploughed field. Though there is one record of a mouse crossing the road, their absence from traps set on the other side suggests that this was an unusual occurrence. Traps set at the edge of the field also caught nothing. The mice, therefore, lived in a strip of vegetation at most two yards wide, and the trapping of marked individuals almost every day in this hedgerow indicated that they wandered from its shelter seldom if at all. Only four mice were repeatedly captured here and the frequency distribution of their movements are shown in Table 6 and Fig. 15. All recaptures were within 60 yards of the last one. In view of the shape of the habitat, there seems little point in expressing the home range as an area, so the total range over which all the animal's movements took place is calculated. Stickel (1954), using artificial populations, found that the estimates are more accurate if half the distance to the next trap is added to the length of range over which the animal moves,and this is carried out here. The total length of the range, adjusted as described, together with the number of captures for each mouse,are shown in Table 7
The length of range for Micromys no. 3 almost certainly includes a dispersal movement because between the last three captures the animal covered long distances (60, 30 and 20 yards) and moved always in the same direction. The first two are the most reliable

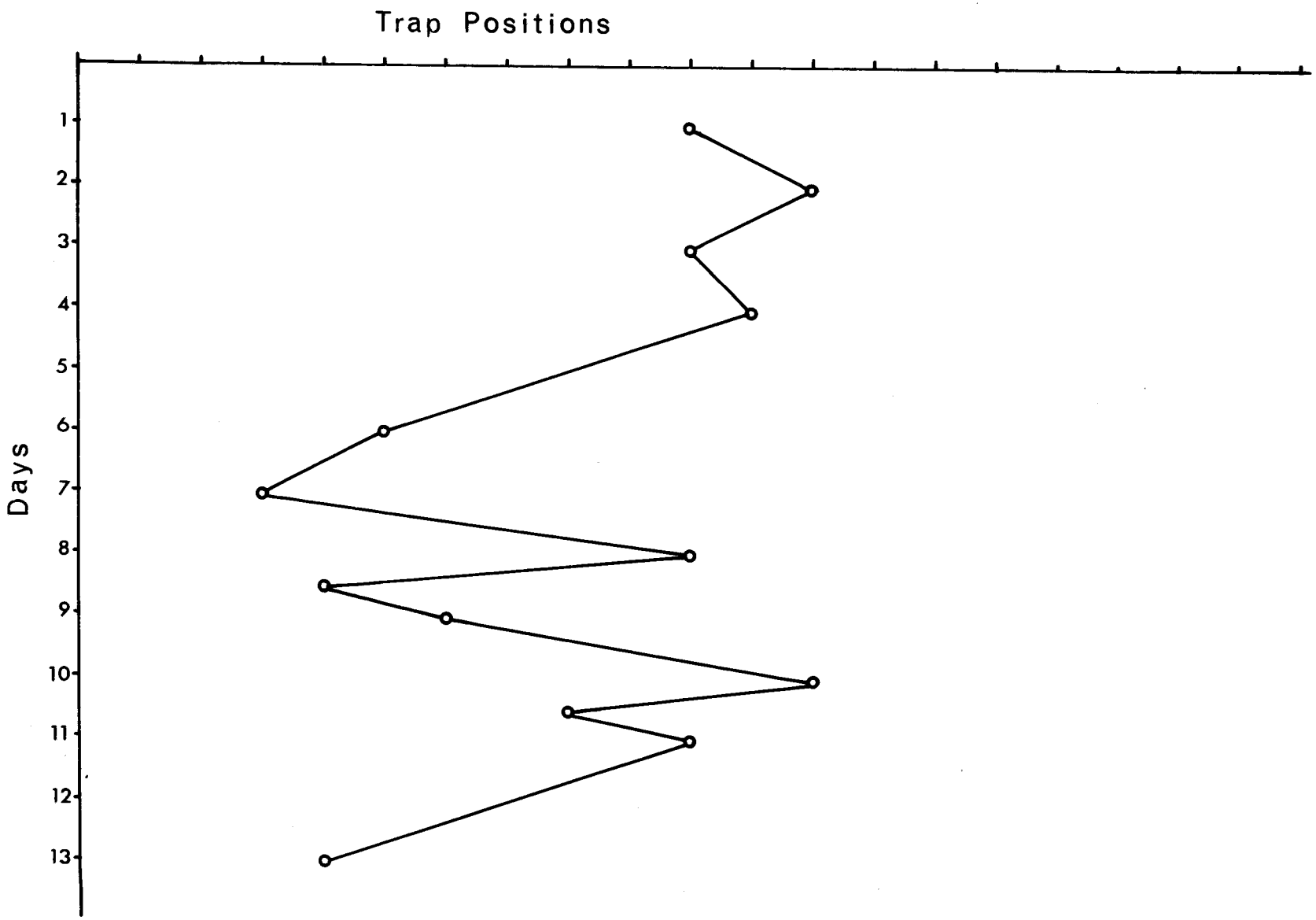
Distance (yards)	Observed frequency		Probability of capture	Adjusted frequency
	No.	%	%	%
0-10	11	42.3	26.4	28.8
11-20	7	26.9	24.8	19.7
21-30	5	19.2	19.9	17.6
31-40	2	7.7	14.6	9.7
41-50	0	-	8.9	-
51-60	1	3.0	2.9	24.4
61-70	0	-	1.3	-
71-80	0	-	0.7	-
81+	0	-	0.0	-

Table 6: Frequency of capture at different distances for Micromys at Spursholt Farm, Romsey.

Mouse No.	No. times captured	Adjusted range length (yards)
1	13	50
2	6	70
3	8	140
4	8	45

Table 7: Adjusted range length for Micromys at Spursholt Farm, Romsey.

Fig. 14: Movements of female harvest mouse no.1 in the hedgerow at Spursholt Farm, Romsey, from February 27th. to March 10th. 1966. The traps were spaced five yards apart.


Trap Positions
Days
1
2
3
4
5
6
7
8
9
10
11
12
13

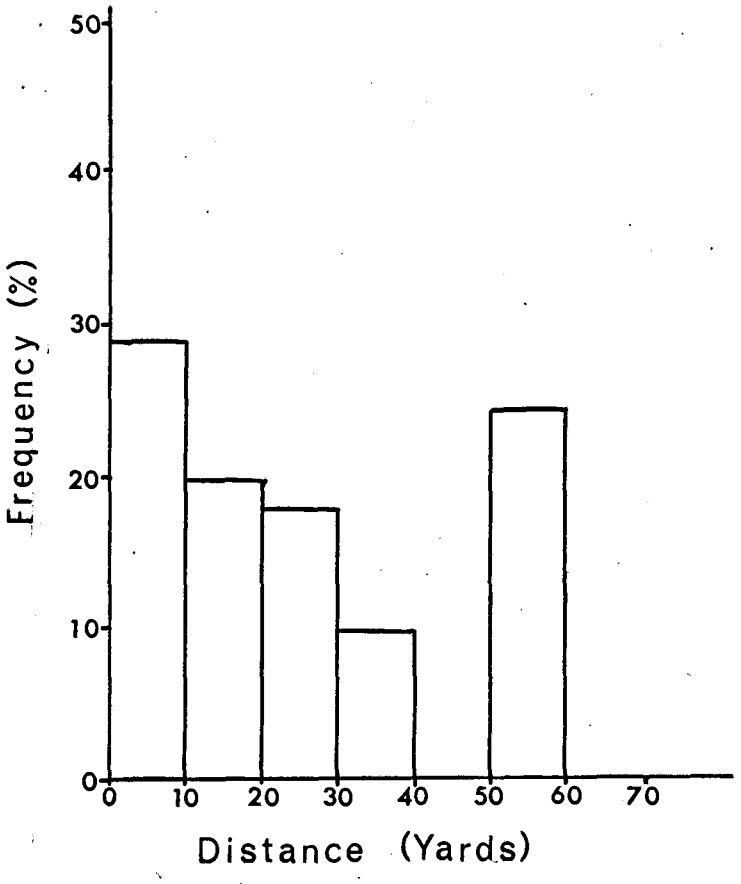


Fig.15: Adjusted frequency distribution of number of movements at each interval of distance shown for animals at Spursholt Farm, Romsey.

estimates of home range because the animals moved backwards and forwards within these limits a number of times. The movements of mouse (1) are shown in Fig. 14 and it is apparent that its daily points of capture were between five and thirty yards of the previous one.

(iv) Discussion

It has already been mentioned that the number of times an animal is recaptured will affect the estimate of home range size. A number of other factors will also influence this estimate. One, for example, is trap spacing. If the traps are set too close together few long movements will be recorded, and if they are set too far apart, the results will include mainly the few, probably unrepresentative, animals that move over those distances. It is probable that the shorter length of movements between captures in the hedgerows, compared with those recorded at Studland, is due largely to the much closer spacing of the traps at Romsey (one every five yards instead of two every twenty yards). For each species of small mammal there will be an optimum trap spacing which can be used only after the approximate range of movements has been determined.

Another factor influencing the estimate of home range is the trapping period, which must not be so long that the animals move to new sites within the home range and thus give estimates that

are too large (Kikkawa 1964). Furthermore, care must be taken not to include dispersal movements within the estimate of home range. Kikkawa (1964) found that a large proportion of an Apodemus population showed wandering and dispersal movements, and he concluded that it was more important to know the proportion of the population showing these movements according to age, sex, season, habitat, and density, than to obtain the average range size.

Clearly the above points apply when the movements are analysed on a frequency distribution or range length basis, as in the present study, as well as when areas of home range are defined. For the above reasons, true range size is difficult to determine and when measurements of home range or range length are obtained, strictly speaking they can only apply to the animals in question at the particular time and in the particular habitat in which the data were collected. However, bearing these factors in mind, where similar methods of estimation are used, comparison of estimates may be made.

There are no figures published for range of movements of Micromys, but comparison may be made with those obtained for other British small mammals. Brown (1956a) found that 92% of Apodemus and Clethrionomys in mixed woodland moved less than 60 yards, while 92% of Microtus in grassland moved less than

30 yards. These figures were not adjusted according to the probability of capture. Miller (1958), whose figures are adjusted, found 92.3% of Apodemus in woodland moved less than 60 yards. All these figures are for males and females combined because, although the authors distinguished between the sexes, it was felt in the present study that the data were not sufficient to provide a reliable measure of any difference between the sexes. Shillito (1963) working on Sorex araneus in woodland, however, found considerable differences in the ranges of males and females. Although some females moved their range at the beginning of the breeding season, once established all their movements were less than 61 yards. The movements of the mature males were so large that they often left the trapping area; however, movements of up to 157 yards were recorded. It would appear, therefore, that of the five species concerned, Microtus has the most restricted range while Micromys, Apodemus, Clethrionomys, and Sorex araneus have similar ranges. However, as stressed above, under suitable conditions much longer movements may take place in all species and this especially applies to males during the breeding season. It must also be pointed out that the figures for movements of Micromys at Romsey are ground range and take no account of the vertical range of the animals. Micromys climbs vegetation and, although in March no breeding

nests would have been built, it is possible that the mice did climb to some extent in search of food. At Studland, the question does not arise because, with the exception of a few Ulex bushes, there was no tall vegetation in the area inhabited by the mice.

The comparative ranges of the small mammals given above can be related to their respective feeding habits. Microtus, which is herbivorous and lives amongst the grass that it eats, has a short range. Apodemus, Clethrionomys, and Micromys are omnivorous and have to search for their food over a wider area than Microtus. Sorex is a predator and might be expected to have the longest range of all; this seems to be true only as far as the males are concerned.

To sum up, it is evident that the ground range of Micromys is comparable with that of other British small omnivorous mammals.

6. General Conclusion on Field Work

As so often happens when a fresh problem is studied, the work on Micromys in the field has brought to light more problems than it has solved. However, some methods of attacking these problems may be suggested. Longworth trapping during

the summer months is particularly unrewarding and as an alternative the use of radioactive tracing methods is suggested. These would be particularly useful for the limited environment of the hedgerow. The small numbers of harvest mice caught compared with other small mammals has also been described by Bauer (1960), Saint-Girons (1955), Ursin (1952), Giban (1957) and Kulicke (1956). The diverse methods and traps used by these authors minimise the possibility that the small catches of harvest mice are due to unsuitable methods of trapping except that, in all cases, the traps were set on the ground. It is suggested here that setting traps on the ground is one of the main reasons why such small catches of Micromys are made during the summer. However, results at other times of the year, when there is little vegetation for the mice to climb, suggest that Micromys is normally rare. The recording of the animal's movements among the grass stalks is a problem that conventional trapping methods cannot solve. Radioactive tracing could help in solving this problem, or a modification of the smoked paper method of tracking small mammals on the ground as developed by Cross and Hedges (see Hedges, unpublished thesis) could conceivably be used.

C. Ecological Experiments in the Laboratory

It has been reported that the harvest mice that do not get carried into grain ricks during the winter, live in burrows in hedgebanks and similar places (White 1789, Matthews 1952, Knight 1963). However, it is not known whether the mice construct the burrows themselves or use those discarded by other species. The following experiment was conducted to investigate this point.

A special cage was constructed to accomodate a layer of soil 10" deep and 2" wide against the glass front so that any burrows could easily be seen. The soil used was soft, damp leaf-mould so that burrowing would be as easy as possible. In order to make conditions as natural as possible some earth was also scattered on the false floor of the cage and plenty of dry grass was provided, together with a log of wood. The cage was placed outside in case the animals' behaviour was influenced by the colder weather in winter. A pair of harvest mice (one male, one female) was introduced into the cage and immediately made a nest from the dry grass, situated on the ground partly beneath the log. This nest was not a woven structure like the summer nest but consisted merely of a heap of shredded leaves. The mice continued to occupy this nest for the next 10 days and made no attempts to build a burrow. The weather during this period varied from mild (c.15^{o}C) to very cold, with temperatures down to -5 ^{o}C at night and rising scarcely above

freezing during the day. At the end of this time the harvest mice were replaced by a male Apodemus sylvaticus which constructed a burrow during its first night in the cage. The field mouse was removed and the harvest mice re-introduced. At first the mice would visit the burrow but continued to live in their nest on the ground. However, after two days it was found that they had abandoned their old nest and taken up residence in the burrow. During the next six days they continued to use the burrow and even enlarged it a little by digging themselves. However, this activity resulted in the extension of the burrow by only 2 - 3" and certainly made no appreciable difference to the main structure. After three more days the burrow partly collapsed and the mice deserted it to return to their old nest on the surface. This experiment was repeated three times with a total of six harvest mice (three males, three females) and in every case the same sequence of events took place, with the mice showing little or no burrowing activity.

It had been observed in a previous experiment when a large piece of turf was provided, that the mice quickly made runways through the vegetation but not through the soil itself - these resembled vole runways. This work, then, shows that Micromys may use the discarded burrows of other species. Furthermore, they may make runways through the vegetation when this is sufficiently dense.

D. Predation

Little information is available on the predators of Micromys and it is generally assumed that it falls prey to the same animals (e.g. owls, small carnivores and foxes) as do other small mammals. Micromys remains turn up fairly regularly in the pellets of the barn owl, Tyto alba (Scopoli), and have also been recorded from those of the short-eared owl, Asio flammeus (Pontoppidan), and the long-eared owl, Asio otus (L.). However, the remains of the harvest mice are always present in much smaller numbers than those of other small mammals. For example, Czarnecki et al. (1955) collected the remains of 15,587 vertebrates from the pellets of the barn owl (Tyto alba) and found that Micromys formed 0.7% of the catch (Sorex araneus formed 16.9% and Microtus arvalis Pallas 52.8%). Again, Czarnecki (1956) found that the harvest mouse formed only 0.11% of the catch of the long-eared owl (Asio otus) in Poland.

It is possible that the small numbers of Micromys usually recorded in owl pellets are the result of the pellets being collected from owls which hunt over areas where the harvest mouse is scarce or absent. In order to test this hypothesis, it was necessary to collect owl pellets in areas where the harvest mouse was known to be present. Accordingly, 40 barn owl pellets were collected at Manor Farm, Studland, a farm on which

Animal	No.	%
Sorex araneus	19	14.7
Sorex minutus	24	18.6
Clethrionomys glareolus	8	6.2
Microtus agrestis	44	34.1
Apodemus sylvaticus	25	19.4
Mus musculus	4	3.1
Micromys minutus	5	3.9

Table 8: Number of animals (estimated from the presence of right dentary bones) found in *Tyto alba* pellets collected from Manor Farm, Studland.

harvest mice are frequently found in straw ricks and are also known to be present in the surrounding area.

The results of the analysis are presented in Table 8 and it will be seen that harvest mice formed 3.9% of the catch. Although the sample is fairly small, the figures obtained represent a greater proportion of the catch than those given by other authors. Evidently, in order to obtain a reliable estimate of the predation on an animal which occurs only in certain areas of its range, as Micromys appears to, it is necessary to collect the data in those areas. Whether the low proportion of Micromys caught is a reflection of a small population present in the area, or whether it is due to discrimination by the owls or some other factor, is not at all clear. If the owls are discriminating in some way against catching Micromys, it is difficult to see on what basis this could be done. Size, which is the most obvious factor, seems to be ruled out by the high catches of shrews. It seems most probable that the owls catch few Micromys because the animal is rare, a conclusion supported by the trapping results presented earlier.

IV ACTIVITY

A. Introduction

Every species of mammal has a pattern of activity in its day-to-day life. This pattern may take the form of a strong diurnal or nocturnal preference, or there may be periods of activity during both day and night. The cyclic nature of these periods has given rise to the concept of activity rhythms, and besides being geared to the natural rhythm of day and night, many small mammals also have a short-term rhythm of activity within each 24 hours. This short-term rhythm is thought to be a result of changes in metabolism causing resting and feeding at regular intervals. In practice, it is difficult to obtain reliable estimates of activity patterns of small mammals in the wild. Periodic trapping is the most generally used method in such studies and this has the disadvantage that, no matter how short a period elapses between visits to the traps, once the animal is caught it cannot do anything until released, and is unlikely in any case to continue with its normal routine. In view of these and other difficulties, most studies of activity rhythms have been carried out in the laboratory.

Laboratory techniques for the study of small mammal activity have been summarised by Chitty and Southern (1954). Such

techniques have included counting the revolutions of an exercise wheel, recording all movements in a cage mounted on springs, and registering the time that the animal passes from one compartment of a cage to another. This latter method has been quite commonly used (e.g. Crowcroft 1954, Miller 1955), but suffers from the disadvantage that activity taking place in the compartment is not recorded. Direct observation is undoubtedly the best method of recording the activity of an animal, provided that precautions are taken so that the presence of the observer is not disturbing. However, besides being time-consuming, it is not possible to use this method for continuous recording over several days unless a number of observers are available. Photography is a method combining many of the advantages of direct observation with continuous recording facilities. A photographic method of studying the activity of small mammals has been developed and used with Micromys as described in the following section.

B. Methods

(i) Direct Observation

Before the photography unit was brought into operation, the activity of four different mice under 15-hour day-length conditions was recorded by direct observation. The animals were observed in

four five-hour shifts and one four-hour shift spread over three consecutive days. The mice were housed together in one large cage (36" x 18" x 24") which contained a clump of growing wheat and had floors at two levels. Nest boxes were provided, and hay was spread on the floors.

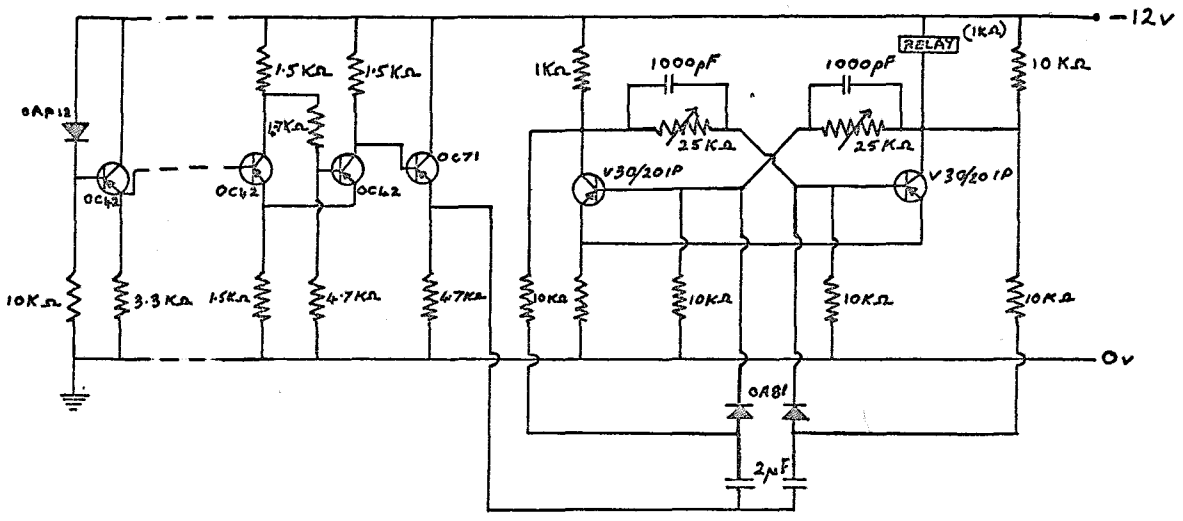
Some form of illumination was necessary so that the mice could be observed during the hours of darkness without disturbing their normal activity. Colour vision is apparently lacking in Rattus norvegicus (Prosser and Brown 1961), and it seems reasonable to assume that this is the case in murids generally. In fact, it has been reported that there are no cones in the eye of Mus (Scheer 1948). Therefore, a dim red light would provide suitable illumination for the observer, since, if Micromys has any visual acuity at all in such a light, it will be poor. A dim red light has been successfully used for watching Apodemus sylvaticus (Southern 1964) and a similar technique has been used in the present study.

(ii) Photography

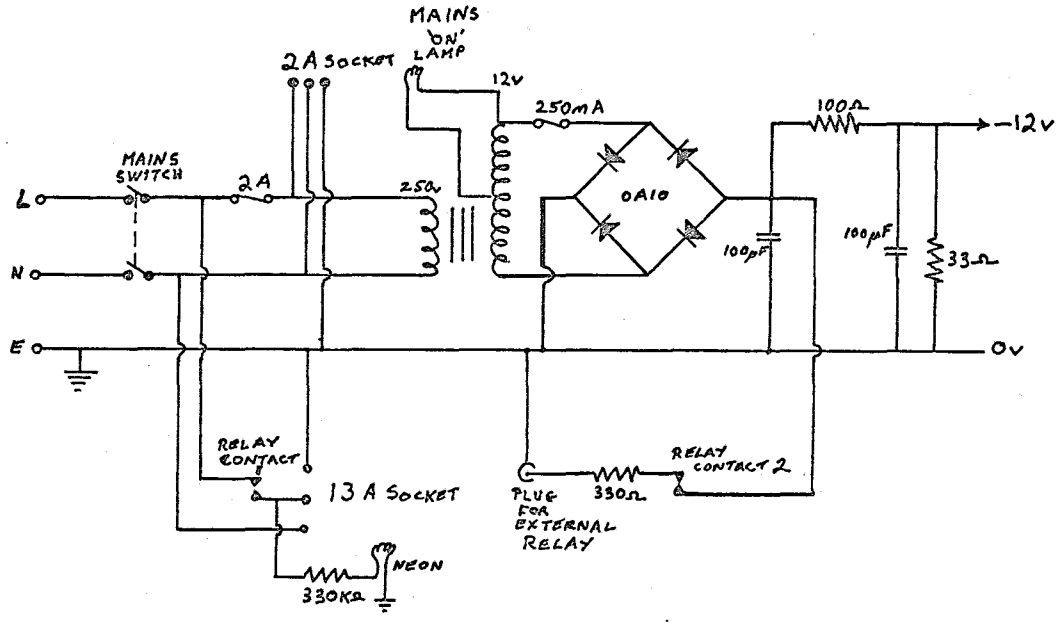
Preliminary observations showed that if a harvest mouse was provided with a small nest box leading into a large cage, the animal would spend much of its time in the cage doing nothing at all - usually just sitting on a piece of twig. Consequently,

if the passage of the mouse from the nest box to the cage was recorded and active periods taken as the time spent in the cage, considerable error would arise. Hence, it was necessary to know exactly what the mouse was doing in the cage, and to this end a time-lapse photography unit was set up which took one picture of the whole cage every minute all the time the mouse was out of its nest box.

A parallel beam of light was passed through a transparent perspex tunnel connecting nest box and cage and was focused on a photo-sensitive diode. This was connected to the camera via a switching apparatus, details of which are shown in Fig. 16. When the mouse passed along the tunnel from the nest box to the cage, the momentary interruption of the light beam caused the camera to be switched on. When the animal passed back into the nest box, it cut the light beam a second time and this switched off the camera. The tunnel was made just large enough for the animal to walk through, and was placed between the pair of convex lenses responsible for producing the parallel beam from the light source and focusing it on to the diode. Infra-red light was used in later experiments so that the mouse should not be startled by the light beam and withdraw to the nest box having switched on the camera. A photograph of the cage and tunnel is provided in Fig. 17.



A. Switching circuit.



B. Chassis wiring.

Fig.16 : Circuit diagram of switching apparatus.

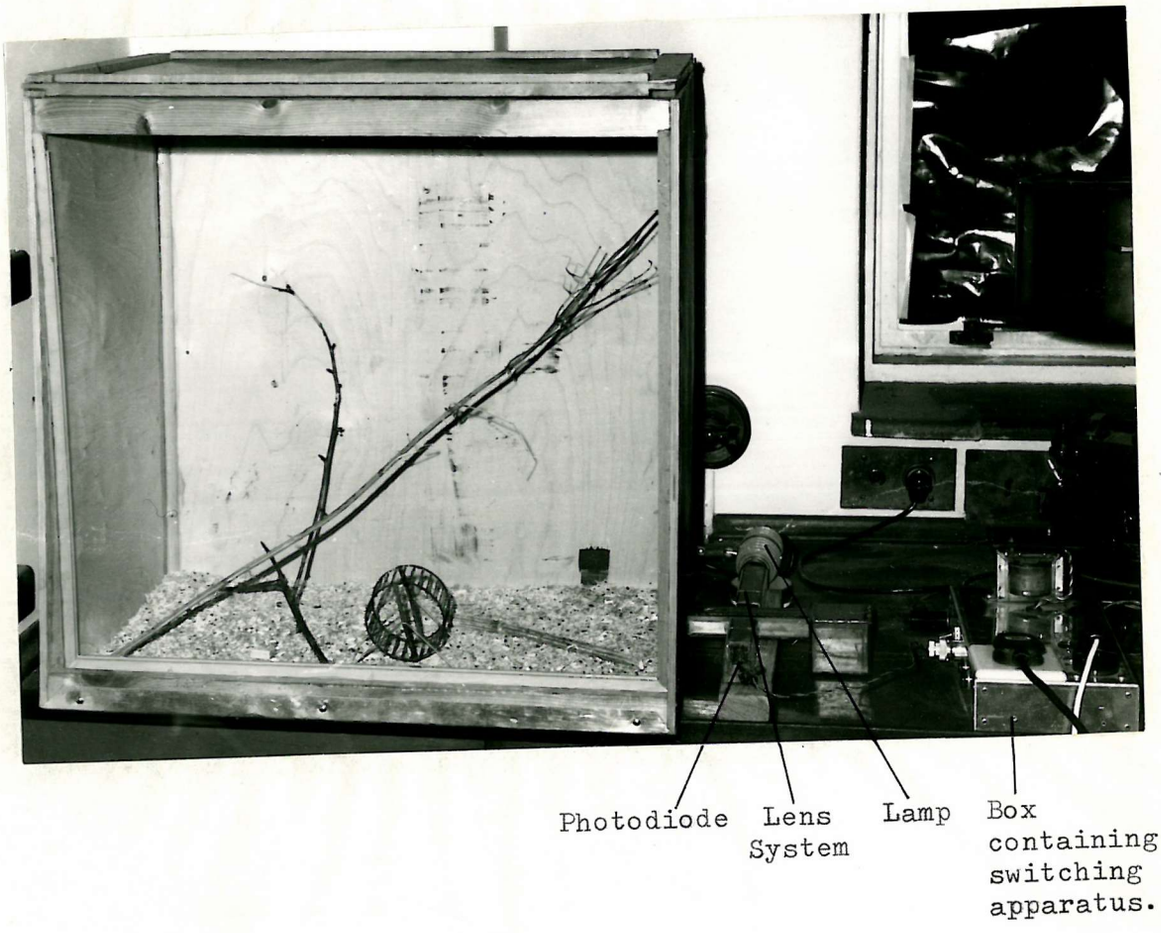


Fig. 17: Activity cage and associated equipment.

The photographic apparatus used was a Vinten Scientific Camera Mk.III with a 200 ft. magazine and Vinten associated equipment of a control box and intervalometer. A 15 mm Dallmeyer wide-angle lens was fitted to the camera which was placed at such a distance from the cage that the latter (measuring 24" x 18" x 24") filled the picture. Kodak 16 mm Plus X negative film was used and the pictures were examined one by one by placing the film in an ordinary enlarger. An electric clock was placed at the back of the cage to give the time each picture was taken. Lighting was provided by Metz electronic flash equipment synchronised with the camera shutter and placed about 12 feet from the cage. Besides the camera and associated instruments, the switching apparatus also activated a relay connected to a pen writing on a kymograph drum. This was principally used to determine the effect of the flash on the activity of the mouse, for the kymograph could be used to record the time spent by the mouse away from the nest box when the camera and flash gun were switched off and when they were working. The flash and the noise made by the camera apparently did not affect most of the mice. Those that did react at first reduced the amount of time spent in the cage, but soon grew accustomed to these effects and their activity returned to normal after 36-48 hours.

Investigation of the activity of the mice under different light conditions, so as to correspond to those at different seasons of the year, were undertaken. Day-lengths of 9, 12 and 15 hours duration were provided by three 150-watt lamps controlled by a time-switch. The light thus provided was checked by an exposure meter and found to be of a similar intensity to that on a bright day outdoors.

Experiments were carried out with a total of five harvest mice (three males, two females), four of these being used at all day-lengths and the fifth at 12 hours only. All the mice were subjected to the prevailing light conditions together with the camera and flash for at least two weeks before the recording began. One mouse was then placed in the activity cage and allowed to become accustomed to it for three to four days. The activity of each mouse was filmed continuously for 48 hours, and when all had been recorded at the particular day-length, this was changed and the mice given another two weeks to become accustomed to the new day-length. In all experiments the cage contained twigs and an exercise-wheel, as well as enough food and water to last for the whole of the recording period.

Throughout the experiments the animals lived in a room with a fairly constant temperature about 20°C. In the following discussion, 'dawn' and 'dusk' are the times that the lights were

switched on and off respectively.

C. Results

The activity of the four mice recorded by observation is shown in Fig. 19. The number of minutes each mouse was active in each hour have been added together and expressed as a percentage of the total activity possible, i.e. 240 minutes in each hour. It will be seen that a high level (up to 100%) was maintained during the hours of darkness, and that it dropped sharply at dawn and rose abruptly at dusk. A variable level of activity was recorded during the day with a peak of 66.7% between 13.00 and 14.00 hours. Day-time activity was 39.2% of the total.

The activity of the mouse recorded by the camera over 72 hours at the 12-hour daylength only is shown, expressed as above, in Fig. 18. A high level of activity was maintained during the latter half of the night but less took place between dusk and 24.00 hours. The amount of daytime activity was generally small (20.7% of total), with two minor peaks between 09.00 and 10.00 hours and between 13.00 and 14.00 hours. The onset and cessation of activity was not as synchronised with dusk and dawn as it was with the animals in the observation cage, since some activity took place during the hour after dawn and in the two hours before dusk.

When considering the photographic record, the problem arose

of determining whether the mouse was active or inactive when it appeared not to have moved its position in successive photographs. Direct observation showed that the mice were rarely if ever inactive on the ground, and when they remained in one place for several minutes they were in fact doing something - eating or grooming for example. Examination of the photographic record revealed that the mice never remained in one place on the ground for more than 15 minutes, and feeding periods could last as long as this. Hence, all the time the mice were on the ground they were recorded as 'active'. They were recorded as 'inactive' if they sat stationary on one of the pieces of twig for more than two consecutive frames. Thus, they may have been recorded as 'inactive' when they were grooming themselves whilst sitting on the twig, but, since this activity rarely lasted more than two or three minutes, it is not thought that this procedure introduced any large error. The mouse was also recorded as 'inactive' when it was in its nest box i.e. out of the cage with the camera switched off.

A more detailed presentation than that used for the other results has been adopted for the four mice used in the complete series of day-lengths. Each 24 hour period is divided into 12-minute intervals and the number of minutes that the mouse was active in each 12-minute period has been determined. This method is used because plotting the results as activity in a

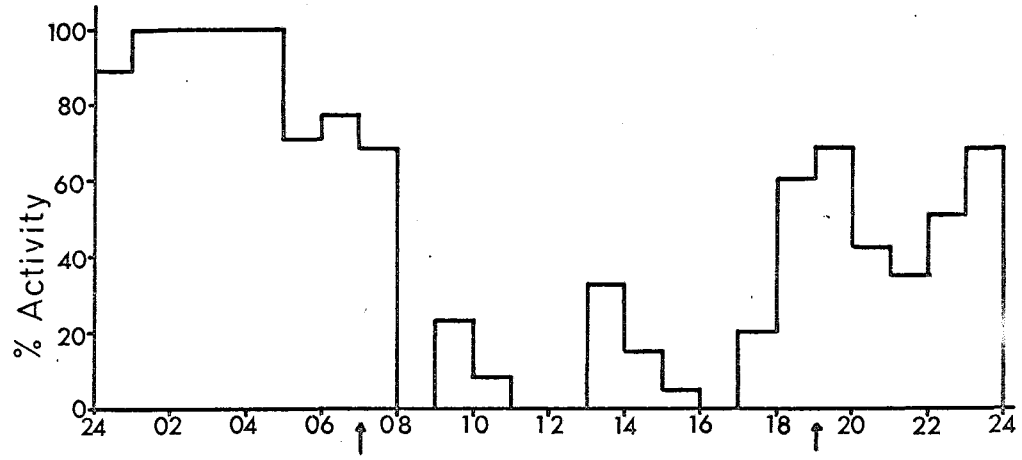


Fig.18 : Summed activity of Mouse E over 72hrs. on a 12-hour day-length. Arrows indicate the onset of day and night.

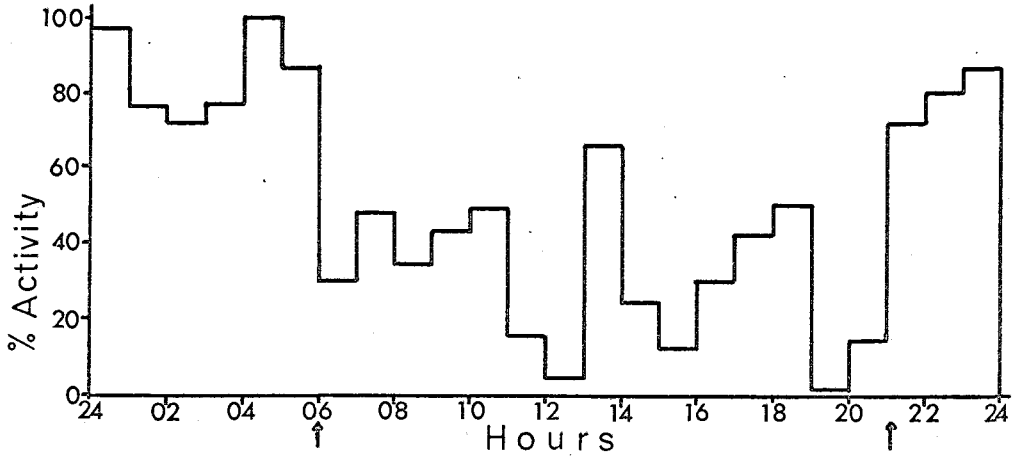


Fig.19 : Summed activity of 4 mice over 24hrs. on 15-hour day-length, recorded by direct observation. Arrows indicate the onset of day and night.

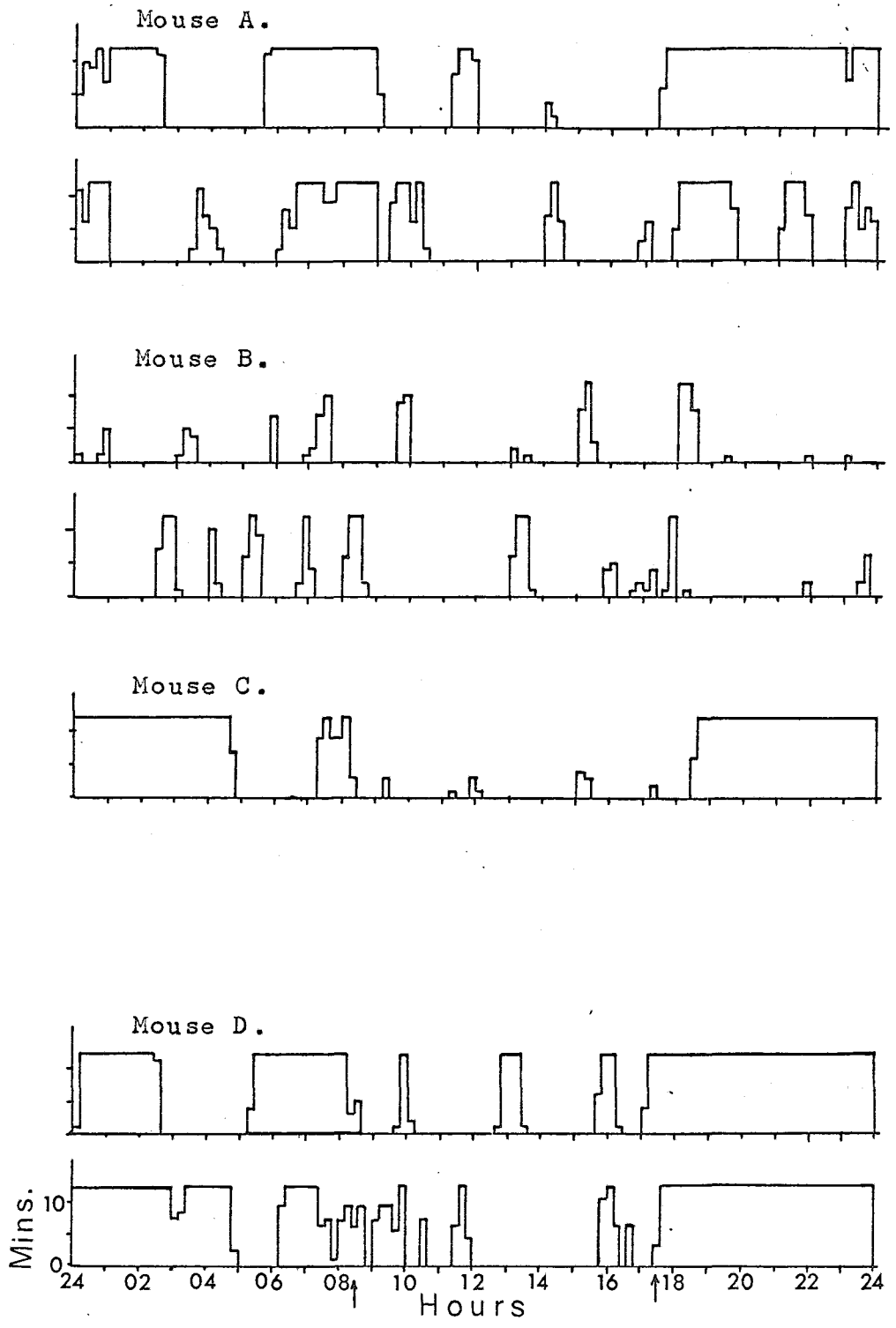


Fig. 20: Activity of individual mice A,B,D over 48hrs. and mouse C over 24hrs. on a 9-hour day-length. Arrows indicate onset of day and night.

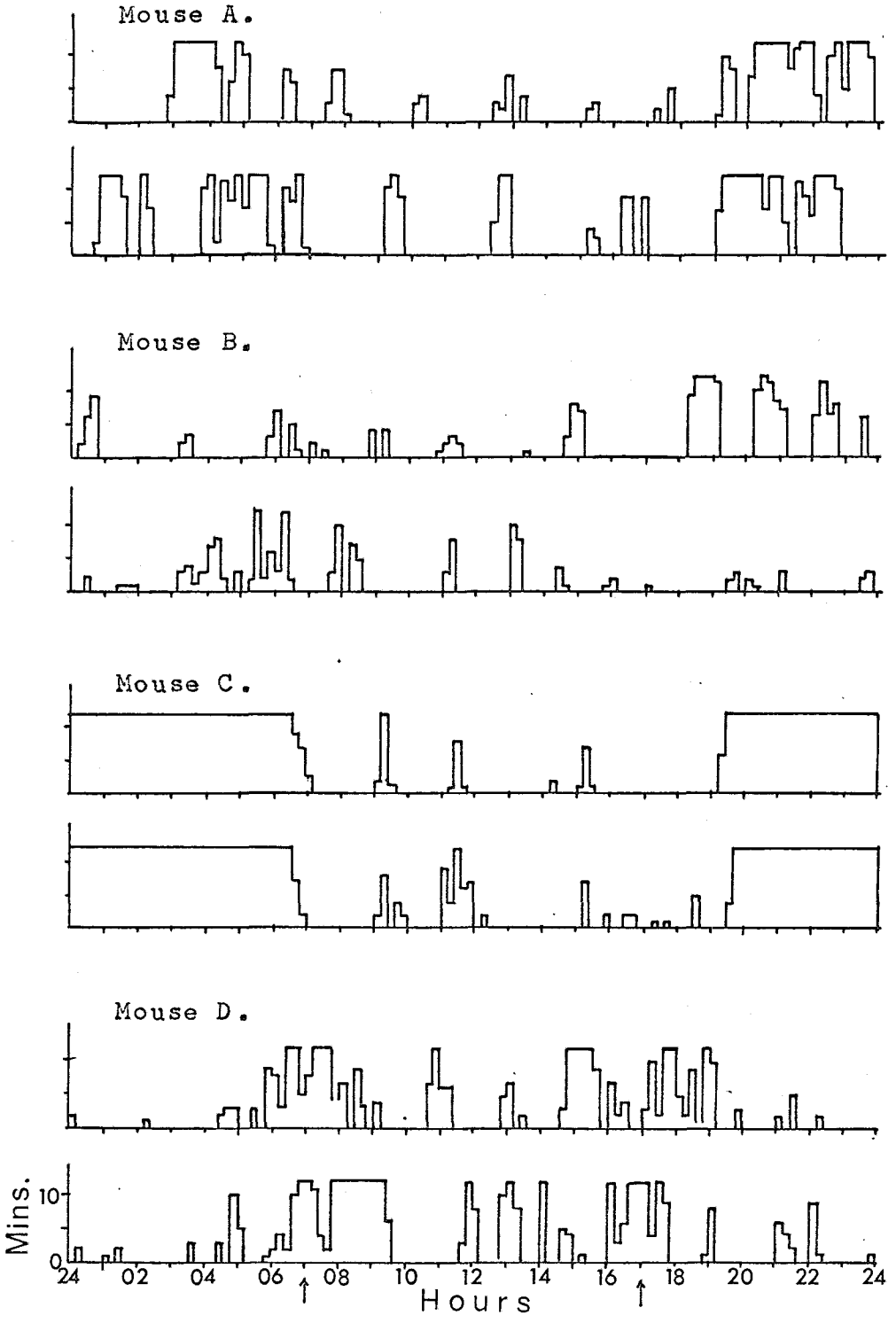


Fig.21: Activity of individual mice A-D over 48hrs. on a 12-hour day-length. Arrows indicate onset of day and night.

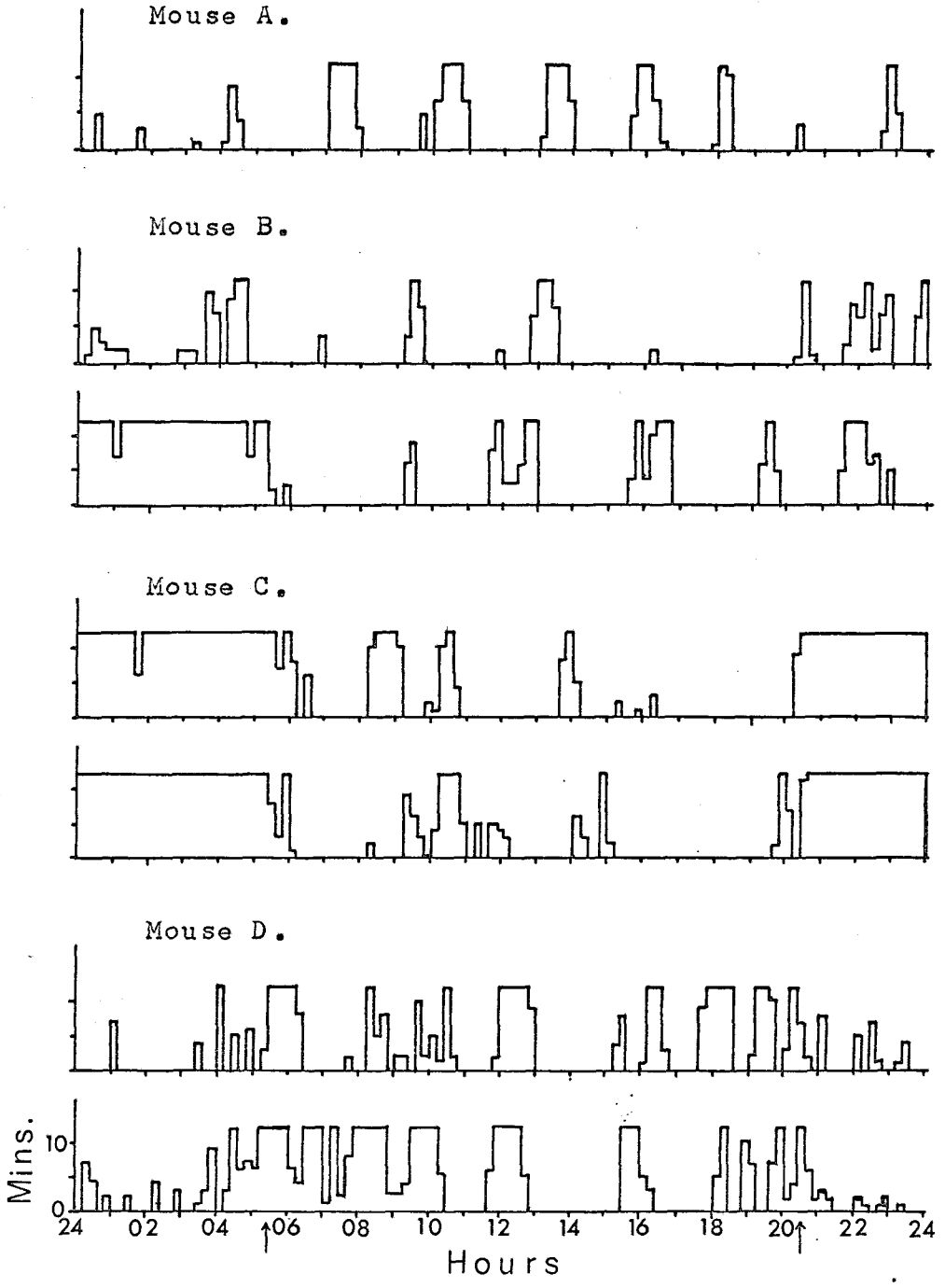


Fig.22: Activity of individual mice B-D over 48hrs. and mouse A over 24hrs. on a 15-hour day-length. Arrows indicate onset of day and night.

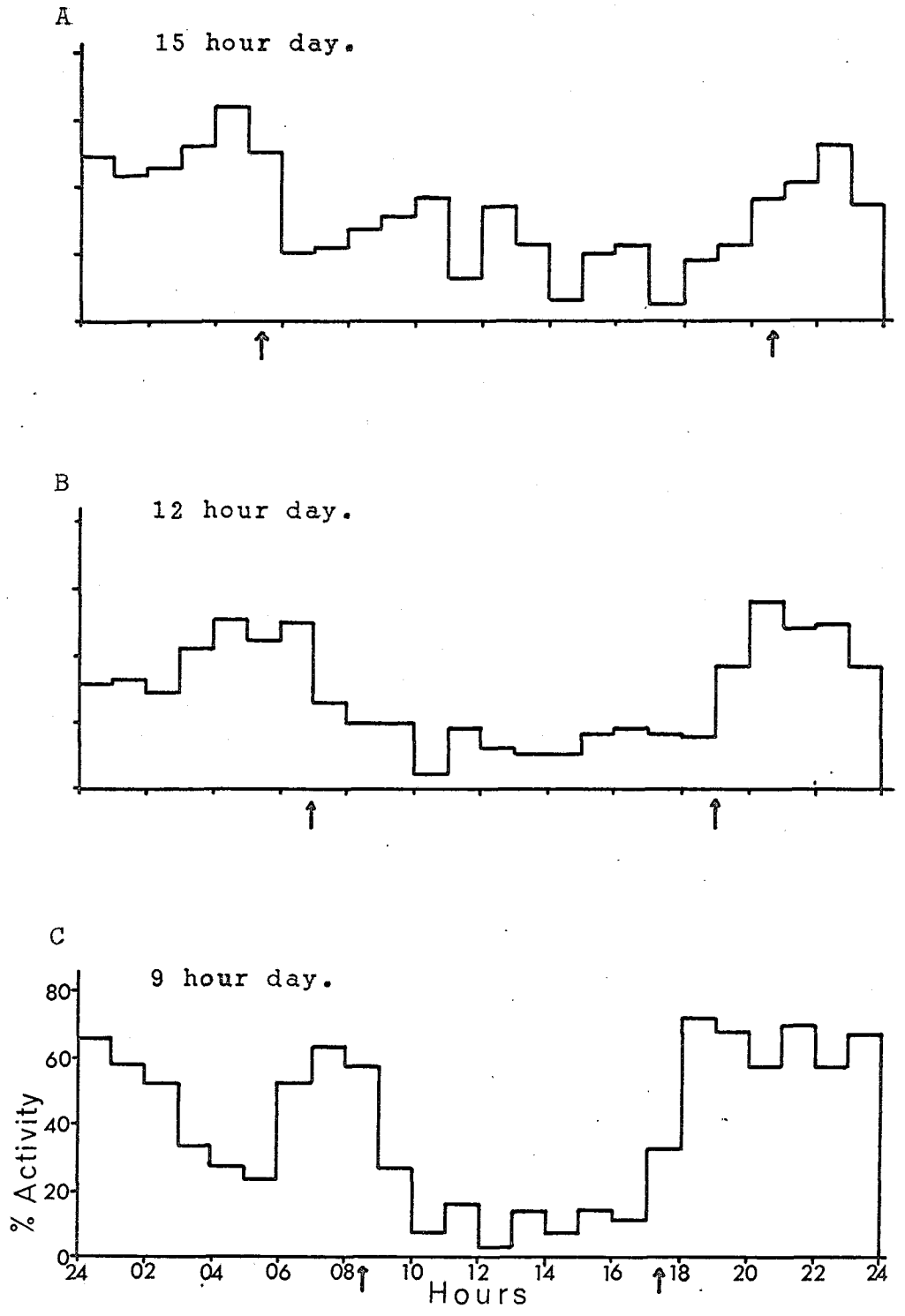


Fig.23: Summed activity of mice A-D over 48hrs. on day-lengths of 9, 12, and 15 hours. Arrows indicate onset of day and night.

larger unit such as one hour could mask any shorter rhythm. The complete 48-hour run for each mouse at different day-lengths is shown in Figs. 20-22. Because of technical difficulties, 24-hour runs only were recorded for mouse A at 15-hour and mouse C at 9-hour day-lengths. The runs for each mouse are added together and plotted as a percentage of the maximum possible activity per hour for the different day-lengths in Fig. 23. This is done to smooth individual variation and for comparison with the other results.

Examination of Figs. 20-22 shows that there is considerable individual variation in both the intensity and the time of activity under all day-length conditions. Under the 9-hour regime the activity of mice A, C and D is fairly similar with much activity in each case during the hours of darkness. Mouse B, however, shows rather less activity altogether, particularly between 19.00 and 02.00 hours. The duration of the activity periods is generally much less during the day. There is an increase of activity at, or just after, dusk, and a decrease at, or just before, dawn. When the activity of the different mice is summed, as in Fig. 23C, the picture becomes clearer. Activity rises to a maximum of 72% about half an hour after dark, and remains at a fairly high level until about 01.00 hours when it begins to die away, only to rise to a second peak of 63% in the period around daybreak. It then decreases and remains at a low

level during the day, with only 15.2% of the total activity taking place during daylight hours.

When the day-length is increased to 12-hours, Mice A, B and C have a rhythm similar to their 9-hour one. Mouse D however, loses its nocturnal preference and is most active during the day. Summation of the activity of all four animals produces the result shown in Fig. 23B. There is a peak of activity just before dawn and one just after dusk, and the percentage of the total activity taking place during the day has risen from the 9-hour day-length figure of 15.2% to 27.9%. Much of the day-time activity is due solely to mouse D. Both peaks of activity are lower than on the 9-hour day, but again that in the hour about dusk (57%) is a little greater than that just before dawn (46%).

During the 15-hour day-length series (Fig. 22), mouse A joins mouse D in being mainly diurnal, but mouse C continues to be strongly nocturnal, starting its activity later and finishing earlier to fit in with the day-length conditions. The summed activity (Fig. 23A) shows a bimodal distribution, with a peak of 64% just before dawn and one of 53% one and a half hours after dusk. The day-time activity is 44.8% of the total, and there are three fairly well-defined minor peaks at 10.00, 12.00, and 16.00 hours.

The total activity of mice A - D at all three day-lengths

is shown in Table 9. In an analysis of variance test on these data (Table 9), $F^2_7 = 0.154$, $P > 0.1$, which indicates no significant effect of changing day-length on total activity. Though the magnitude of the individual variation may be largely responsible for this result, no consistent trend with changing day-length can be detected for individuals.

Table 10 summarises the results of all the activity experiments.

From examination of the detailed 48-hour records it is difficult to discern any consistent short-term rhythm of rest and activity. In order that any such rhythm might be more easily displayed, the data are rearranged as follows. The duration of each period of rest of each mouse was measured and expressed in 12-minute units. Because the records of each individual last for only 48 hours at each day-length, the duration of periods of rest for all four animals are summed at each day-length. This operation hides any individual variation but results in larger figures to compare in order to detect any change in the pattern of rest periods at different day-lengths. The frequency of occurence of rest periods of different lengths is calculated and shown in Table 11. The use of the 12-minute unit introduces the possibility of an average underestimate of 12 minutes and a maximum underestimate

Mouse	Day-length(hours) 9	12	15
A	19.78	14.38	
B	5.28	6.18	12.22
C		24.70	23.18
D	28.52	12.02	14.65

Source of variation	Sums of squares	Degrees of freedom	Mean squares	Variance ratio
Day-length	22.99	2	11.49	0.154
Residual	521.13	7	74.45	
Total	544.12	9		

Table 9: Total activity (in hours/48 hours) of Micromys A-D under different day-lengths.

Mice	Day-length (hours)	Mean 24hr activity/ mouse (hrs)	Day-time activity (%)	Activity peaks (%)	
				Dawn	Dusk
	9	9.55±2.48	15.2	63	72
A-D	12	7.16±1.93	27.9	46	57
	15	7.32±1.55	44.8	64	53
E	12	11.4	20.7	75	65
F-I	15	12.35±0.22	39.2	80	100

Table 10: Summary of experiments on the activity of all mice. For mice A-D, which were recorded over 48 hours, column 3 is the mean (±S.E.) 24hr activity/mouse of the mean 24hr activity of each mouse.

A-D Mice photographed at all day-lengths.

E Mouse " " 12-hour day-length.

F-I Mice observed at 15-hour day-length.

No. days	Day-length (hrs)	Duration of rest periods in 12-minute units																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20 or over
7	15	22	10	6	5	3	4	2	5	2	5	4	2	3	1	0	1	0	0	2	1
8	12	26	9	11	7	10	3	5	3	6	6	4	3	1	1	1	0	0	1	0	0
7	9	5	5	4	6	5	2	2	1	3	6	2	4	1	1	2	1	2	0	1	1

Table 11: Frequency of occurrence of rest periods of different lengths. Compiled from mice A-D at each day-length.

of 23 minutes in the duration of any period of rest. Allowing for this, it is clear that under 15 and 12-hour day-lengths the usual period of rest is of fairly short duration, lasting 12 minutes (or less), though 62% last up to 60 minutes, and a few over two hours. Under a 9-hour day-length, however, the duration of rest periods is not concentrated at 12 minutes but spread fairly evenly up to 144 minutes. The longest period of rest recorded at any day-length was 22 12-minute units, or, more precisely, 284 minutes, since the mouse was active for one minute in the 12-minute period at each end (see Fig. 22, Mouse C). The actual number of rest periods is less at the 9-hour day-length (54) than at the 12 or 15-hour day-lengths (97 and 78 respectively). This is due to the fact that both rest and activity periods are generally longer at the shortest day-length, especially for mice A, C, and D.

Due to the large cage, the image of the mouse on the film was so small that, when the animal's position on the ground did not change, it could not be determined whether it was feeding or performing some other activity (see Fig. 24). Consequently, examination for evidence of a feeding rhythm was made on the records obtained by direct observation. The length of time occurring between two successive periods of feeding is split into 6-minute units in order to smooth the data, and any break

of six minutes or less is taken arbitrarily as being part of the same period of feeding, i.e. is not used in the analysis. The frequency of occurrence of feeding periods of different lengths is shown in Table 12, and it will be seen that the majority of intervals between feeding last from 6 - 12 minutes. Feeding occurs most frequently during periods of activity and the longer intervals represent periods of rest.

D. Comparison with other small mammals.

It has been known for many years that Micromys is partly diurnal but little detailed work has been carried out. In one study it was found that the mouse was completely nocturnal when constantly supplied with food, but that it would come out during the day if food was withheld during the night (Saint-Girons, 1959). The results of the present study, however, show that though the mouse is mainly nocturnal, some activity normally takes place during the day, and this conclusion is supported by the results of Smirnov (1957). The fact that two mice (A and D) changed their nocturnal preference when the day-length was increased, suggests that this preference is not an inflexible pattern and may be fairly easily changed in response to environmental conditions.

As might be expected in an animal that shows no strong nocturnal preference, the proportion of the total activity

	Length of time (in 6-minute units) occurring between two successive feeding periods.													
Minutes	12	18	24	30	36	42	48	54	60	66	72	78	84	88 and over
Frequency	70	29	10	11	3	6	3	0	2	1	1	0	2	7

Table 12: Frequency distribution of intervals between feeding, showing the occurrence of a short-term rhythm in the feeding of Micromys in the direct observation cage.

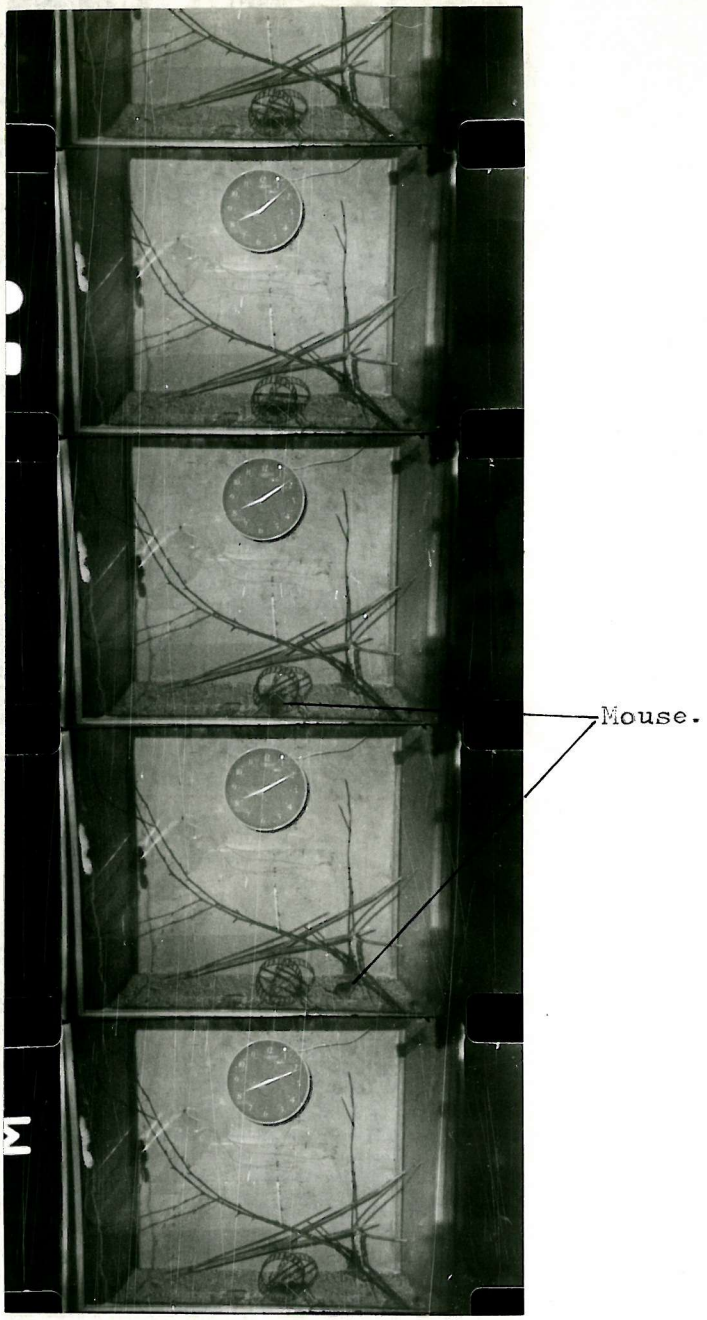


Fig. 24: Print of section of 16mm film record of harvest mouse activity. (The print is of poor quality because the record was not intended for printing but only for examination as a negative.)

taking place during daylight hours rises with increasing day-length - 15.2% with a 9-hour day-length and 44.8% during a 15-hour day-length (see Table 10). In laboratory experiments, Apodemus sylvaticus and Clethrionomys glareolus also show such an increase, though the daylight activity of Apodemus was only 28% even on a 16-hour day-length (Miller 1955). In contrast, Clethrionomys seems slightly more diurnal than Micromys, with 51% of its activity taking place in daylight on a 16-hour day-length. Activity peaks at dawn and dusk were also found for Apodemus and Clethrionomys, and Miller (1955) suggests that the intensity of the first peak of activity at night is determined by the nocturnal preference of the animal coupled with day-length and feeding habits. Thus, as a result of not feeding during the day, a strongly nocturnal animal such as Apodemus will have a strong peak of activity at dusk. Animals such as Clethrionomys and Micromys, which feed during the day, will not exhibit such a large peak at this time. The magnitude of the dusk and dawn peaks for all the present experiments are shown in Table 10. There is certainly no consistent trend as far as day-length is concerned, and this underlines the considerable individuality in activity rhythms displayed by Micromys, and the lack of a rigid nocturnal/diurnal preference.

Within each 24-hour cycle of activity there is evidence in

small mammals of a short term activity rhythm which is caused by a cycle of physiological changes within the animal. Although the exact cause of this rhythm is not known, it may primarily be a feeding rhythm based on the energy necessary for the animal to maintain its basal metabolic rate plus that required for searching for food and extra activities (see Physiology section). In addition, there is clearly a physiological need for a period of rest following one of intense activity. Thus, the short term rhythm is probably controlled by these two factors.

The duration of periods of rest of Micromys (Table 11) resembles the pattern described for the common shrew, Sorex araneus (Crowcroft 1954). The chief difference is that Micromys has a few periods of very long duration (up to 284 minutes), while the longest for Sorex lasted 120 minutes. The longer periods of inactivity sometimes shown by Micromys may be associated with the different food of this animal. Sorex is insectivorous and its diet contains a high percentage of water, while Micromys feeds mainly on grain and seeds, which contain considerably less water (see Physiology section for calorific values of different foods). Therefore, on a wet weight basis, Micromys can consume more energy per gram of food than Sorex, and a full stomach could probably provide it with energy for longer periods.

The intervals between feeding periods show a similar frequency distribution (Table 12) to those between periods of activity, but this is because they sometimes coincide. However, a mouse may have several feeding periods during one activity period. A feeding rhythm has been found in all small mammals investigated. The length of the period tends to decrease with decreasing body size e.g. Rattus norvegicus four hours, Apodemus sylvaticus two hours, and Mus musculus three-quarters to one and a half hours. It is not surprising, therefore, to find that the feeding rhythm of Micromys is similar to that described for Sorex araneus (Crowcroft 1954), for they are roughly the same size and their metabolic rates appear to be similar (see Physiology section). However, as discussed above, Micromys can go without food for longer periods than Sorex.

It will be seen from Table 11 that the pattern of the short term rhythm of rest and activity in Micromys under a day-length of 9-hours is rather different to that under longer day-lengths. Under the shortest day-length the activity occurs in longer periods at greater intervals than under the 12 or 15-hour day-lengths, and it is suggested that this is due to the habit of taking food into the nest box as described below. Since the mice are now taking some food into the nest box, it is unnecessary for them to make some of the shorter excursions into

the cage for feeding only, such as occurred at the longer day-lengths.

It has been found that in Apodemus and Clethrionomys the total amount of activity per 24-hour period falls with decreasing day-length, and this is correlated with food-storing under short day-length conditions (Miller 1955). In Micromys A - D no significant difference has been detected in the amount of activity occurring at different day-lengths, and it is possible that the decrease shown by the other species is absent in Micromys because it does not store food. Although food-storing was never observed in Micromys, all four animals A - D frequently took food into their nest box and ate it there. Whole food was never found in the nest box, so it would appear that the mice ate it soon after taking it in. This activity mainly took place under the 9-hour day-length and few food-remains were found at the longer day-lengths.

E. Discussion

One of the difficulties involved in any study of the activity of a wild animal in captivity is to decide how far the observed activity is a true picture of that in the wild. In the wild the animal has not only to search for food but also must explore its living space regularly, for it is of great importance for a small mammal to be thoroughly acquainted with the area in which it lives. Consequently, confining the animal to a small compartment so that

it has nothing to do but rest and feed could modify its normal activity. Since no studies were made of the activity of Micromys in the field, the laboratory activity pattern cannot be compared with that in the wild. However, the direct observation cage was arranged to provide conditions as natural as possible (see above), and comparison may be made between the activity of the mice in that and those in the photographic cage.

The mice in the direct observation cage were very active for much of the night, running up and down the corn stalks and exploring the cage generally. Table 10 shows that the mean 24-hourly activity of these mice is considerably higher than that for mice A - D on the same (15-hour) day-length, and this difference is significant, $t_{(3)} = 3.21$, $P < 0.05$. However, the large standard error for mice A - D suggests that this lower activity is not characteristic of them all, and reference to Fig. 22 shows that the activity pattern of mouse C resembles markedly that of the observed animals (Fig. 19), while that of mice A, B, and D does not. In fact, mouse C shows almost continuous activity throughout the night and during this time the photographs show that it was running in the exercise wheel, an activity which the other photographed mice (A, B, D) showed only occasionally. In this connexion, it is worth noting that mouse E also used the wheel for long periods and shows a similar

pattern of activity to mouse C on the same day-length (12-hours).

Apparently, therefore, when the mice can explore a large cage or choose to run in a wheel, their activity may vary from that of those mice that do little but eat and sleep and whose exploration of their surroundings is soon complete. Consequently, extrapolation of laboratory results to indicate conditions in the wild must be made with caution as far as total activity is concerned. However, there is no evidence that a mouse will change its nocturnal or diurnal preference when its living space is restricted. Although mice A and D show more diurnal than nocturnal activity at the 15-hour day-length, they do not at the other day-lengths. Hence, this change is probably not due to the cage, but to the experimental variable of increasing day-length together with the lack of a rigid nocturnal preference.

Since, because of the nature of the switching device, it was necessary to record the activity of one mouse at a time in the photographic cage, it is pertinent to enquire whether the presence of other mice would affect an individual's activity rhythm. Consequently, special attention was paid to this point whilst observing the four mice in the observation cage. No fighting occurred, though one particular mouse sometimes robbed the others of food. Two nest boxes were provided for the four mice and they all slept in both of them at times, as well as in

nests they made for themselves in the hay on the floor of the cage. If one mouse was occupying a nest box, another would either join it or go elsewhere to rest. Therefore, the fact that one mouse was resting did not prevent the others from doing so, and it seemed that each individual expressed its personal activity rhythm without interference from the others. The activity of one individual recorded alone is therefore probably not very different from that when other mice are present.

In concluding this section it may be said that, as in other small mammals, two activity rhythms appear to be present in Micromys. The first of these is the short term feeding rhythm in which the mouse satisfies its basic energy requirements. Within the limits of this rhythm is a longer 24-hour cycle of activity in which the mouse can express a diurnal or nocturnal preference. Micromys generally shows a nocturnal preference in this second rhythm, which is less noticeable on long day-lengths than on short ones, and which is evidently not an inflexible pattern since it may be completely reversed.

In the present study no detailed work on activity was carried out in the wild. However, visiting at dawn and dusk the traps set at Studland always resulted in a larger catch of Micromys in the morning, though the fact that one or two mice were usually caught in the evening suggests that activity was taking place during the day as well as at night. Other authors have also recorded that activity takes place during the day in the wild (e.g. Southern 1964). It is likely, therefore, that the activity described here

for mice in the laboratory is similar to that in the wild, at least in respect of the general pattern of night and day activity. As discussed above, without further evidence from the field it cannot be automatically assumed that laboratory results give detailed information on activity in the field. However, by its intrinsic nature, the short term rhythm is less likely to modification by laboratory conditions than the 24-hour cycle, which, in the present case, has been shown to be quite flexible.

V. PHYSIOLOGY.

A. Introduction.

The energy acquired by an animal from its food is chiefly used in maintaining the life of the animal and any surplus is accumulated in the form of growth. Such accumulation is commonly called production. Since the release of energy from food is an oxidative process, it is directly proportional to the oxygen consumption of the animal. Hence, the energy assimilated from food that is utilised directly will equal respiration, while that accumulated will appear as production. The sum of these processes is termed energy flow. Knowledge of the energy flow through a population forms an adjunct to the study of its numbers since the calorie provides a common unit for describing populations of animals of different sizes.

The energy flow through a population may be summarised as follows (Southwood 1966):

Assimilation = Respiration + Net Production

Assimilation = Ingestion - Egestion.

It is generally necessary to determine some or all of these values on animals in the laboratory and then, with the aid of information from the field, the energy flow through populations in the wild may be estimated. The energy assimilation may be regarded as the maintenance energy requirement of the animal when it is just sufficient to maintain the body weight (i.e. no production takes place). In the present series of experiments

the energy assimilation of Micromys and Apodemus has been studied by measuring food consumption.

The energy necessary for maintaining the body weight of a mammal includes the basal energy requirements, the energy cost of utilising food and excreting waste, the energy cost of activity, and the cost of maintaining the body temperature. The basal energy requirement is usually expressed as the basal metabolic rate (BMR), which is defined as the heat production during complete rest in a thermo-neutral environment in a post-absorptive condition. The basal metabolic rate is correlated with body size in mature mammals, and when expressed per unit of body weight it is found that a small mammal has a much higher metabolic rate than a large one. This follows because a small mammal has a greater surface area/volume ratio than a large one and consequently loses heat faster. In general, metabolism is more uniform when expressed as a power function of body size, and when the BMR is expressed as a ratio to the 0.73 power of body weight it is independent of body size and is approximately constant (Brody 1945).

The rate of metabolism per gram body weight rises so steeply with small size that it would be virtually impossible for a mammal weighing less than 3.5g to obtain sufficient food when active (Pearson 1948). Micromys, weighing about 6g, is one of the smallest rodents, and experiments have been carried out in

the present study to establish how far it adheres to the metabolic functions relating to other mammals. In addition, because of the relationship between respiration and assimilation, as described above, the repiratory and food consumption studies can be compared to estimate the reliability of the respective methods for determining the energy flow through small mammal populations.

The range of habitats in which a small mammal can live is governed by a number of physiological considerations, one of the most important of which is that the animal must be able to maintain its water balance. In this connection the ability of a small mammal to conserve water must have some bearing on its habitat - in an extreme case, e.g. the desert rat Dipodomys, water loss is considerably lower than that of small mammals living under moist conditions. Water loss may be controlled by restricting urine flow, or evaporative loss or both. The evaporative water loss, which takes place through the lungs and general body surface, is affected by the humidity of the surrounding air and can amount to between 28 and 56% of the total daily water loss (Chew 1955). Within a particular habitat, the humidity to which a small mammal is exposed will vary according to whether the animal is nocturnal or diurnal, and with the extent to which is uses microhabitats of high humidity such as burrows or runways beneath the vegetation. Micromys is partly diurnal

and, in summer at least, lives well above ground level. Consequently, it will be exposed to lower humidities than a nocturnal burrowing mammal such as Apodemus. A preliminary series of experiments has been carried out to determine whether or not Micromys can control its evaporative water loss more effectively than Apodemus.

The physiological experiments carried out in this work, though interrelated, are described under three headings:- food consumption, respiration, and evaporative water loss.

B. Food Consumption.

(i) Methods.

Because of the influence of activity on the energy requirements of an animal, it is necessary to measure food consumption under constant activity conditions and the most accurate way of achieving this is to restrict activity to a minimum. The mice were housed singly in small (12" x 18" x 18") cages and provided with a piece of twig to sit on and some cotton wool to use as nest material. Under these conditions activity was reduced to a minimum and yet the animal was not under undue stress. The floor of the cage was detachable to facilitate collection of food remains. Each mouse was weighed every day at the same time to minimise the effects of daily variation. Also at this time the remains and the uneaten

portion of the food was removed and weighed, and a fresh, known amount introduced. Two diets were regularly given, one consisting of mixed corn, sunflower seeds and mealworms (larvae of Tenebrio molitor). The mixed corn, which consisted of whole - grain wheat and oats together with broken maize, was sometimes given alone. The second diet was the commercially-prepared, balanced food known as Diet 41B, and this was introduced because it is easier to handle and has a known calorific value. Water was freely available to the mice. The changes in weight of the different foodstuffs after standing at room temperature for several days were found to be negligible.

The determinations of the calorific values of food (except mealworms and Diet 41B) and faeces were carried out on a Gallenkamp adiabatic bomb calorimeter. In the case of the mealworms and Diet 41B the calorific values were obtained from Hawkins and Jewell (1962). The food intake was calculated in terms of kilocalories per gram body weight per day. The dry matter content and calorific value of food and faeces is presented in Table 13.

The limited availability of the bomb calorimeter and the relatively large amount of material required for combustion (2g dry weight) made it necessary to combine the faeces collected from two mice on each diet for the determination of the energy lost in the faeces. The percentage assimilation thus

Substance	Dry Matter %	Kcals/g dry weight
Food		
Mealworms	40	6.1
Grain	89	4.0
Sunflower seeds	94	7.1
Diet 41B	86	4.4
Faeces		
Micromys		
on mixed diet	79	5.0
on Diet 41B	79	4.3
Apodemus		
on Diet 41B	79	4.3

Table 13: Dry matter content and calorific value of foodstuffs and faeces.

Mouse	Sex	Expt. No.	Diet	Activity conditions	Duration of Expt. (days)	Mean weight of mouse (g)	Mean daily food intake			Kcals/ g body weight
							Wet wt. (g)	Dry wt. (g)	Kcals	
Micromys										
A	♀	1	Grain	Minimum	7	5.43	2.44	2.17	8.74	1.61
		2	Mixed	"	6	5.61	4.97	2.34	13.20	2.35
B	♀	3	Grain	"	7	5.63	2.47	2.20	8.87	1.57
		4	Mixed	"	6	6.18	2.66	1.88	10.38	1.68
C	♀	5	Grain	"	5	5.85	2.40	2.14	8.62	1.47
		6	Mixed	"	9	6.10	4.76	2.38	13.59	2.23
D	♂	7	41B	"	11	7.44	2.05	1.76	7.74	1.04
E	♂	8	41B	"	9	7.07	2.77	2.38	10.47	1.48
F	♂	9	41B	"	14	7.16	2.49	2.15	9.46	1.32
G	♂	10	41B	"	6	5.73	2.11	1.81	7.96	1.39
H	♂	11	41B	"	8	8.81	2.98	2.56	11.26	1.28
I	♀	12	Mixed	Wheel provided	6	5.79	3.21	1.79	10.53	1.82
J	♂	13	Mixed	"	6	6.41	3.08	1.99	11.03	1.72
Apodemus										
K	♂	14	41B	Minimum	14	26.98	5.77	4.96	21.82	0.81
L	♀	15	41B	"	11	17.77	2.62	2.25	9.90	0.56
M	♂	16	41B	"	6	22.06	4.38	3.77	16.59	0.75

Table 14: Summary of feeding experiments on Micromys and Apodemus.

obtained was used for all mice on that diet.

The air temperature in the laboratory was maintained between 18°C and 22°C during the experiments. It is unlikely that this variation caused any but slight changes in food requirements.

The experiments were carried out on eight Micromys under conditions of minimum activity, and on two mice which were provided with an exercise wheel. The experiments were repeated using three Apodemus sylvaticus under minimum activity conditions. Experiments one and two were performed consecutively on the same animal, being distinguished only by a change of diet. Similarly with experiments three and four, five and six. (See Table 14).

(ii) Results.

Table 14 shows the mean daily food intake for all experiments. Figures 25-27 are representative runs for different diets and activities, showing the relative amounts of the different foods eaten and the fluctuations in body weight and food intake.

Of the eight harvest mice studied under minimum activity conditions, three were fed on the mixed diet and five on Diet 41B. The first three were given only mixed corn for an initial determination of food consumption (experiments one, three, five), and then sunflower seeds and mealworms were added to the diet (experiments two, four, six). Faeces were collected in experiments

four and six (Mice B and C) for the calculation of assimilation. In every case, the change of diet resulted in an increase in the wet weight of food consumed (see Fig 25) due to the high proportion of mealworms taken. In terms of dry weights, however, the increase was slight and in experiment four there was actually a decrease. Owing to the fact that mealworms have a greater calorific value per gram dry weight than grain, the actual calorific intake in these experiments was greater than in those in which grain only was given. During experiment four, mealworms were in short supply and had to be restricted; hence the smaller increase in calorific value ingested. The higher calorific intake resulted in an increase of 0.55g in the weight of the animal in experiment four, and of 0.60g of that in experiment six. In experiment two, as Fig 25 shows, the increase in weight was only 0.25g, indicating that some of the extra food was voided in the faeces.

This increase in calorific intake when mealworms are given may be apparent because, when eating mealworms, Micromys removes the exoskeleton and ingests only the soft parts. In calculating the energy obtained by the mouse from mealworms, the actual weight eaten was taken because the discarded exoskeleton was included with the food remains. However, the exoskeleton will have a higher dry matter content and probably a higher calorific value than the mealworm as a whole, and the portion of the meal-

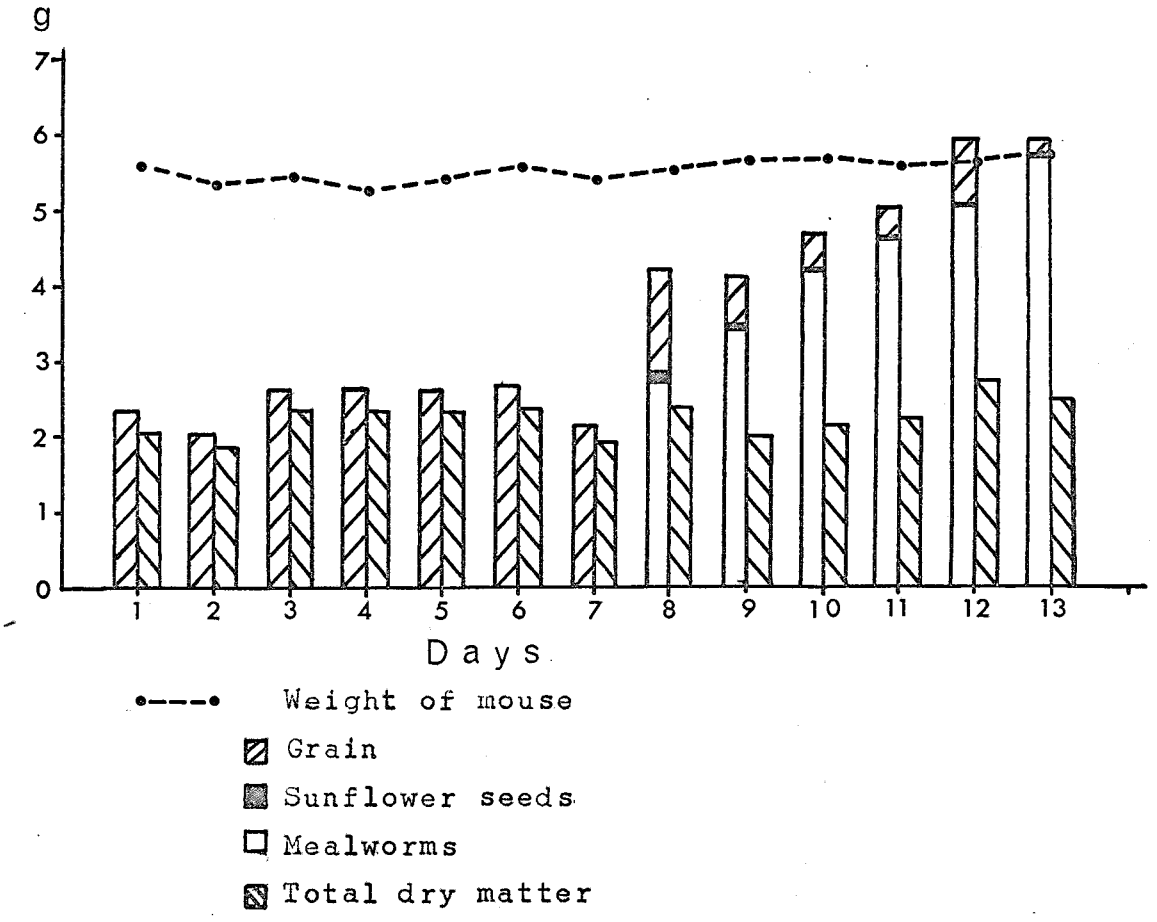


Fig.25 The food intake, day by day, of harvest mouse A in Experiment 2.

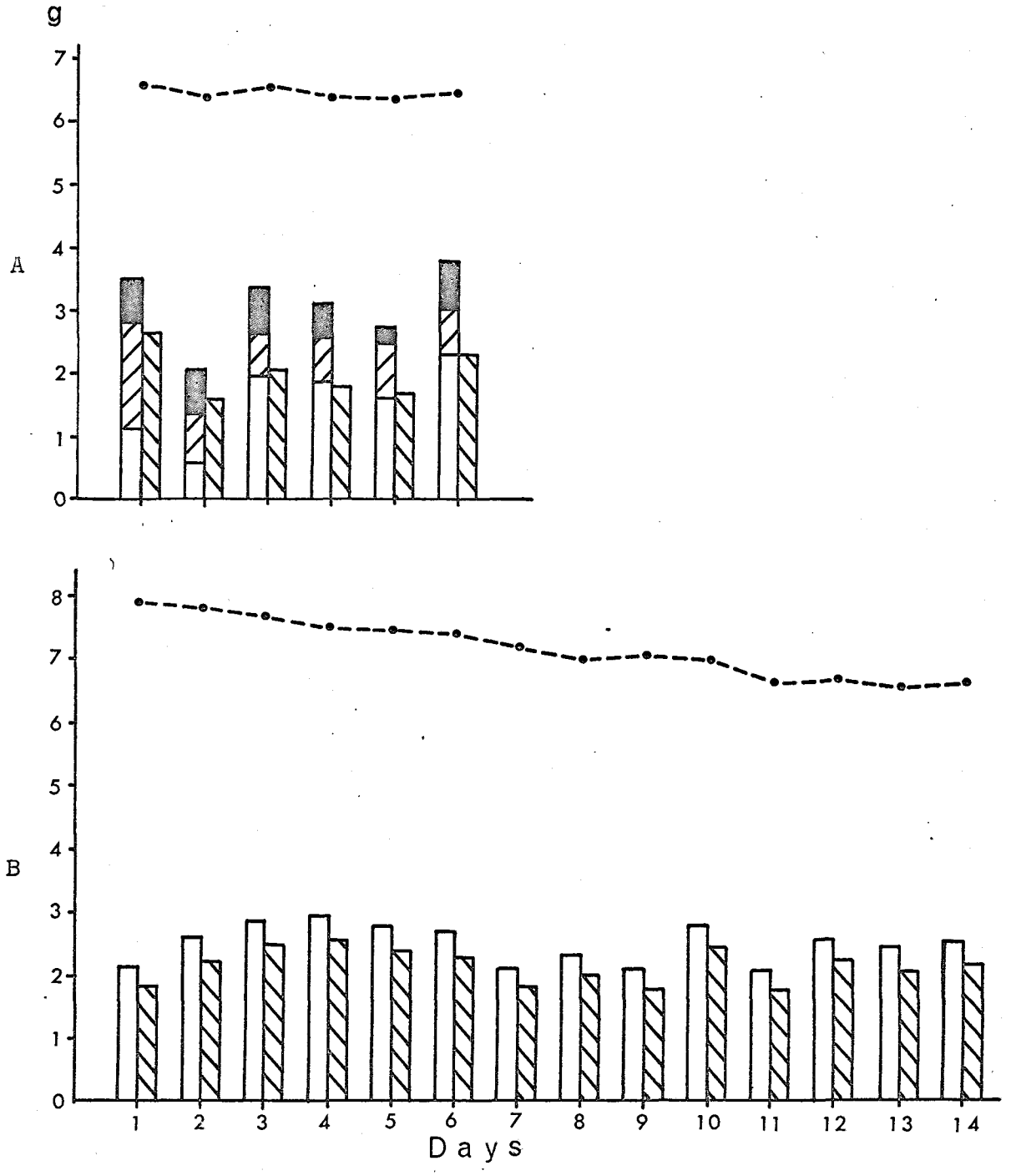


Fig. 26: A. The food intake, day by day, of harvest mouse J in Experiment 13. Legend as in Fig. 25.

B. The food intake, day by day, of harvest mouse F in Experiment 9. Legend as in Fig. 27.

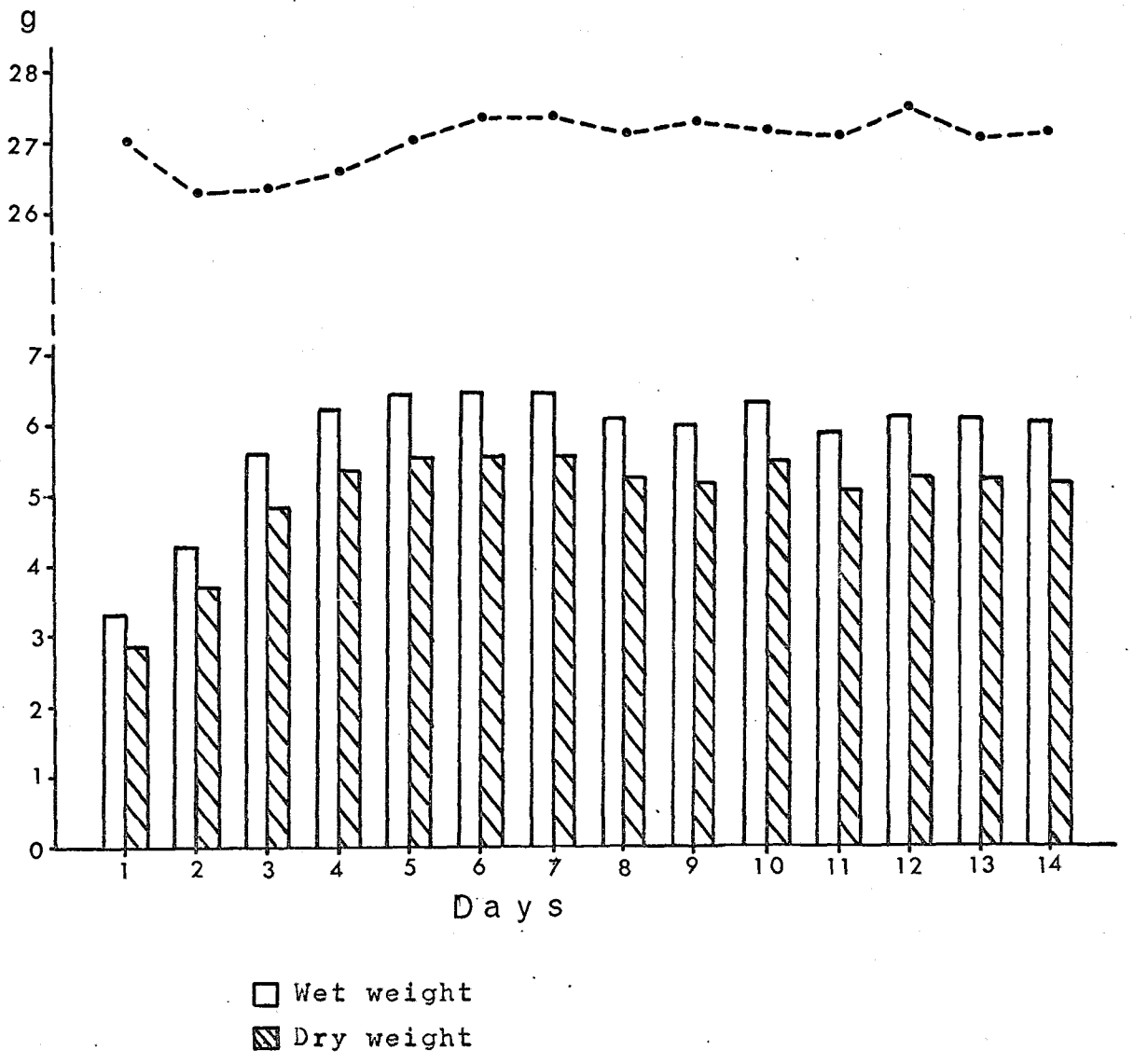


Fig.27 : The food intake, day by day, of wood mouse K fed on Diet 41B in Experiment 14.

worm that the mouse eats will therefore have a lower dry matter content and probably a lower calorific value than the mealworm as a whole. Since the dry matter and calorific value conversions were based on whole mealworms, this could introduce an error, and consequently the calculated calorific intake from the mealworms is too high. If this fact, together with the increase in weight of the mouse, is taken into consideration, the energy intake required for constant body weight on this diet will be nearer the values obtained for Diet 41B. Although the weight of faeces produced per day on the mixed diet was lower than that produced on Diet 41B, the former were found to have a higher calorific value (see Table 13). In fact the percentage assimilation was greater on the mixed diet (92.6%) than on 41B (79.6%), so much of the apparent surplus energy intake cannot have been lost in the faeces. However, it could have been lost as urea in the urine, but this was not measured. In view of these discrepancies, the values obtained for the mice fed on Diet 41B are almost certainly nearer the minimum energy requirements, for this diet is homogeneous and the mice cannot select certain parts.

The mice showed different reactions to Diet 41B. It is produced in large pellets and as such has a different form and constitution to the animals' natural diet. However, it is easier to handle from the experimenters point of view and has a known

calorific value. Mice G and H maintained a constant weight on this diet and mouse E gained 0.11g, but mice D and F both lost weight (Fig 26B).

These feeding experiments were also carried out on Apodemus which, apart from being housed in slightly larger cages, were under identical conditions to Micromys. All the Apodemus were fed on Diet 41B. Mouse L gained 1.5g in weight over 11 days, while mouse K, after an initial drop, maintained a fairly constant weight (Fig 27). Mouse M also maintained a steady weight and varied 0.33g over six days.

The proportion of the energy ingested as food that is used by the mouse depends on the efficiency of the digestive system, and this is measured by calculating the assimilation efficiency according to the following equation:-

$$\text{Assimilation Efficiency} = \frac{\text{Potential Energy ingested - faeces energy}}{\text{Potential Energy ingested.}}$$

The assimilation efficiency for the two species on Diet 41B are shown in Table 15, together with the conversion of food intake to assimilation. Only Micromys E, G and H on Diet 41B are included since the others on this diet lost weight. For these calculations faeces were collected from mice E and G (experiments eight and ten). As explained above, the food consumption of the Micromys on the mixed diet does not give as reliable an indication of maintenance energy requirements

Species	No.	Mean weight (g)	Mean intake (Kcals/mouse/day)	Mean faeces output(Kcals/mouse/day)	Assimilation (%)	Mean assimilation Kcals/mouse/day	Kcals/g/day
Micromys	3	7.20	9.89±2.84	2.01	79.7	7.88±0.79	1.10±0.04
Apodemus	3	22.27	16.10±3.45	2.86	82.2	13.24±2.84	0.58±0.06

Table 15: Assimilation of Micromys and Apodemus on Diet 41B under minimum activity conditions. The mean values for intake and assimilation are the mean values per mouse of the mean value per day of each mouse.

as that of those on 41B, and so calculations based on the mixed diet were not made.

In order to estimate the maintenance energy, the figures for assimilation must be corrected for the energy used in growth. The average daily increase in wet weight of the Micromys was 0.005g while that of Apodemus was 0.012g. These figures are so small that they can be ignored since if all the increase in weight was due to the deposition of fat (which has a high calorific value of 9.3 Kcals/g), the daily energy expenditure on growth for Apodemus would be only 0.11 Kcals/mouse, or 0.86% of the daily assimilation. This is well within the individual variation of the mice and so no allowance has been made for growth.

Hence, the maintenance energy of Micromys is 7.88 Kcals/mouse/day or 1.10 Kcals/g/day and that of Apodemus is 13.24 Kcals/mouse/day or 0.58 Kcals/g/day.

Mice I and J were provided with exercise wheels so that the increase in calorific intake with activity could be measured. However, only mouse J was observed to use the wheel to any extent. Reference to Table 14 shows that its energy intake per gram body weight was rather less than that of the mice on a similar mixed diet (experiments two, four, six), but was greater than that of those on Diet 41B. In view of the

probable discrepancies in the analysis of the mixed diet, it is not felt that any firm conclusions can be drawn from this experiment.

(iii) Comparison with other small mammals.

The percentage assimilation of Micromys and Apodemus on Diet 41B is a little higher than the figure of 75% for Mus musculus on the same diet (Hawkins and Jewell 1962). However, higher values for assimilation have been obtained for other small mammals. For example, Peromyscus polionotus showed 93.5% assimilation efficiency (Davis and Golley 1963), while Microtus pennsylvanicus had a 90% efficiency when fed alfalfa, and 82% on a diet of lettuce, carrots and oatmeal. In the present study the assimilation efficiency of Micromys increased from 79.6% on Diet 41B to 92.6% on the mixed diet. This increase is probably due to the large proportion of mealworms taken since these will have a higher digestibility than plant food. Because of this greater digestibility of animal material, it has been suggested that carnivores will have a higher assimilation efficiency than herbivores (Davis and Golley 1963). However, Sorex spp. fed on mealworms, baby mice and earthworms had an assimilation efficiency (92.5%) (Hawkins and Jewell 1962) no higher than that of the rodents mentioned above. This anomaly between the observed and expected results may be due to the

effect of laboratory conditions and diets on the secretions of the gut. The energy content of the faeces is not due solely to undigested food, but also includes secretions and cells sloughing into the digestive tract. Thus, the assimilation energy indicates only the excess of food energy entering the blood stream over excretion into the gut.

It is of interest to compare the maintenance energy requirements of Micromys with those of Sorex spp., for these are also very small mammals. Using an assimilation value of 92.5% (measured on Neomys fodiens), the mean energy assimilation of four Sorex araneus with a mean weight of 8.6g was 1.89 Kcals/g/day (Hawkins and Jewell 1962). These animals were not under minimum activity conditions and were at a lower environmental temperature (c.16°C) than the mice in the present study, factors which would increase the maintenance energy requirement. Thus, the figure of 1.89 Kcals/g/day cannot be regarded as the maintenance energy requirement comparable to that of Micromys but, if allowance is made for the greater activity and lower temperature, the figure will approach more closely to that of Micromys (1.10 Kcals/g/day).

Hawkins and Jewell (1962) calculated the mean daily intake of Micromys fed on mixed grain with a calorific value of 4.9 Kcals/g dry weight to be 0.97 Kcals/g. This is marginally lower than the values obtained in the present series of

experiments for mice on Diet 41B, and about 0.6Kcals/g lower than those mice fed on a roughly comparable diet. This difference is probably due to different experimental conditions and individual variation. Hawkins & Jewell (1962) suggest that the higher values obtained for shrews over harvest mice are due to the greater activity of shrews rather than the possession of a higher metabolic rate, and the results of the present experiments lend much support to this argument by showing that, when due allowance is made for differences in activity and temperature, the metabolic rates of the two species are similar.

(iv) Discussion.

The maintenance energy expenditure of a small mammal will be greater than that of a larger one because of its greater proportional heat loss. In the present experiments Apodemus and Micromys were kept under similar conditions of minimum activity and temperature, and were fed on the same kinds of food. When allowance has been made for the slightly different assimilation efficiencies, the difference in the maintenance energy requirements is a measure of the greater requirements of the smaller mouse. The mean assimilation of Micromys was 1.10 Kcals/g/day while that of Apodemus was approximately half as much at 0.58 Kcals/g/day.

From the little that is known, Micromys and Apodemus

utilise similar foodstuffs in the wild, though Micromys may take a higher proportion of insects. The food chain in which the two species participate is therefore similar, since they also form the food of the same predators:-

VEGETATION ——————→ MOUSE ——————→ PREDATOR

as seeds, berries, etc. Owls, Weasels, etc.

From the results presented here, it is apparent that a biomass of Apodemus double that of Micromys could be maintained on the same amount of food energy. Consequently, when the energy flow through the food chain is considered, it is clear that Apodemus is a more efficient converter of the energy available from the primary producers and more of it will be retained for consumption by the secondary consumers. The extra energy used by Micromys will be lost to the food chain (i.e. the secondary consumers) since it will be dissipated in respiration. (This will be discussed more fully in the following section).

In general, large mammals are more efficient in converting the energy assimilated to biomass than small ones, since they use less energy per unit of body weight in maintenance. This study has measured the difference in efficiency of energy conversion between two small mammals which utilise similar foods and frequently live in the same habitat.

C. Respiration.

(i) Methods.

It is possible to determine the basal metabolism of a mammal by measuring the heat production in a calorimeter, but this method is complicated and rarely used. Instead determinations are usually made by indirect calorimetry, in which the volume of oxygen consumed or carbon dioxide produced is measured and converted to energy values.

The numerous methods used in indirect calorimetry have been reviewed by Brody (1945). They may be classified into two main systems: 1) open circuit, in which it is possible to compare the oxygen and carbon dioxide contents of the expired air with those of the inspired air and hence determine the respiratory quotient (R.Q.) directly, and 2) closed circuit, in which either the pressure or volume in the system is kept constant, and changes in the volume or pressure as a result of respiration are measured.

In the present study an open circuit system was set up based on the Beckman 777 oxygen analyser described below. However, great difficulty was experienced in maintaining a flow of air through the system at a sufficiently low level for accurately measurable changes in the partial pressure of oxygen to occur, and the system was eventually abandoned in favour of the closed circuit constant pressure apparatus described below.

Morrison (1947) described a respirometer which has since been successfully used in many studies on small mammals (e.g. Morrison 1948, Morrison et al 1959, Pearson 1960). The apparatus is based on the closed circuit constant pressure principle, and has proved accurate and reliable. It has the advantages that oxygen consumption is measured over a succession of periods of time which can be easily varied to suit the circumstances, and operation, calibration and calculation are quick and simple.

The apparatus used here was not automatic as was Morrison's, but was similar in all other respects. It consisted of the following parts:-

1) animal chamber, which was a glass vessel of approximately one litre capacity and which contained soda lime to absorb carbon dioxide and wet calcium chloride to keep the humidity in the chamber within reasonable limits. If this was not done, water vapour condensed on the animal's fur. The chemicals were separated from the animal by a zinc gauze sheet which allowed free passage of air. The lid of the chamber was formed from ¼" perspex drilled to take the inlet pipe, thermometer and oxygen meter sensor. The lid was sealed to the chamber with silicone grease.

2) spirometer, which supplied oxygen to the animal chamber. The spirometer consisted of an aluminium

cigar-tube, delicately balanced at the end of a brass rod, and suspended in a bath of water to which a small quantity of detergent (Tee-pol) had been added to decrease surface tension. The tube had a number of divisions marked on its exterior on which calibration was based.

3) a reservoir of oxygen under slight pressure, to refill the spirometer.

4) a Beckman 777 oxygen analyser, to keep a check on oxygen tension within the chamber. This apparatus uses a sensor which is basically a polarographic oxygen electrode. Oxygen in a sample of gas reacts at the electrode and causes a current to flow proportional in magnitude to the amount of oxygen present in the sample.

5) a thermometer, to measure the temperature inside the chamber.

6) a water bath, to keep the chamber at constant temperature. This is most important as a very small change in temperature will affect oxygen consumption. Morrison

calculated that a change of 0.1 - 0.2% in the temperature of the chamber during a single measuring period would introduce an error of 1%.

Fig. 28 is a diagram of the apparatus.

The apparatus was calibrated by withdrawal of air from the chamber by a syringe which was itself calibrated by delivery of water. Over 10 trials the mean volume of oxygen delivered by the spirometer was 21.07 $\pm$ 0.01 ml.

Later the apparatus was modified so that two experiments could be conducted at the same time. The oxygen analyser was the only piece of equipment that could not be duplicated, so arrangements were made to transfer it from one chamber to another without affecting the equilibrium within the apparatus. A large-bore glass tap was introduced into the lid of the chamber and an air-tight seal effected between the tap and the sensor of the oxygen analyser by a suitable piece of rubber tubing. Air from the chamber was circulated up to the oxygen sensor by operating a syringe at the end of a length of polythene capillary tubing, the other end of which was just beneath the sensor (see Fig.28). The air in the chamber could thus be thoroughly mixed and a true reading of the partial pressure of oxygen obtained. While the chamber air was pumped in and out of the syringe, the chamber was isolated from the

Fig. 28: Diagram of apparatus used for measuring oxygen consumption.

E = Electrode of Beckman oxygen meter.

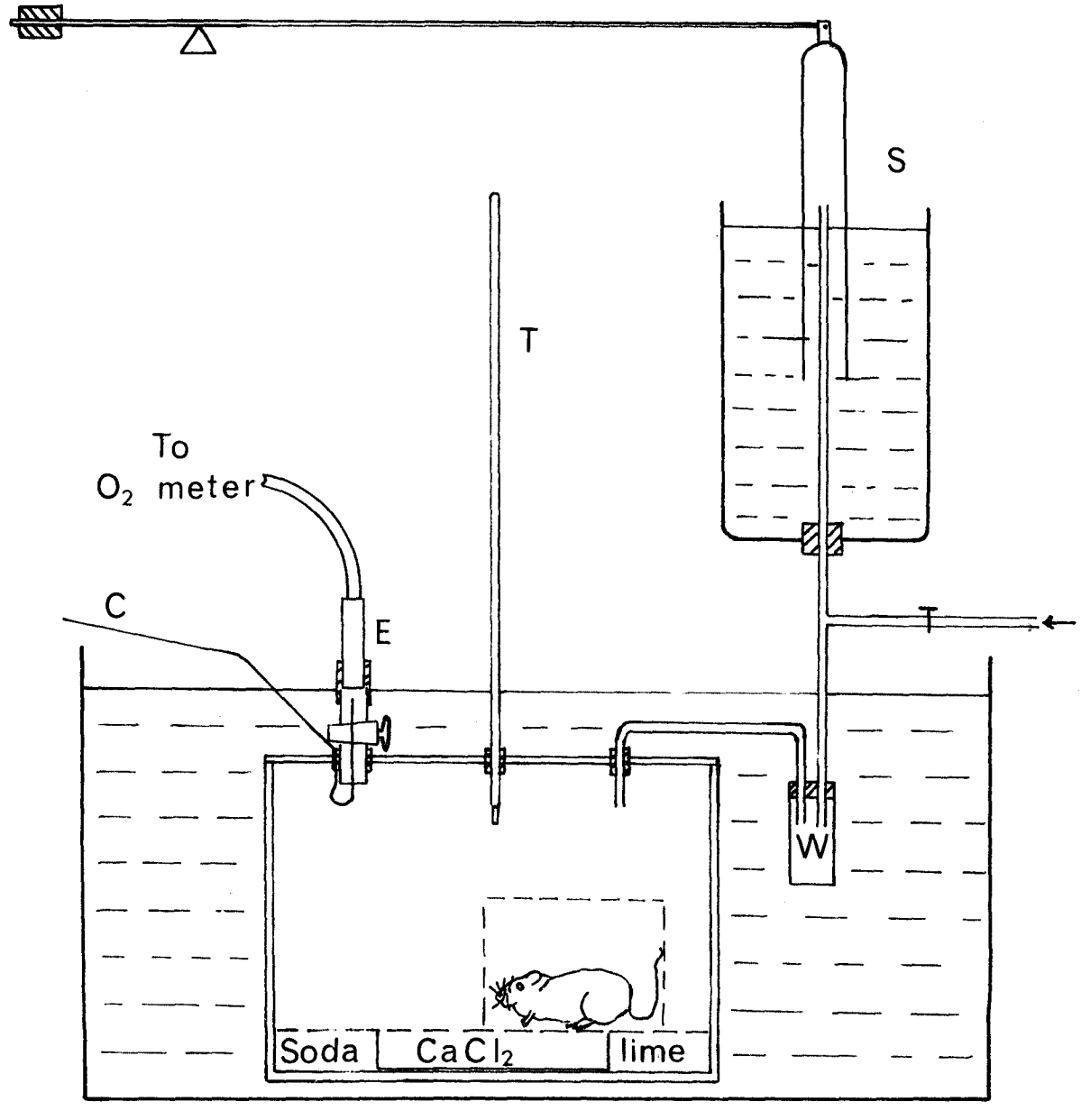
C = Polythene capillary tubing.

S = Spirometer.

T = Thermometer.

W = Water trap - to prevent water from the spirometer bath accidentally entering the respiratory chamber.

Arrow indicates the direction of oxygen flow from the reservoir to the spirometer.


S
T
To
O_2 meter
C
E
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W
Soda
$CaCl_2$
lime

spirometer to prevent oxygen entering. When a reading of the oxygen tension had been taken, the tap was closed, the oxygen sensor removed, and the spirometer reconnected to the chamber.

(ii) General method of operation.

Bearing in mind the above method for determining the oxygen tension in the chamber when more than one chamber was in use, the general procedure for the rest of the experiment was as follows. The mice were starved for four to five hours before experiments commenced to ensure that they were in a post-absorptive state. To keep the mice under conditions of minimum activity, they were placed in a perforated zinc box only a little larger than their body. This box, which had a perspex lid so that the mice could be seen during the experiments, was then placed in the prepared chamber and the whole apparatus allowed to equilibrate in the water bath for 60 minutes. During the equilibration period the oxygen tension was maintained at atmospheric level by periodic withdrawals of air from the chamber, the volume of air withdrawn being replaced by an equal volume of pure oxygen from the spirometer. Before measurements began the partial pressure of oxygen in the chamber was again adjusted if necessary to 159mm i.e. atmospheric level.

The spirometer was calibrated as described above so that

the volume of oxygen delivered to the chamber was known at three stages in the descent of the spirometer. Thus, for every full spirometer of oxygen that was used, three readings of consumption were taken. In each experiment on one mouse the spirometer was usually filled five times, thus giving a total of 15 measurements of the rate of oxygen consumption. The length of time between successive measurements varied from about six to 15 minutes according to the rate of consumption at the different temperatures, and hence each experiment on one mouse varied from one and a half to four hours according to the temperature of the chamber. At each temperature, two experiments on separate days were carried out on each mouse, thus giving a total of 30 measurements of oxygen consumption at that temperature.

When only one chamber was in use the oxygen tension was checked after every three readings, i.e. after one spirometer of oxygen had been consumed, but when two chambers were operated at the same time, the oxygen tension was checked after every two or three spirometers of oxygen had been used. Generally it was not necessary to adjust the oxygen tension since it was maintained at atmospheric level (159 mm) throughout the experiments. If it was found to have varied by more than 1 mm the results for that run were discounted.

Three Micromys and three Apodemus were used at each

temperature. Experiments were carried out on both species at 20°,25°,30°,31°,32°,33°,34°, and 35°C but as Apodemus appeared to have a wider range of thermoneutrality, experiments on these mice were also carried out at 27°,28°,29°, and 36°C. Once the temperature of thermoneutrality had been found using these mice, the basal metabolic rate was determined for a further three Micromys and an additional Apodemus.

Measurements of oxygen consumption were also made on Micromys number two under fairly normal conditions to determine the increase in metabolic rate due to activity and food digestion. The mouse was allowed the full run of the respiration chamber and was provided with food and water.

(iii) Results.

The mean and minimum of the 30 measurements taken for each mouse at each temperature are calculated and the volume of oxygen consumed is expressed as dry gas at NTP. Morrison (1947) pointed out that there can be a lag in the absorption of carbon dioxide after a period of activity, which can give rise to errors in a given period. Although in these experiments the mouse was capable of only very limited movements, these were sufficient to cause some variation in the rate of oxygen consumption at each temperature (see Fig.35). The mouse could be seen within its box inside the chamber and any activity was

noted. Therefore, for calculation of the minimum rate of oxygen consumption, only a period preceded and followed by one of comparable length was used.

The responses of the individual Micromys to different environmental temperatures are shown in Figs. 29-31. At each temperature, the minimum values recorded in either experiment are plotted together with the mean of both runs. Similar data for Apodemus are shown in Figs. 32-34. A representative run for each species is shown in Figs. 35 and 36. The basal metabolic rate data for all animals studied are summarised in Table 16.

For Micromys it will be seen that in all three cases (Figs 29-31) the oxygen consumption was lowest at an environmental temperature of 33°C. This temperature may therefore be regarded as the temperature of thermoneutrality, which is that temperature at which the animal is in thermal equilibrium with its environment, needing to use no energy to keep its body temperature constant. By definition, the basal metabolic rate is measured at this temperature on animals in a post-absorptive condition, and so the BMR for these harvest mice is seen from the data shown to be between 2.25 and 2.75 ml O_2/g/hr. These results, together with those of the three additional animals whose BMR was determined once the temperature of thermoneutrality had been found, are shown in

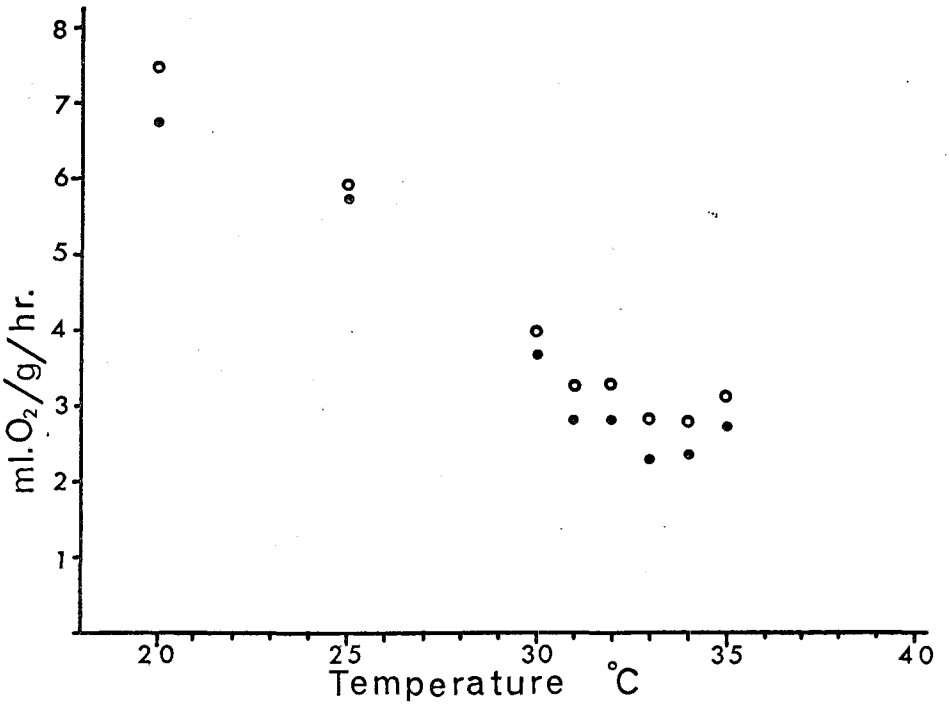


Fig.29: Minimum and average rates of oxygen consumption at various temperatures for Micromys No.1.
Closed circles = minimum.
Open circles = average.

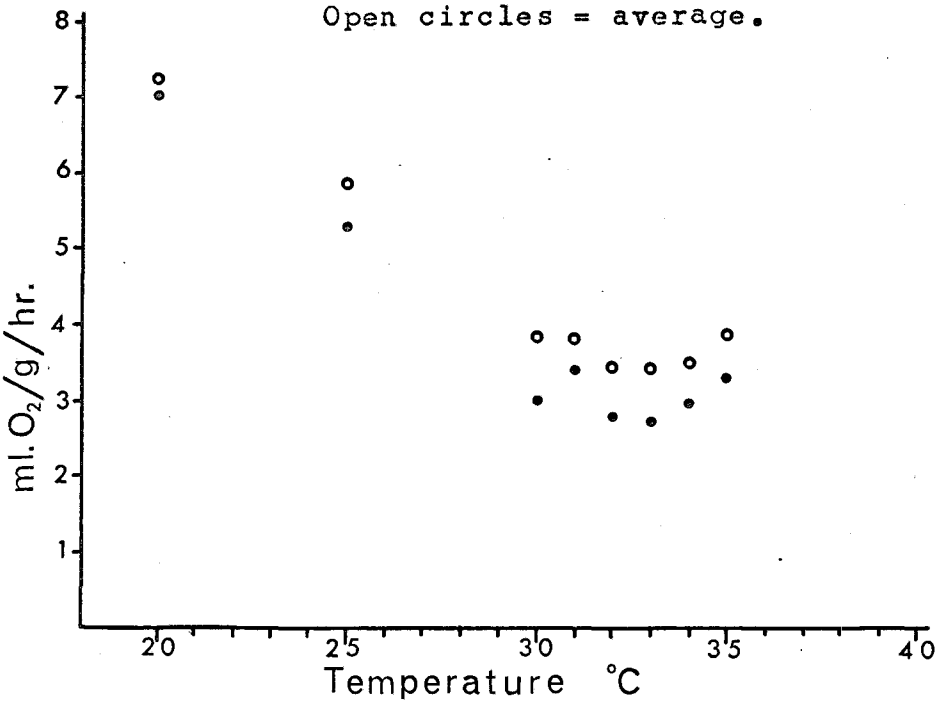


Fig.30: Minimum and average rates of oxygen consumption at various temperatures for Micromys No.2.

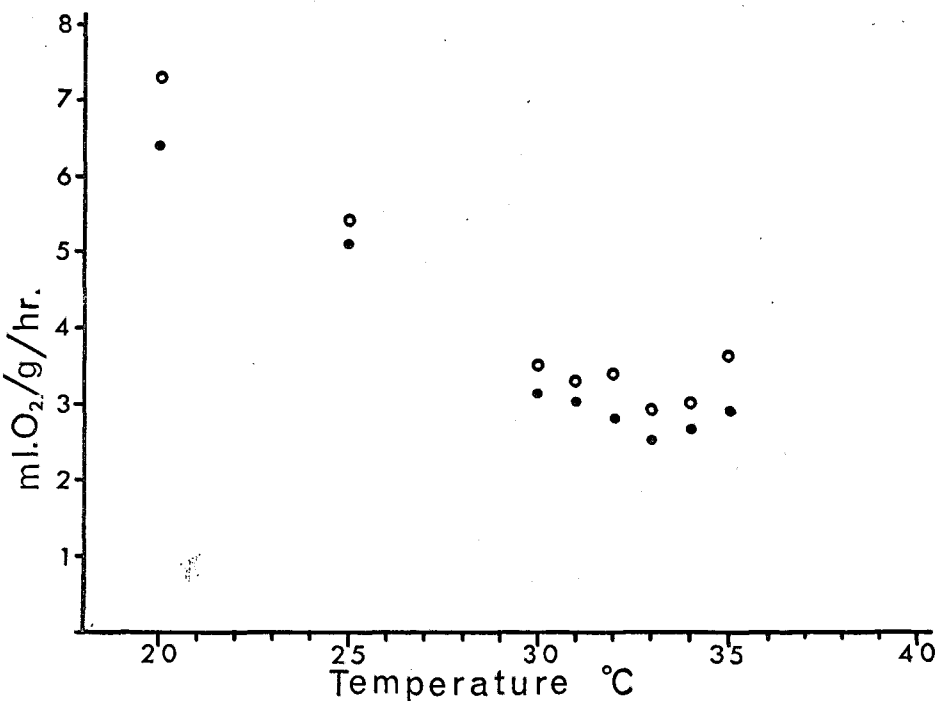


Fig.31: Minimum and average rates of oxygen consumption at various temperatures for Micromys No.3.

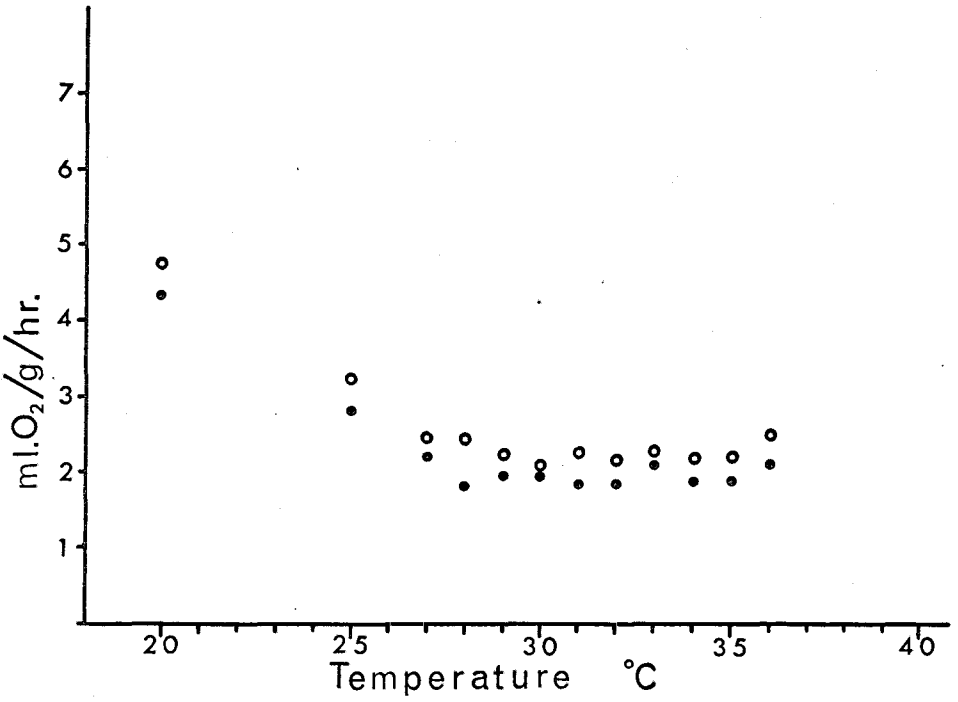


Fig.32: Minimum and average rates of oxygen consumption at various temperatures for Apodemus No.1.

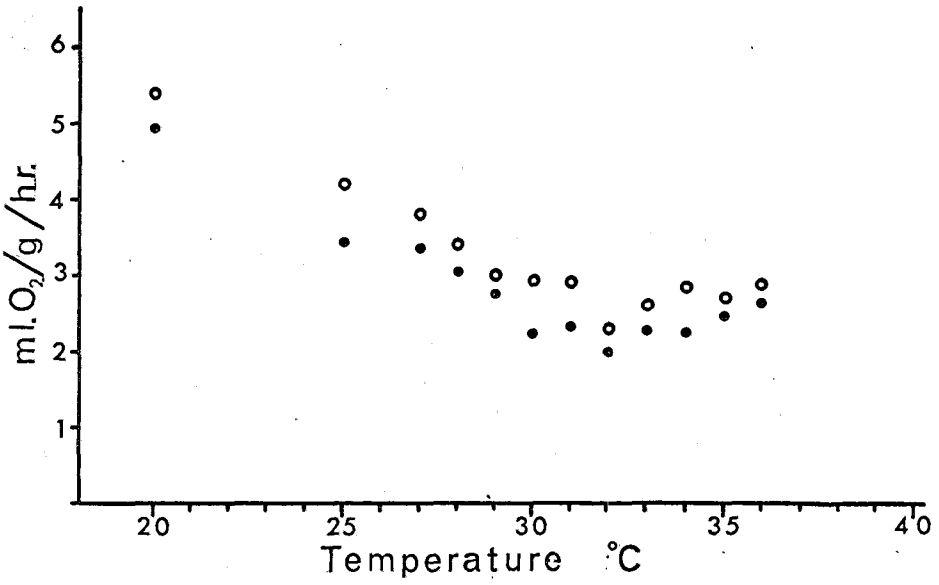


Fig.33: Minimum and average rates of oxygen consumption at various temperatures for Apodemus No.2.

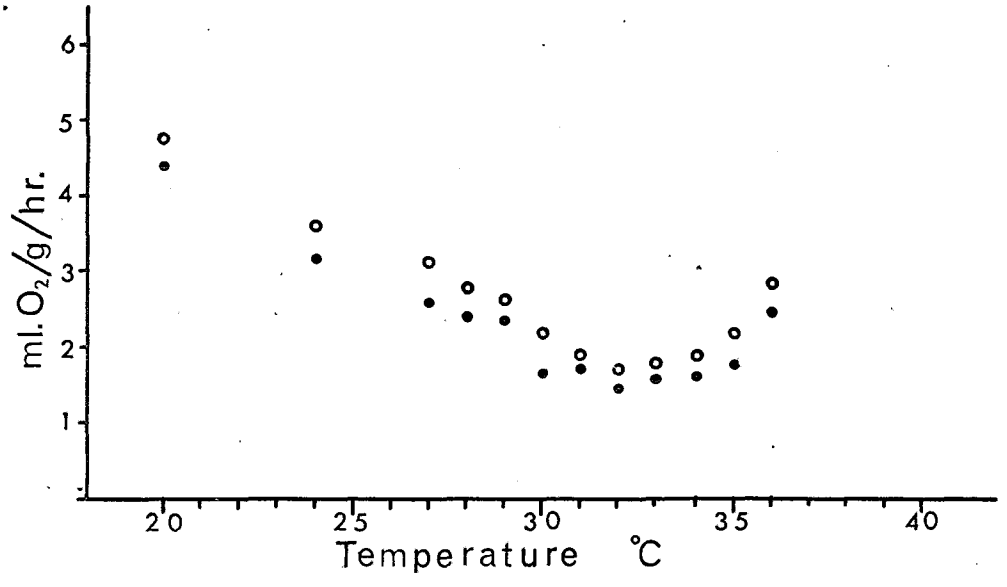


Fig.34: Minimum and average rates of oxygen consumption at various temperatures for Apodemus No.3.

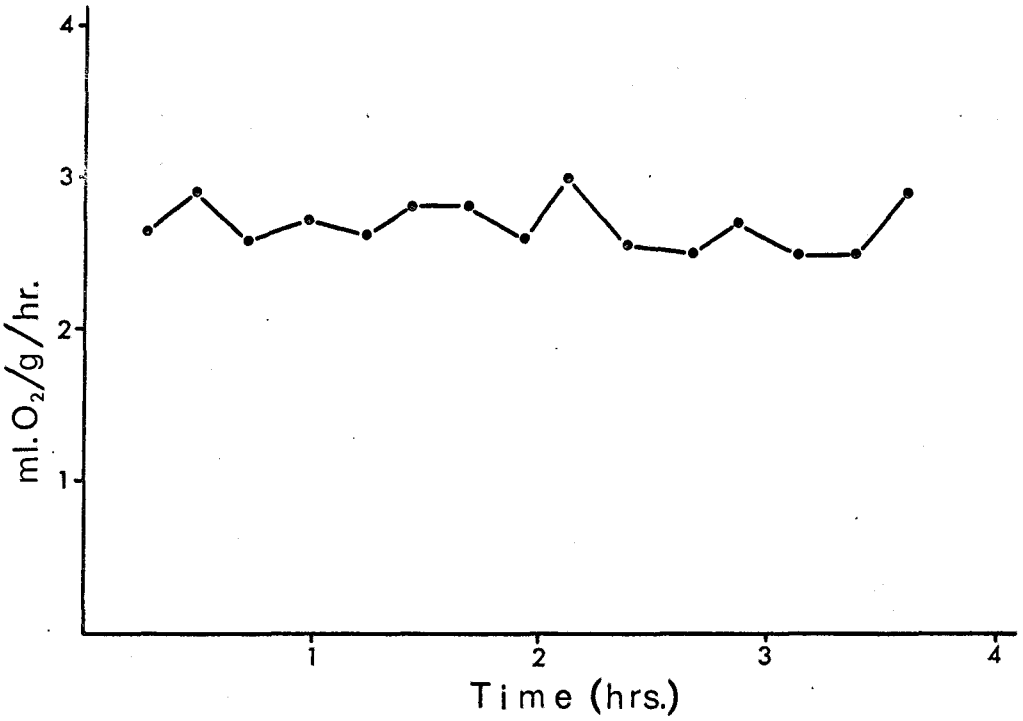


Fig.35 : Representative run on Micromys. Rate of oxygen consumption of Micromys 3 at 33°C.

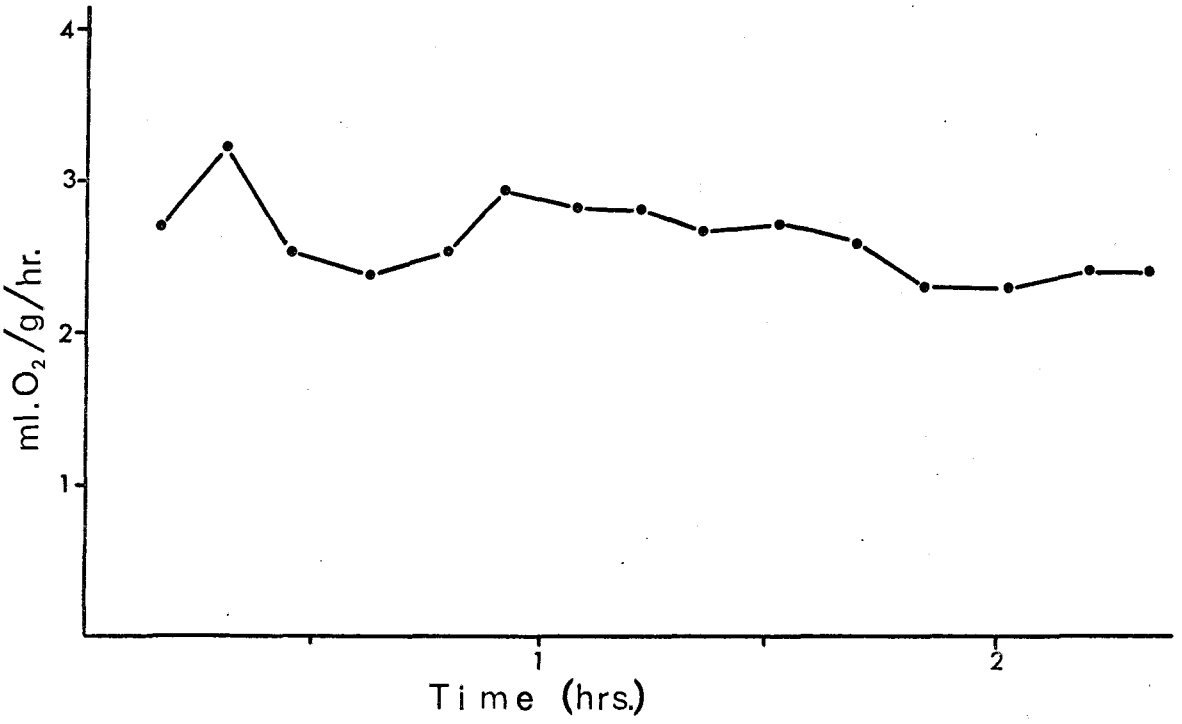


Fig. 36: Representative run on Apodemus. Rate of oxygen consumption of Apodemus 3 at 28°C.

Micromys No.	Sex	Weight (g)	ml O_2/g/hr	BMR cals/g/hr	Kcals/day	Mean BMR Kcals/day
1	♂	9.31	2.25	10.57	2.36	
2	♂	6.44	2.76	12.97	2.00	
3	♀	9.83	2.50	11.75	2.76	2.41 ± 0.10 for mice 1-6
4	♂	7.84	2.73	12.83	2.37	
5	♀	7.85	3.02	14.19	2.67	2.43 ± 0.12 for mice 1-5
6	♀	5.41	3.78	17.76	2.30	
Apodemus No.						
1	♀	15.47	1.86	8.74	3.25	
2	♂	17.04	2.00	9.40	3.84	
3	♂	20.59	1.44	6.77	3.35	3.86 ± 0.34 for mice 1-4
4	♂	26.84	1.65	7.76	4.99	

Table 16: The basal metabolic rates of Micromys minutus and Apodemus sylvaticus.

Table 16. Although individual variation is only to be expected, the high value for mouse number six is probably due to activity as the animal was observed to be restless during the experiments. Hence, this value is not included in the determination of mean BMR, which for the five animals under consideration is 2.65 ml O_2/g/hr. BMR is usually expressed in terms of the heat production of the animal, so the values obtained here for oxygen consumption were converted into calorific output. Since no respiratory quotients were determined in the present study, an R.Q. of 0.72 has been assumed and the corresponding value of 4.70 Kcals/litre O_2 used in the calculation. This is the same or close to the value used by other authors in studies on Mus musculus and shrews (Brody 1945, Morrison 1948). Expressed in this way, the mean BMR of harvest mice is 12.4 cals/g/hr or, without taking weight into account, the average animal needs 2.43 Kcals/day.

According to Brody (1945), the relationship between metabolism and body weight in all sizes of mammals may be expressed by the equation:-

$$M = aW^b,$$

where M is the BMR, W is the body weight, a is a constant derived from the ratio $\frac{\text{Kcals/day}}{(\text{body weight in kg})^{0.73}}$, b is a power transforming weight into "metabolically active weight."

The accepted values for a and b are 70.5 and 0.73 when W is expressed in kilograms; hence the equation becomes

$$BMR = 70.5 \ W^{0.73}$$

When the mean weight of the harvest mice involved in these experiments is inserted in this equation, the calculated BMR is 2.12 Kcals/day, which is in close agreement with the experimentally determined value of 2.43 Kcals/day.

It will be seen from Table 16 that the smaller individuals have a rather higher rate of metabolism per gram body weight than the larger ones.

The increase in the rate of metabolism between 33° and 20° is almost linear, each drop of 1°C causing an increase of approximately 0.30 ml O_2/g/hr in the case of mice one and three, while the increase is nearer 0.35 ml O_2/g/hr for mouse two.

Since a mammal follows Newton's law of cooling, the slope of the curve relating basal metabolic rate and environmental temperature also represents the basal thermal conductance. (Morrison et al 1959). Thermal conductance is a measure of the rate of loss of heat from the interior of the animal to the environment and is inversely related to the efficiency of insulation, with relatively high conductance values reflecting relatively poor quality insulation. The basal conductance values for Micromys are 0.30 ml O_2/g/hr/°C for mice one and three, and 0.35 ml O_2/g/hr/°C for mouse two.

The temperature at which the animal is in thermal

equilibrium with its environment is represented in most animals by a zone rather than a single temperature. From Figs. 29-31 it is obvious that the BMR is maintained at its lowest level only at 33°C, and from this it follows that the zone of thermoneutrality in the harvest mouse is of the order of 1-2°C around 33°C.

The results for Apodemus are shown in Figs. 32-34. As for Micromys, the individual measurements do not vary much at each temperature, and the mean values follow the same trend as the minimum. Variation between different mice is again recorded. In the case of Apodemus, however, no single temperature stands out as the one at which the lowest oxygen consumption was measured, and the zone of thermoneutrality is much more extensive than for Micromys. For mice two and three it appears to extend from 30° to about 34°C and for mouse one, from 28-35°C. The fourth Apodemus was recorded at 31°C and the average lowest value of all four mice was 1.74 ml O_2/g/hr or 3.86 Kcals/day. The calculated BMR, arrived at as described for Micromys, was 4.05 Kcals/day and so again there is close agreement with the experimental value.

The basal conductance of Apodemus was calculated to be 0.3 ml O_2/g/hr/°C.

The maximum oxygen consumption of Micromys two, which was measured under normal conditions, was 8.65 ml/g/hr at 23°C. This represents an increase of 44% above the calculated basal

metabolism for this animal at 23°C.

The respiratory energy loss can be compared with the maintenance energy intake as measured by food consumption. Therefore, the oxygen consumption of both species of mice at the temperature at which the feeding experiments were conducted (20°C) are presented separately in Table 17. The figures given are the mean consumption per mouse of the mean consumption per day of each mouse.

(iv) Comparison with other small mammals.

It might have been expected that the relationship BMR = 70.5 $W^{0.73}$ would not hold for extremes of small body size since it was formulated from the results of experiments on a variety of much larger mammals. However, the present study has shown that the relationship does hold for the lower limits of mammalian size. Micromys is not the smallest of all mammals; a few species of shrews hold this position, and several determinations of BMR have been made on one of them, Sorex cinereus (Morrison and Pearson 1946, Morrison et al 1959, Buckner 1964). The experimental BMR values obtained for S. cinereus (9.0 ml O_2/g/hr) do not adhere to the calculated value mainly because, owing to its almost ceaseless demands for food, it is not possible to experiment with the animals in a post-absorptive condition. It is, however, possible to

Species	No.	ml O_2/g/hr		Kcals/g/day	
		Minimum	Mean	Minimum	Mean
Micromys	3	6.68±0.22	7.32±0.07	0.75±0.02	0.82±0.02
Apodemus	3	4.55±0.17	4.94±0.18	0.51±0.02	0.56±0.02

Table 17: The oxygen consumption of Micromys and Apodemus at 20°C. The mean values given are the mean consumption per mouse of the mean consumption per hour (day) of each mouse.

adjust the values in these cases to bring them near the calculated value. Nevertheless, the harvest mouse, as one of the smallest rodents, represents the smallest class of mammals on which the BMR can be experimentally determined.

For shrews, the oxygen consumption per gram body weight rises slowly from about 4.0 to 6.5 ml O_2/g/hr for different species with body weights between 21g and 7g. However, below 7g body weight, the rate of oxygen consumption rises steeply (Pearson 1948). Similarly, the curve relating oxygen consumption per gram body weight to body weight in rodents remains at a fairly constant level of 3.5 to 4.0 ml O_2/g/hr for body weights between 26 and 10g. The present study shows that, for rodents as for shrews, oxygen consumption rises considerably with small body size, since the comparable values (at 24°C) calculated from the present results are 5.7 ml O_2/g/hr for the three smallest Micromys with a mean body weight of 7.4g.

The mean minimum oxygen consumption of Reithrodontomys megalotis, one of the smallest American rodents, is 2.5 ml/g/hr for individuals with a mean weight of 9g (Pearson 1960). This is close to the value obtained here for Micromys of 2.65 ml O_2/g/hr for a mean weight of 8.25g. Pearson also found a very small zone of thermoneutrality (not more than 3°C) for Reithrodontomys, and that the minimum metabolism was achieved at 33°C. It seems, therefore, that the metabolic requirements

of Reithrodontomys megalotis and Micromys minutus are similar, and this is evidently due to their comparable small size. However, adult Micromys can be smaller than adult Reithrodontomys and then, as Table 16 shows, the BMR rises even further.

The BMR of Apodemus sylvaticus is similar to that of other mice of this weight. Pearson (1947) found values of 1.6 ml O_2/g/hr for Peromyscus maniculatus gracilis, 1.5 ml O_2/g/hr for P. leucopus noveboracensis, and 1.7 ml O_2/g/hr for Mus musculus. Too close comparison should not be made between these figures and the value of 1.7 ml O_2/g/hr obtained here for Apodemus sylvaticus because of the former may not have been made within the zone of thermoneutrality. A number of authors have determined the BMR of Mus musculus and the values obtained vary from 6.8-13.0 cals/g/hr (Morrison 1948). The most consistent figures, however, are between 7.4 and 7.8 cals/g/hr. Apodemus sylvaticus, with a BMR of 8.1 cals/g/hr, appears to have a slightly higher basal metabolism than Mus.

The zone of thermoneutrality for the white laboratory mouse, Mus musculus, has been reported as 28°-34°C, while that of the wild Mus musculus was 32°-34°C (see Morrison 1948, for review). The zone for Apodemus, therefore, falls between these two values. Micromys, with its very small zone of thermoneutrality, appears to have little power to regulate

its body temperature by physical means. Physical means of temperature regulation, such as varying the position of the hairs to trap a larger or smaller amount of insulating air, are the only ones open to the animal in the zone of thermoneutrality. The poor ability of Micromys in this respect is in contrast to that of Sorex cinereus, as Morrison et al. (1959) found its zone of thermoneutrality to extend from 22.5-30.5°C, a range of 8°C. The zone of thermoneutrality is directly proportional to the minimum metabolism and inversely proportional to the basal metabolism (Morrison et al. 1959). This explains why S. cinereus has a wider zone of thermoneutrality than Micromys, since although its basal conductance (0.59 ml O_2/g/hr/°C) is about twice that of Micromys, its metabolic rate (9.0 ml O_2/g/hr) is more than three times that of the rodent. The shrew's high basal conductance also shows that, although the animal's physical powers of regulating its body temperature are greater than those of Micromys, outside the zone of thermoneutrality its oxygen requirements rise twice as fast as those of the harvest mouse.

The greatest influence of activity on the metabolism of Micromys is shown by the rise of 44% over the basal level. This was measured over a 16 minute period and it is probable that for brief intervals the activity may be slightly higher. Observations in the laboratory show that the mice can maintain

a high level of activity for a long time. For example, they have been observed to use exercise wheels for hours on end, stopping only briefly. It would seem, therefore, that this value of 8.65 ml O_2/g/hr at 23°C is probably a fairly normal metabolic rate for an active mouse, rather than a peak rate under strenuous exercise. The mouse did not have a wheel in the respiratory chamber, but was seen to be moving about rapidly.

D. Discussion of Food Consumption and Respiration Results.

An equation for the energy budget of a population has already been given i.e.

ASSIMILATION = RESPIRATION + NET PRODUCTION

In the present study, assimilation and respiration have been measured, but whereas the respiration experiments lasted only a few hours, food consumption was measured over 6-14 days. The mice used in the experiments were all adult and the production during the feeding experiments was estimated to be negligible. In both cases the energy flow was measured on mice at the same environmental temperature and under minimum activity conditions appropriate to the experiment. Hence, assimilation should be approximately equal to respiration, since all the energy ingested was used in the maintenance of the animal's body weight. Comparison of Tables 15 and 17 show that the maintenance

energy income of Micromys (1.10 Kcals/g/day) was greater than the minimum loss of energy through respiration (0.75 Kcals/g/day), though the difference is not so great if the mean loss of energy through respiration is considered (0.82 Kcals/g/day). In the case of Apodemus, the maintenance energy intake (0.58 Kcals/g/day) is more nearly balanced by respiratory loss (0.51 Kcals/g/day minimum and 0.56 Kcals/g/day mean). The measurements of respiratory loss were made on starved animals and hence would not include the energy cost of metabolising food. Furthermore, the mice were confined to a small chamber and showed very little activity. With these considerations in mind, it is evident that even the mean respiratory loss will be smaller than if the mice had been supplied with food and had been able to move about to a limited extent, as they were in the feeding experiments. This is born out by the Micromys number two, whose maximum energy loss, when provided with food and space in the respiration chamber, was 0.97 Kcals/g/day at 23°C, a figure which approaches even more closely to the mean assimilation energy when allowance is made for the 3°C difference in temperature (feeding experiments were carried out at about 20°C). The food and activity factors, therefore, account for much of the variation between the observed values for energy assimilation and loss.

Odum et al. (1962) found similar discrepancies in measurements of food assimilation and respiratory loss in

Peromyscus. They suggest that, because of the longer time intervals and more natural activity patterns exhibited by mice in large cages, food assimilation studies are to be preferred to oxygen consumption for estimating metabolised energy. However, the results of the Activity section of this work show that activity is by no means constant under different laboratory conditions. Therefore, to enable meaningful comparisons to be made between the results of different workers, it is preferable to measure oxygen consumption under standard minimum conditions, preferably with post-absorptive and inactive animals. Further results, presented separately and stipulating activity conditons, could be given for the additional energy necessary for maintenance of body weight over longer periods of time, either by feeding studies as in the present work, or by measuring the oxygen consumption of animals supplied with food in a large chamber over several days.

Measurements of energy flow have not yet been made on small mammals in the field, so it is not possible to relate laboratory measurements to the energy flow through wild animals in their normal environment. However, it has been demonstrated that man and animals working in the field require at least twice the calorific intake of sedentary individuals (Brody 1945), and this factor has been used to estimate the maintenance energy costs of animals in the wild from laboratory measurements (e.g. Odum et al. 1960). Doubling the laboratory measurements allows

for the interaction of temperature, activity and other factors in the field that require energy. Because of the lack of suitable information on the numbers and productivity of populations, the yearly energy flow through a Micromys population cannot be estimated. However, using the factor of two proposed by Brody (1945), it can be concluded that the approximate maintenance energy requirement of adult Micromys in the wild is 2.2 Kcals/g/day, while that of adult Apodemus is 1.2 Kcals/g/day (both figures based on assimilation, they would be a little lower if based on respiration). The significance of this difference between the two species has already been discussed.

As pointed out in the introduction to this section, comparison of the numbers and densities of different species provides limited information as to their relative importance in a community in terms of the utilisation of the energy resources of the community. Much of the energy assimilated by an animal will be used in maintaining the life of the animal and will be dissipated in respiration. Thus, this maintenance energy will be lost to the community as a whole since it will not be available as an energy source to other species. The role of a species in a community may be judged by the efficiency with which it converts its food into an energy source for other members of the community, such as

predators or decomposers. More information on populations in the field, combined with the results presented here, will undoubtedly indicate more clearly the relative roles and interrelationships of Micromys and Apodemus within the community.

E. Evaporative Water Loss.

(i) Method.

The evaporative water losses of Micromys and Apodemus were measured under two different humidities. Dry air was used for one series of experiments and air at an absolute humidity of 13.6 mg H_2O/litre of air for an animal chamber temperature of 21°C for the other. This constant humidity, which was equivalent to a Relative Humidity of 76%, was obtained by drying the air and passing it through tubes of calcium chloride or silica gel.

The apparatus used in the experiment was set up in the following order:

1) air pump,

2) U-tubes containing silica gel for drying the air,

3) saturated sodium acetate solution,

4) expansion chamber to smooth flow of air,

5) valve to allow delicate control of flow rate,

6) flow meter,

7) animal chamber,

8) U-tubes containing silica gel to collect water.

The animal chamber was the same as that used for the oxygen consumption experiments. Liquid paraffin was placed at the bottom of the chamber to collect faeces and urine and so prevent water from these adding to the water vapour collected.

The animal chamber was maintained at 21°C in a water bath. The mice were enclosed in a small perforated-zinc box to restrict their activity. The flow rate of air through the system was maintained at 140 ml/minute.

All the mice were starved for four hours before experiments began and an equilibration period of 45 minutes was allowed before the start of each series of runs. Each experimental run lasted 30 minutes and four such runs were made on three Micromys and three Apodemus at each humidity. The tubes of silica gel collecting the water vapour from the chamber were weighed before and after each run to determine the weight of water lost from the mouse.

At 76% Relative Humidity, the water content of the air passing through the chamber was determined by taking the mean of 10 runs without the mouse in the chamber. This value 57.60($\pm$0.52)mg H_2O/run, was subtracted from that obtained with the mouse present to give the amount of water lost by the mouse.

Checks were kept on all absorbing tubes to ensure that they were collecting all the water vapour.

(ii) Results.

The results are summarised in Tables 18 and 19. The mean value given is that of all four runs, while the minimum

HUMID AIR

	Mouse	Sex	Weight (g)	Water loss (mg/hr) Mean	Minimum	Water loss (mg/g/hr) Mean	Minimum
	1	♀	7.78	31.73±2.09	28.4	4.08±0.27	3.65
	2	♂	7.79	29.65±1.45	26.8	3.82±0.19	3.44
	3	♀	5.71	30.40±4.45	18.8	5.32±0.79	3.29
Mean			7.09	30.59	24.7	4.40	3.46

DRY AIR

	1	♀	6.36	25.00±4.32	19.0	3.93±0.68	2.99
	2	♂	7.54	38.13±4.53	29.4	5.07±0.60	3.90
	3	♀	5.55	26.58±2.98	19.0	4.79±0.54	3.42
Mean			6.48	29.90	22.5	4.60	3.45

Source of variation	Sums of squares	Degrees of freedom	Mean squares	Variance ratio
Change in humidity	0.001	1	0.001	0.0008
Residual	0.480	4	0.120	
Total	0.481	5		

Table 18: The evaporative water loss of Micromys under humid (13.6 mg H_2O/ litre of air) and dry air conditions, together with the analysis of variance table.

HUMID AIR

	Mouse	Sex	Weight (g)	Water loss (mg/hr) Mean	Minimum	Water loss (mg/g/hr) Mean	Minimum
	1	♀	19.00	32.80±1.42	28.8	1.73±0.07	1.52
	2	♂	23.64	26.75±1.04	24.8	1.13±0.04	1.05
	3	♂	18.37	26.80±1.07	24.8	1.46±0.06	1.35
Mean			20.34	28.78	26.1	1.44	1.31

DRY AIR

	1	♀	18.85	56.05±8.32	41.0	2.97±0.44	2.18
	2	♂	21.89	61.80±5.76	50.2	2.82±0.26	2.29
	3	♂	18.77	81.05±5.20	65.6	4.32±0.28	3.49
Mean			19.84	66.30	52.3	3.37	2.65

Source of variation	Sums of squares	Degrees of freedom	Mean squares	Variance ratio
Change in humidity	2.721	1	2.721	9.224
Residual	1.179	4	0.295	
Total	3.890	5		

Table 19 : The evaporative water loss of Apodemus under humid (13.6 mg H_2O/ litre of air) and dry conditions, together with the analysis of variance table.

is based on the minimum value obtained in any of the runs on that mouse. Analysis of variance for the effect of the two humidities on the minimum water loss of the three Micromys shows that very little is attributable to the change in humidity ($F_4^1 = 0.0008$, $P > 0.2$). In the case of Apodemus, a similar test shows that most of the variability is attributable to the change in humidity ($F_4^1 = 9.379$, $P < 0.05$). The variability within, and possibly to some extent between, the species probably reflects slight differences in activity, since it has been found in Peromyscus that the rate of evaporative water loss is very sensitive to activity (Chew and Dammann 1961).

(iii) Discussion.

These experiments were really of a preliminary nature and were intended to show whether there was a basis for more detailed research. For this reason, no definite figures can be given. However, it is evident that the increase in the evaporative water-loss in Micromys is lower than for Apodemus at the two humidities concerned.

Evaporative water loss occurs through the lungs and general body surface; it has been found that 46% of the total evaporative loss of Peromyscus occurs through the general body surface (Chew 1955). Also, evaporative water loss from the lungs is tied up with respiration, since it depends mainly on

the humidity of the inspired air, the volume of which is dependent on the respiratory rate and oxygen requirements. Thus, although not directly correlated with small body size, the evaporative water loss per gram body weight will be greater in a small mammal than in a larger one because of the greater surface area/volume ratio. This is shown by the difference in evaporative water loss of Apodemus and Micromys at 76% RH. When, however, the humidity is reduced to zero, Micromys continues to lose water at the same rate, while the loss from Apodemus increases to approximately double that at 76% RH.

The partially diurnal activity cycle of Micromys, together with its niche in the "stalk-zone" of grasses, cause the mouse to be exposed to lower humidities than the nocturnal and burrowing Apodemus. It is suggested that the ability of Micromys to restrict its water loss at the low humidity to the level at the high humidity is an adaptation to its relatively dry habitat.

For every animal there will be an optimum level of evaporative water loss at which it will be in both water and heat balance with the environment. If the evaporative water loss rises above this level, the animal will have to increase its water intake to replace that lost, and it will also require more energy to make good the extra heat lost through the latent heat of evaporation. If the evaporative loss is less than the

optimum, the water intake can easily be regulated but the heat balance may again be upset. Therefore, some evaporative water loss is obligatory, and it can account for between 28 and 56% of the daily water loss (Chew 1955). Although a reduction in the evaporative loss is not the only way to conserve water in a dry environment - more concentrated urine or drier faeces could be produced - this loss can be reduced to the least amount and becomes the critical point in the water economy of the animal (Chew 1951). Evaporative water loss, therefore, can be most important, especially to an animal such as Micromys which lives under relatively dry conditions, and it would be interesting to extend these experiments at different temperatures and humidities.

VI VARIATION.

A. Introduction.

(i) Review of the subspecific situation.

Micromys refers only to the Eurasian harvest mice. These are now all placed in a single species, M. minutus, which is found over most of Europe north of the Pyrenees and south of the Baltic, extending east into Finland and European Russia, across most of the U.S.S.R., and into S.E. Asia and Japan. Over this vast range a number of subspecies have been described - in the last overall review Ellerman and Morrison-Scott (1951) list 14 and comment "there seem to be far too many standing subspecific names in this species." Since then, Miric (1966) has reduced the number to 13 by deciding that the two specimens on which the subspecies M.m. mehelyi Bolkay was erected are in fact young Mus musculus.

The 13 standing subspecies are listed below, together with the type locality:

M.m. minutus Pallas - banks of the River Volga, Russia.

M.m. soricinus Hermann - Strasbourg, France.

M.m. subobscurus Fritsche - Wesermünde, W. Germany.

M.m. pratensis Ockskay - Western Hungary.

M.m. brauneri Martino - Kraljevo, Serbia, Yugoslavia.

M.m. fenniae Hilzheimer - Mantsala, Finland.

M.m. ussuricus Barrett-Hamilton - Ussuri, E. Siberia.

M.m. batarovi Kastschenko - Transbaikalia, E. Siberia.

M.m. japonicus Thomas - Shikoku, Japan.

M.m. aokii Kuroda - Tsushima, Japan.

M.m. hondonis Kuroda - Hondo, Japan.

M.m. erythrotis Blyth - Assam, India.

M.m. takasagoensis Tokuda - Formosa.

Many of these subspecies are known only from the type locality; where the geographical range is known, it will be given later in the "materials" section.

The chief characters on which the subspecies have been erected are differences in overall size and coloration from M.m. minutus. Some of the original descriptions of the subspecies were not available to the author; those that were are reviewed briefly below.

M.m. soricinus Hermann (1780) is a difficult subspecies to review because there are many synonymous names; Miller (1912) lists 19. These were largely distinguished by slight differences in the pelage coloration of specimens collected over most of western Europe. As it now stands, this subspecies may be described as having a light reddish-brown pelage dorsally, tending to foxy-red or even ginger, especially on the haunches. The underside is white. The head and body is usually slightly longer than the tail; Southern (1964) gives the mean head and body and tail measurements of 72 males as 57.0 mm and 53.1 mm respectively.

M.m. subobscurus Fritsche (1934) was based on 29 specimens. No mean measurements were given. Head and body 60-65 mm and tail approximately the same. Dorsal pelage is dark brown tending to light grey at the sides and rusty-brown on the upper part of the thighs. Underside is silver-white or yellow white.

M.m. pratensis Ockskay (1831) was based on one specimen but later more were described by Miller (1912). This subspecies appears to be rather larger than the others in Europe, with a mean head and body length of 69.7 mm and the tail the same (Bauer 1960). However, as originally described by Miller (1912), the chief characteristic is that the dorsal pelage is two-coloured - grey anteriorly and yellowish-brown posteriorly. This characteristic has been disputed by Bauer (1960), who found that only 20% of his specimens agreed with this description and the rest resembled soricinus. The underside of pratensis is white or grey.

Szunyoghy (1958) working on the three subspecies so far described (soricinus, subobscurus, pratensis), found that the pelage coloration varied seasonally. He concluded that there is no essential colour difference between soricinus and pratensis, and that subobscurus is a winter-coloured form of soricinus.

M.m. ussuricus Barrett-Hamilton (1899) was described on the basis of one dried skin and the corresponding skull. The specimen is large, with the head and body of the skin measuring

78 mm and the tail 62 mm. It is dark brown dorsally, dull red on the rump, and the underside is washed with dirty yellow.

M.m. batarovi Kastschenko (1910) was described from two specimens with a mean head and body length of 51.5 mm and mean tail length of 38.9 mm. The description of the pelage dorsally is similar to that of soricinus, but the underside is dark grey.

M.m. erythrotis Blyth (1855) originally described on one specimen, has had M.m. pygmaeus Milne-Edwards included with it by Ellerman and Morrison-Scott (1951), and certainly the descriptions are similar. The original M.m. erythrotis had a head and body length of 57.2 mm and a tail length of 60.5 mm. Allen (1940) reports the mean head and body and tail length of 11 specimens of pygmaeus to be 63.2 mm and 68.3 mm respectively. The descriptions of the coloration are also similar - dorsal surface a dull russett, evenly and minutely lined with black hairs, and tending to a ruddy coloration on the rump. The underside is dull white or fawn.

The colour difference between these subspecies are clearly unreliable (Szunyoghy 1958, Bauer 1960). Measurements may provide a rather better guide, but, as has been discussed recently by Fullagar and Jewell (1966), different methods of measuring body and tail lengths of small mammals can give different results. Too much reliance cannot be placed on

comparison of the measurements given above. However, it does appear that the S.E. Asian subspecies M.m. erythrotis has a tail slightly longer than the head and body, whereas the other subspecies have the tail equal to or rather shorter than the head and body. With this exception, it would be little more than guesswork to classify any specimen unless the geographic locality from which it came was within the known range of a particular subspecies.

(ii) Review of methods.

Several types of variation have been studied in small mammal populations. Matthey (1952) examined the chromosomes of several species of murids and Kalabuchov (1937) compared populations of Apodemus sylvaticus ciscaucasicus on the basis of the amount of haemoglobin in the blood. However, the majority of studies on continuous variation have dealt with linear measurements of the whole animal or skeletal parts, especially the skull (e.g. Delany 1964, Corbet 1964). The system of numerical taxonomy recently introduced allows the use of many different types of characters to be combined in the estimation of affinity between groups. Numerical taxonomy has been defined as "the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities." (Sokal and

Sneath 1963). By converting information about taxonomic entities into numerical quantities, physiological, cytological and even distributional information can be included with morphological characters. The main criterion for choosing characters is that they should be genetically determined and contain, as far as is known, only one piece of taxonomic information. Phylogenetic considerations and the problem of homology between characters, with which one is usually concerned in orthodox taxonomy, play no part in numerical taxonomy, since by this process affinity is estimated solely on phenetic grounds (Sokal and Sneath 1963).

Thus, in the study of variation and the erection of taxonomic groups, many types of characters can be combined to give an estimate of affinity, a procedure which will more clearly reflect the overall similarity between the groups than the few characters conventionally used. In the present study, however, only morphological characters could be included, since museum specimens consisting of skins and skulls were all that were available for examination.

Conventional taxonomic methods usually give more weight to certain characters on the basis of their presumed importance. In numerical taxonomy each character is given equal weighting. The taxonomic equivalence of all characters is clearly seen if attempts are made to construct an objective criterion for weighting the characters. Characters cannot be weighted unless

exact rules for estimating the weight can be given, i.e. should one character be given twice, 20, or 200 times the weight of another. There seems to be no way of deciding this. Furthermore, the concept of taxonomic importance has no exact meaning - if, for example, "importance" means basic or fundamental, then it is a summary of other characters; if it means essential to survival, then the taxonomy would estimate viability but not resemblance. "Importance" also varies according to the use of the taxonomy. A "natural" or orthodox taxonomy is a general arrangement that can be used by the majority of scientists; if special weight is given to certain characters it ceases to be a general arrangement.

Thus, if no decision can be made on how to weight the characters, they must be given equal weight unless weight is allocated on irrational grounds.

The main aims of numerical taxonomy are repeatability and objectivity. Its chief differences from conventional methods are in the large number of characters used and the equal weight given to each character. The methods used in this study are based upon these concepts and will be described in detail later.

(iii) Epigenetic variation.

As outlined above, discontinuous characters controlled

by genes may be included with continuously variable characters in one analysis. Discontinuous variation in the form of genetic polymorphism has been shown to be of value in evolutionary studies (e.g. Ford 1964). However, another type of discontinuous variation, termed epigenetic polymorphism, depends not only on genes but also on the action of the environment during the development of the character (Waddington 1953). Although, as discussed below, populations can be characterised on the basis of epigenetic variants, in view of incomplete genetic control over such characters it is better to separate the analysis of epigenetic variation between populations from that of genetic variation.

Epigenetic variants have been investigated by a number of workers (e.g. Grüneberg 1952, Deol 1955, Grewal 1962) on laboratory populations of Mus musculus. It has been demonstrated that a threshold mechanism is involved in this type of variation which results in the splitting of an originally continuous distribution into sharply distinct adult phenotypes (Grüneberg 1951). Over 50 of these discontinuous variants have now been described in inbred lines of Mus musculus, and most of these characters are skeletal, such as double instead of single foramina in vertebrae and skulls. However, it must be remembered that there will be corresponding changes in the nerves and arteries concerned.

Searle (1954) and Deol and Truslove (1957) have carried

out studies to determine the cause of these variants. They found that the occurrence of any particular variant is determined by the attainment of a critical size at the relevant stage of development. If the mother was fed on an abnormal diet, the incidence of variants could be altered, and this variation was partly due to differences in maternal physiology and hence the intra-uterine environments of the abnormally-fed mice.

Thus, each epigenetic character is determined by many genes, as well as by environmental factors, some of which may be tangible, such as maternal physiology, but most of which are intangible and act unilaterally. (Searle 1954). In addition, the expression of the character is subject to the action of a threshold which must itself be partly under genetic control. A change in the frequency of a particular character within a population may be brought about not only by a gene tending to shift the mean of the underlying continuous variable, but also by any gene which tends to alter the threshold parameter.

Because so many factors can affect the expression of an epigenetic variant, it is likely that isolated breeding populations of a species will show different frequencies of the same variants. Weber (1950) showed that there were in fact well-marked frequency differences of epigenetic characters between wild populations of Mus musculus. Several other

workers (e.g. Berry 1963 on Mus musculus and Grüneberg 1961 on Rattus rattus) have found marked frequency differences with respect to some variants when very close, as well as distinct, populations were examined. Berry and Searle (1963), examining a large sample of Mus musculus (585 specimens) from one locality, did not find some variants which are known to occur in this species. It seems, therefore, that the spectrum of variation exhibited by a population is a characteristic of that population.

Berry and Searle (1963) found that different species of rodents had different patterns of variation, and the characters themselves showed a number of individual characteristics when their frequencies in the different species were compared. When comparisons were made between three species of Cricetidae and five of Muridae, six variants were found only in the Muridae and none only in the Cricetidae. There is thus some evidence for a phylogenetic change in the pattern of variation.

Berry and Searle (1963) have surmised that a threshold variant can be brought entirely under genetic control, and hence fixed in a population, by a process similar to the "genetic assimilation" postulated by Waddington (1953). In this, selection is considered as affecting factors controlling the capacity for response to the environment. Such selection would tend to alter some of the interrelations which constitute

development and, by lowering the threshold, allow the character to be produced over a wider and wider range of environments until it eventually becomes more or less under genetic control in certain individuals.

The characterisation of populations by the frequency distribution of epigenetic characters means that the study of epigenetic variation can form a useful complement to the study of genetic characters, though it would not be advisable to classify populations solely on these "minor variants."

(iv) General Introduction.

The present work deals largely with populations of Micromys from western Europe, but small numbers of some of the Asiatic subspecies (all that could be obtained) have been included. Only preserved material in the form of skins and skulls was available, and as the pelage coloration has been shown to vary seasonally in some subspecies (Szunyoghy 1958), it was decided to use only the skulls. Both linear measurements and epigenetic characters were studied and were analysed independently. It was anticipated that by using these two independent methods, the patterns of genetic variability would appear and thereby clarify the position with regard to subspecific relationships, as well as providing information on variation within the species in general.

B. Material and Measurements.

A total of 367 skulls was examined, representing seven subspecies. (Despite intensive searches, these were all that could be obtained.) The mice from Studland Heath and Norfolk were collected by the author, and those from Odiham were kindly donated by F.P. Rowe. The rest of the collection was obtained from the following sources:-

1. Natural History Museum, Paris, France.
2. Natural History Museum, Brussels, Belgium.
3. Natural History Museum, Leiden, Holland.
4. Museum Alexander Koenig, Bonn, W. Germany.
5. Natural History Museum Senckenburg, Frankfurt, W. Germany.
6. Humboldt University, Berlin, E. Germany.
7. Martin Luther University, Halle/Saale, E. Germany.
8. Zoological Museum of the University, Moscow, Russia.
9. Natural History Museum, Chicago, U.S.A.

The material obtained was divided for analysis in two ways. Firstly it was separated into the subspecies. Secondly, because the populations belonging to M.m. soricinus had been obtained from a number of distinct areas, these populations were kept separate so that variation within this subspecies could be studied. Further details of the material follow below:

1. Subspecies examined, numbers, and localities.

The letters in brackets refer to the map, Fig. 37.

M.m. soricinus

(A) England. 21, Studland Heath, Dorset.

(B) England. 7, Norwich, Norfolk.

(C) England. 53, Odiham, Hampshire.

(D) Belgium. 40, Wynckel St. Kruis.

(E) Holland. 22, 16 localities all over the country.

(F) France. 19, Lagny (Seine et Marne).

(H) Halle/Saale, E. Germany. 36, 4 localities all within 20 miles of each other.

(I) Berlin, E. Germany. 25, 5 localities within 30 miles of each other. (18 in this group from Furstenwalde Spree).

(K) Ukraine, Russia. 9, 3 localities (6, Poltava, others from different parts of the Ukraine)

The range of soricinus is roughly equivalent to the total area enclosed by these samples with the addition of White Russia and Poland.

M.m. subobscurus

(G) 85, Garthesheide and Emsbek, near Oldenburg, W. Germany. This subspecies is found only in this region and is thus completely surrounded by populations of soricinus.

M.m. pratensis

(J) 6, Kisbalaton, Hungary. This subspecies is found in Hungary, Roumania, and parts of Yugoslavia.

M.m. minutus

9, 4 localities. This is the type subspecies and its range extends over the European part of the U.S.S.R. to the River Ob in western Siberia, north and east Kazakhstan.

M.m. batarovi

6, 4 localities. This subspecies is found in central Siberia from the River Ob to the Lake Baikal region.

M.m. ussuricus

5, the Khabarovsk area, the only locality where this subspecies is found.

M.m. erythrotis

23, various localities in the Szechwan province of China. This subspecies is also found in the Yunnan, Fukien, Hupeh, and Shensi provinces of China, and in Assam, N. Burma, and N. Vietnam.

The ranges or localities of the mice in this collection are shown in Figs. 37-38.

The numbers of mice given above are the numbers included in the epigenetic analysis, except for the omission of the subspecies minutus, batarovi, and ussuricus on account of the small and heterogeneous samples. Multivariate analysis could only be carried out on skulls for which a complete set of

Fig. 37: Map showing the localities in Europe from which populations used in the present study originated. For explanation of letters, see text.

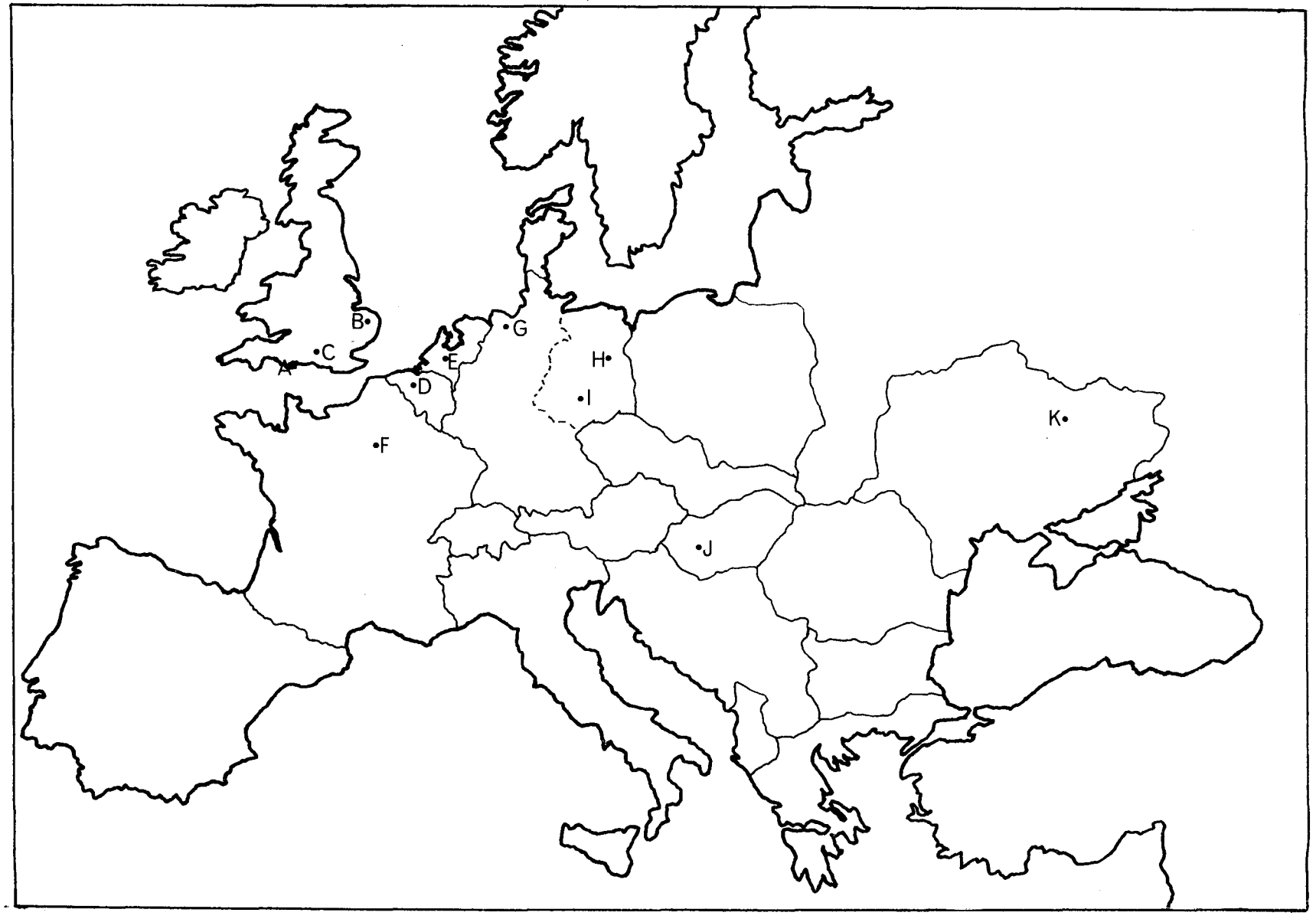
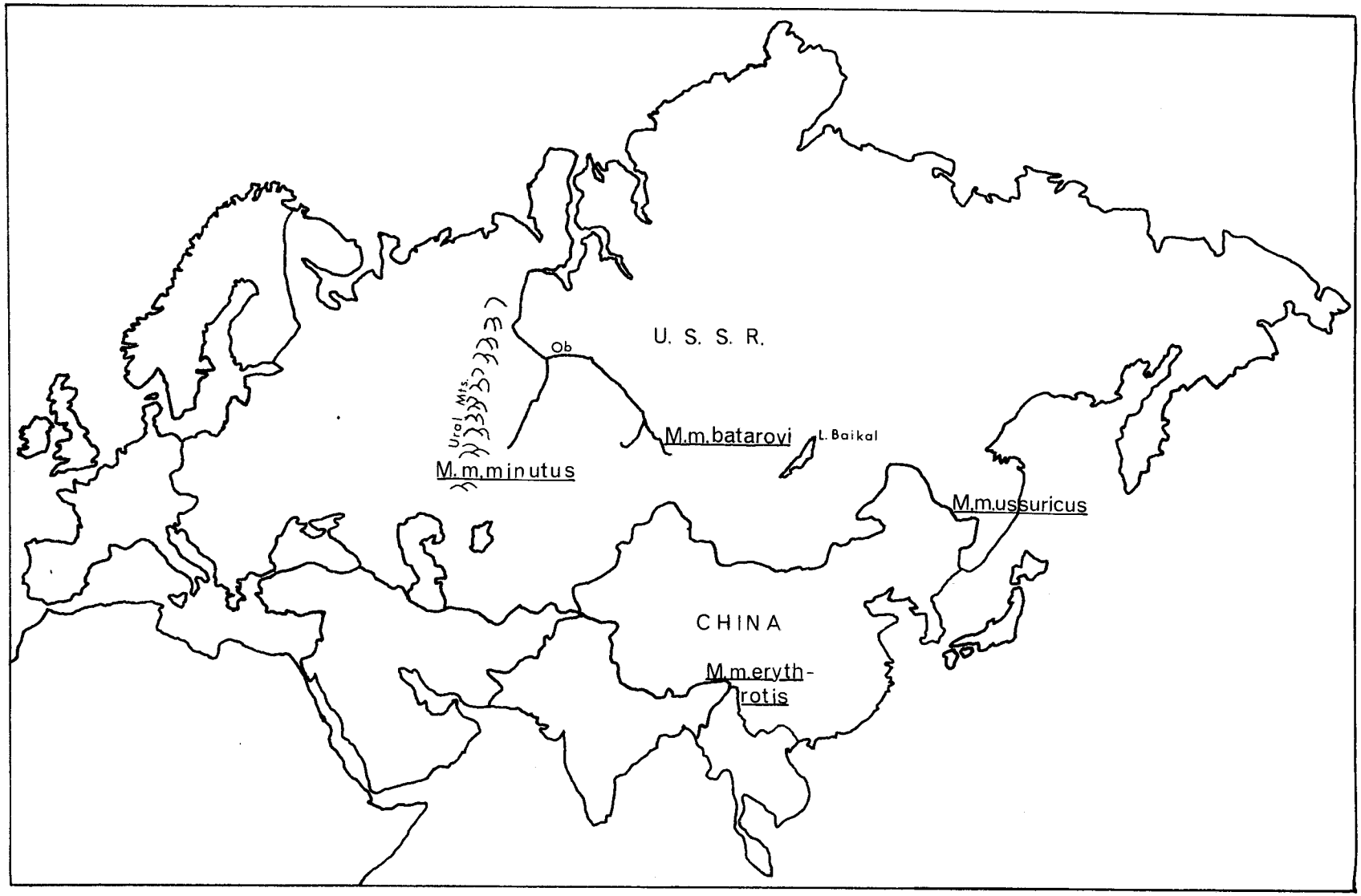

A
B
C
D
E
F
G
H
I
J
K

Fig. 38: Map showing the location of the Asiatic subspecies of Micromys minutus.


U. S. S. R.
Ob
Ural Mts.
M.m.batarovi
L. Baikal
M.m.minutus
M.m.ussuricus
CHINA
M.m.eryth-
rotis

measurements was available and as many of the specimens were damaged, the numbers were somewhat smaller than those used in the epigenetic analysis. The numbers of the different populations taking part in the multivariate analysis were as follows: M.m. soricinus: Studland 18, Odiham 49, Belgium 10, France 13, Halle 26, Berlin 15, Ukraine 9; subobscurus 73; pratensis 6; minutus 9; batarovi 6; ussuricus 5; erythrotis 7. The Dutch and Norfolk pupulations were omitted from the multivariate analysis because of too few complete skulls.

2. Measurements.

(i) Linear characters.

For reasons already explained,only skulls could be used for the analysis and so choice of characters was necessarily limited to this part of the body. The measurements were chosen with the object of obtaining as much information as possible on the size and proportions of the skull. The fact that characters were only taken on the skull does not mean that information was only obtained concerning a special class of genes. A gene having a conspicuous effect on one part of the body is likely to affect other characters as well.

The larger measurements were made with the same pair of Vernier callipers, which measured to an accuracy of 0.1 mm. Measurements of diastema, tooth rows, palatal foramina ,and distance between first molars were made using a micrometer

eyepiece in a low-power monocular microscope. The graticule was graduated in units of 0.07mm. The measurements taken are mainly those described by Southern (1964), and are illustrated in Figs. 39-41.

1. Greatest length of skull (GL). The greatest measurement that can be taken of the long axis of the skull.
2. Cranial width (CW). The greatest width across the cranium, excluding the roots of the zygomatic arches.
3. Inter-orbital constriction (IC). The narrowest width of the frontal bones at the interorbital constriction.
4. Condylo-incisive length (CIL). Measured from the hindmost surface of the occipital condyles to the foremost surfaces of the incisors.
5. Basal length (BL). Another measure of the length of the skull, this time taken from the mid-point of the lower margin of the foramen magnum to the foremost surfaces of the incisors.
6. Length of maxillary tooth row (MXT). Measured from the anterior margin of the first cheek-tooth to the posterior margin of the last.
7. Length of diastema (LD). Measured from the posterior margin of the alveolus of the incisor to the anterior margin of the first molar.
8. Distance between first molars (DM). Measured as the minimum distance between the inside edges of the first molars.

Fig. 39: Dorsal view of the skull of Micromys showing the measurements and epigenetic characters studied; the former are referred to by letters and the latter by numbers (see text).

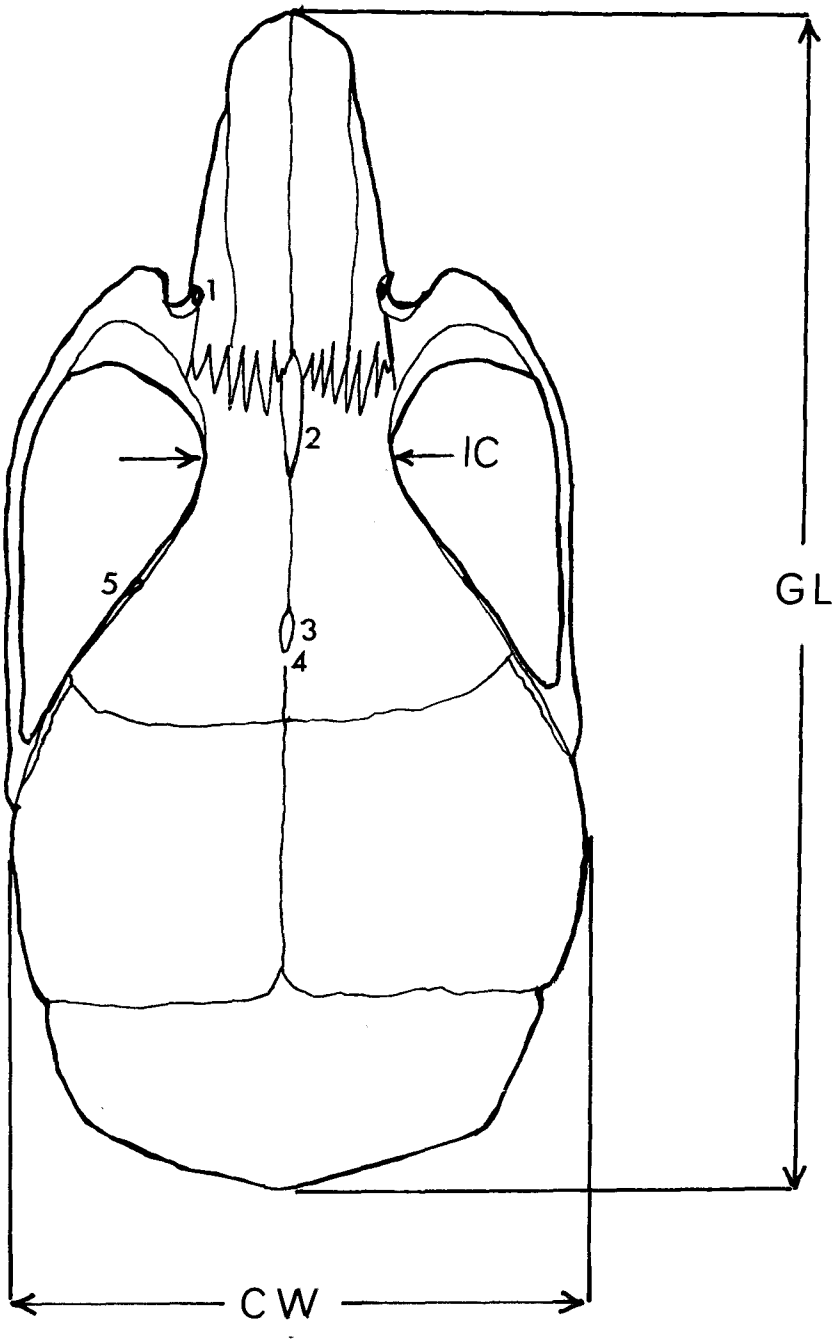

1
2
IC
5
3
4
GL
CW

Fig. 40: Ventral view of the skull of Micromys showing the measurements and epigenetic characters studied.

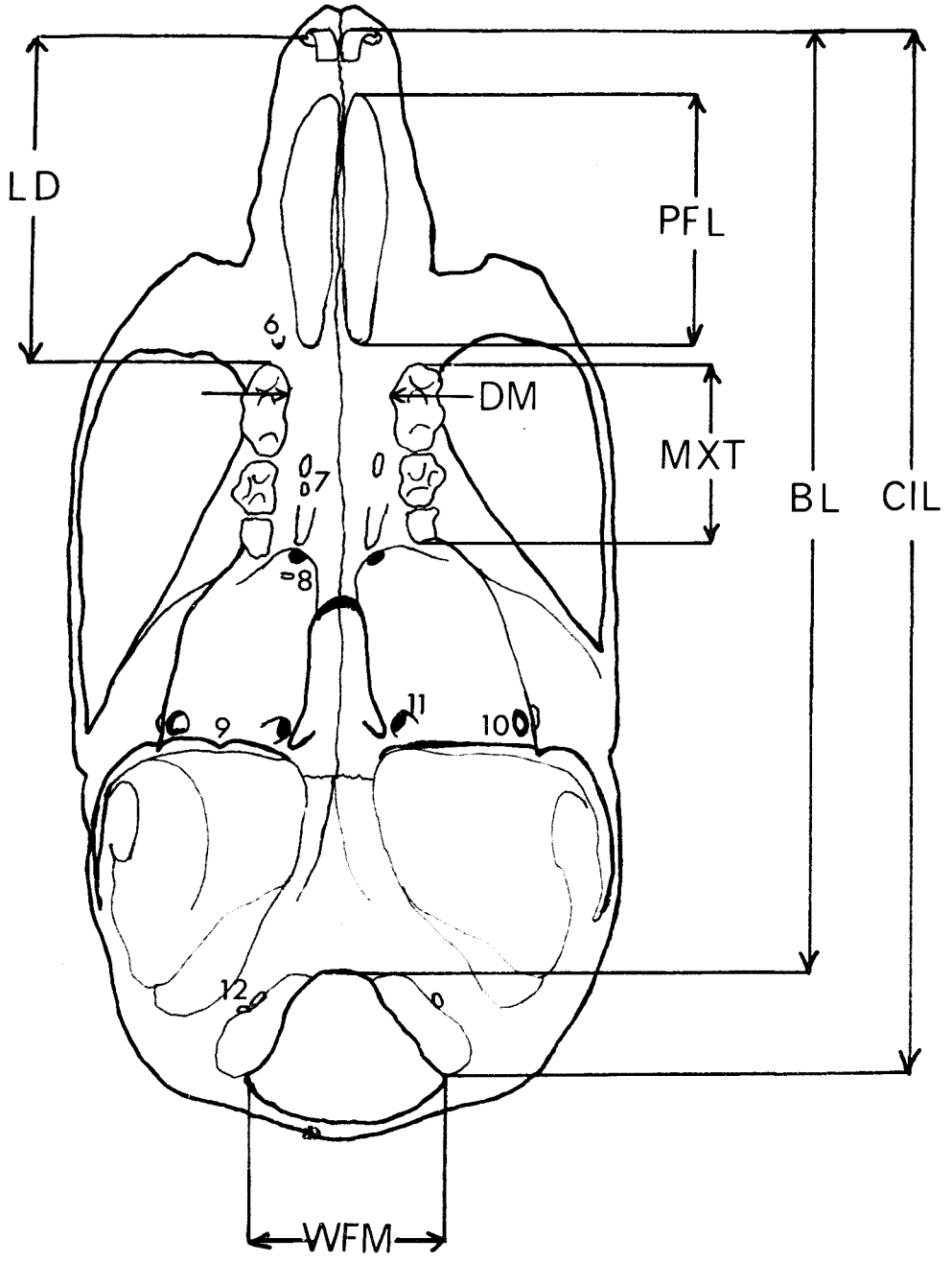
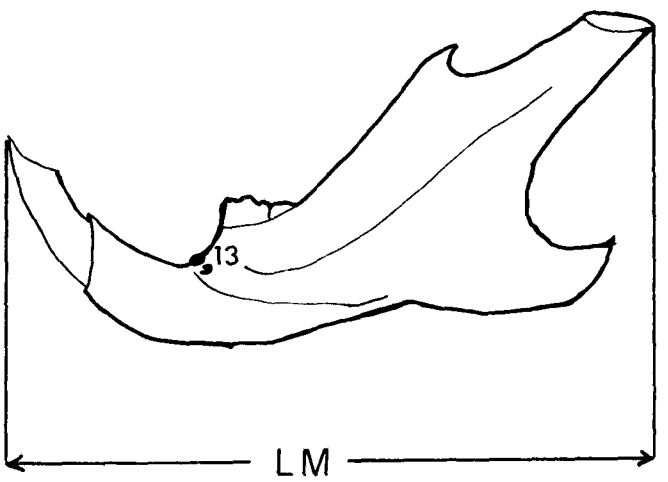
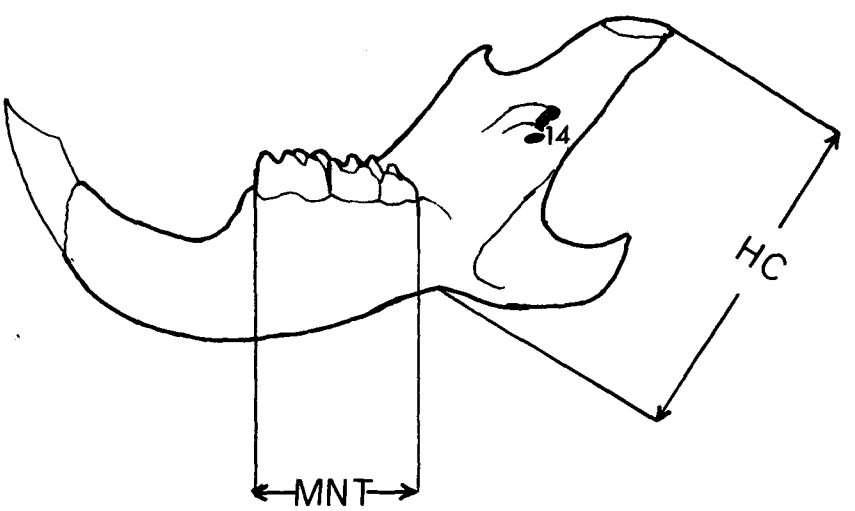

LD
PFL
DM
MXT
BL
CIL
WFM
6
7
8
9
10
11
12

Fig. 41: Lateral view of left mandible and medial view of right mandible of Micromys, showing the measurements and epigenetic characters studied.


13
LM


14
HC
MNT

9. Length of palatal foramen (PFL). The greatest length of the palatal foramen.
10. Width of Foramen magnum (WFM). The greatest width of the foramen magnum, taken just above the occipital condyles.
11. Mandibular length (LM). The greatest length of the mandible plus incisor, taken from the anterior surface of the incisor to the hindmost point of the articular process.
12. Height of mandible (HC). Taken from the notch on the lower margin of the mandible to the hindmost point of the articular process.
13. Length of mandibular tooth row (MNT). The maximum length of the lower molar tooth row.
14. Tooth wear. A count was made of the number of cusps visible on the upper molar tooth row. For further details, see later.

(ii) Epigenetic characters.

The epigenetic characters studied are similar to those used by Berry (1963) on Mus. Owing to the poor cleaning of many of the skulls and their small size, many of the characters described by Berry (1963) could not be used. The following characters could generally be easily identified and they are shown in Figs. 39-41.

1. Preorbital foramen double.

   This foramen occurs on the lateral side of the skull anterior to the canalis infraorbitalis, and is usually on the suture between the maxilla and premaxilla. It is occasionally double.

2. Interfrontal present.

   This bone is found in the suture between the frontals anterior to the transverse sinus.

3. Parted frontals.

   This is represented by a widening of the suture between the frontals behind the transverse sinus

4. Fused frontals.

   Partial fusion of the frontal bones along the dorsal suture. This character was never found in these populations of Micromys.

5. Frontal foramen double.

   This foramen occurs on the lateral surface of the frontal bone just below the dorsal edge of the orbit. It is occasionally double.

6. Maxillary foramen I present.

   This occurs on the ventral surface of the maxilla anterior to the tooth row. It is sometimes absent in Micromys.

7. Foramen palatinum majus double.

   The foramen palatinum majus is sometimes divided into two by a bridge of bone.

8. Foramen palatinum minus anterius present.

The character studied is shown on one side of the skull in Fig. 39. Occasionally there was another foramen posterior to the one shown, but this was not scored.

9. Processus pterygoideus present.

This process on the posterior surface of the sphenoid bone varies in size from a small prominence to a large angular projection. It was scored as present, regardless of its size, or absent.

10. Foramen ovale single.

The absence of a septum of bone dividing the foramen ovale classifies it as single. The foramen ovale was always double in these specimens of Micromys.

11. Foramen pterygoideum double.

The foramen pterygoideum occurs in the sphenoid bone medial to the foramen ovale and lateral to the petrosal process. It was never found to be double.

12. Foramen hypoglossus double.

This foramen occurs on the occipital bone on either side of the foramen magnum on the ventral surface. It may be single or double.

13. Accessory mental foramen.

The mental foramen was occasionally accompanied by another small foramen.

14. Mandibular foramen double.

The mandibular foramen, which occurs on the inner surface

of the mandible, was occasionally double.

C. Methods of Analysis.

1. Methods based on linear measurements.

(i) Age adjustment.

Some of the variation between populations is likely to be due to their different age compositions for Haitlinger (1962) has shown that the skull of Apodemus continues to increase in size throughout the animal's life. To eliminate this variation, it is usual in studying linear characters to introduce a factor to correct all the measurements to the size of a uniform age group. For Apodemus, Delany and Davis (1961) introduced a method based on tooth wear to estimate relative age. They found that the cusps on the teeth wear down and are eliminated in a fairly regular sequence, and that by counting the number of cusps remaining, a measure of the relative age was obtained. Since the cheek teeth of Micromys are essentially the same as those of Apodemus (Barrett-Hamilton and Hinton 1910-21), this method was followed to estimate the age of the mice in this study. The upper molar tooth row was examined under a low-power binocular microscope and the skull tilted so that cusp $M^1 1$ was directly opposite cusp $M^1 x^1$ (cusp notation as in Barrett-Hamilton and Hinton 1910-21), and the number of cusps visible was counted. 12 cusps show in a very young animal,

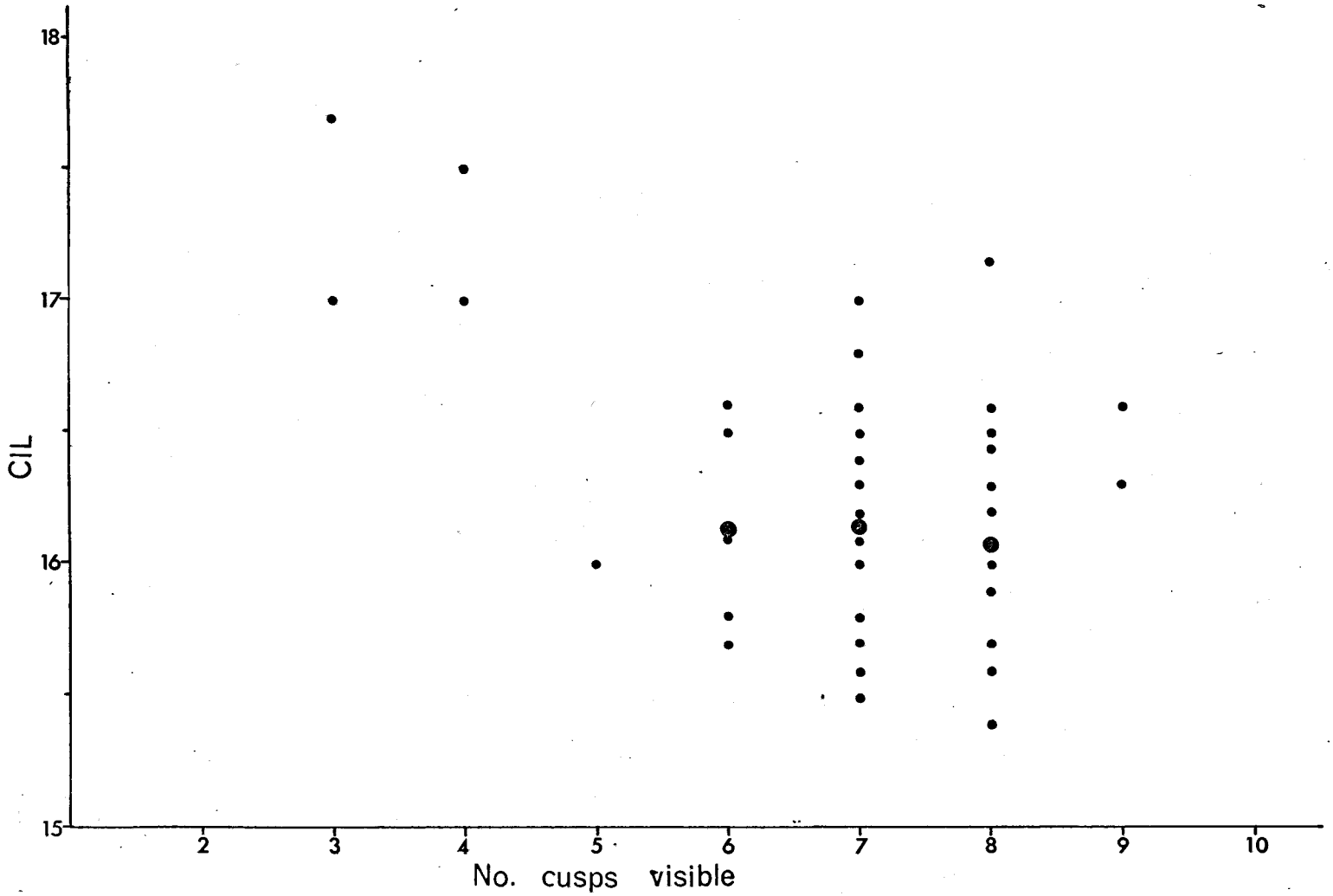


Fig.42: Scatter diagram for the regression of condylo-incisive length on tooth wear for the Odiham population. (● = mean).

POPULATION	No. cusps visible	No. skulls
M.m.soricinus		
Studland	7.9	18
Odiham	7.2	49
Belgium	7.9	10
France	8.1	13
Berlin	7.7	15
Halle	7.5	26
Ukraine	7.4	9
M.m.subobscurus	7.3	73
M.m.pratensis	8.3	6
M.m.minutus	8.2	9
M.m.batarovi	7.5	6
M.m.ussuricus	8.2	5
M.m.erythrotis	7.1	7

Table 20: Mean tooth wear, in terms of the number of cusps visible, for each population taking part in the multivariate analysis.

However, examination of the tooth-wear values revealed that the great majority of the animals had six, seven or eight cusps visible and thus would belong to a similar age group. When a scatter-diagram for the regression of condylo-incisive length on tooth-wear is plotted for the largest homogeneous population available (Odiham), little or no increase in the length of the skull occurs for tooth-wear values of six, seven or eight (Fig. 42). Furthermore, too few skulls were available with different tooth-wear values for a reliable estimate to be made of any variation in length outside these values. In consequence, only skulls with a tooth-wear value of five, six, seven, eight or nine were included, and these were taken to be members of the same age-group; hence no age-adjustment was necessary. This procedure, which was carried out mainly to simplify analysis, was justified by the lack of correlation between tooth-wear and the length of the skull at these values, and by the fact that a few skulls had tooth-wear values outside this range so that the numbers in each population were reduced only slightly. Table 20 shows the mean tooth-wear values (in number of cusps visible) of the different populations for the skulls included in the analysis. All populations fall between 7.1 and 8.3.

(ii) Statistical Methods.

It has already been stressed that large numbers of

characters are used in numerical taxonomy. The question now arises of how to make the best use of these data. In conventional methods, characters are compared singly, or as ratios, between each pair of populations, but when many characters and populations are used there will be so many comparisons, each providing evidence on the similarities of the groups, that the resulting picture will be extremely complex. Moreover, since the various aspects of living organisms are intimately associated, many if not all of the characters taken on a single individual will be correlated. Hence, tests based on these characters will not be independent and it will not be known to what extent the single measurements provide independent measures of distinctness between the populations. The correct statistical method is to treat the set of characters as a single coherent matrix. Such a technique, known as a multivariate analysis, considers all the characters simultaneously and allows for correlations between them.

There are two main methods of multivariate analysis which have both been used on rodent populations. The first of these is known as factor analysis and has been employed on studies of variation in Apodemus sylvaticus by Delany (1965). Factor analysis is a statistical technique for reducing a large number of correlated variables (which are the correlations among the individuals on the basis of the measurements taken)

to terms of a small number of uncorrelated variables (called "factors"). Thus, by means of factor analysis one is able to determine a few common factors which represent the variational patterns of the group being studied. The analysis is carried out on all the data collected, which is pooled irrespective of any subdivisions previously recognised (such as localities, subspecies etc.). From these pooled data, the components responsible for most of the variance within the group are distinguished. Factor analysis is thus concerned with finding the principal components of the variance within the group (all the pooled data) as a whole, and the variation between any existing subdivisions is minimised. Since the greatest variation component of body dimensions within a group is generally age and size (Teissier 1955), the results of factor analysis are chiefly based on these features. For example, factor analysis suggests that life history and genetical size account for much of the variation within populations of Apodemus sylvaticus (Delany 1965).

In the second type of multivariate analysis, which is based on the discriminant function, the initial groupings (in localities, subspecies etc.) of the data are kept separate and measures are obtained of the variation between the groups. Thus, in discriminant function analysis the differences between the groups are emphasised and the between-group covariance matrix is standardised by the within-group covariance matrix (pooled

for all samples). As already mentioned, size and age account for most of the within-group variation and so standardisation of the between-group variation by the within-group variation emphasises other factors of variation besides age and size. (Jolicoeur 1959). Discriminant function analysis has been used in studies on Peromyscus spp. by Foster (1963), and on Apodemus sylvaticus by Delany and Healy (1964) and Whittaker (1965).

If the principal components of variation within a group are extracted by factor analysis, a classification of the group may be based on these components. Factor analysis is used in this way in many studies in numerical taxonomy, and it can also be applied when any previous subdivisions of the group are ignored and it is desired to know whether the principal components of variation within the group correspond to these previous subdivisions (see Delany 1965). If, however, it is desired to keep the subdivisions of the data separate and to examine the affinity between them and reorganise them on the basis of this affinity, then discriminant function analysis is called for. For these reasons, discriminant function analysis was chosen in the present study since it was desired to test the validity of the subspecies of M. minutus, and in discriminant function analysis any variation between the subspecies is maximised. Hence, this provides a better measure of discrimination than factor analysis, in which between-subspecies

variation is minimised. Furthermore, the results of discriminant function analysis are likely to be easier to interpret than those of factor analysis, since the components extracted by factor analysis may not correspond to the original groups and do not provide any measure of the distinction between them.

The discriminant function was introduced by Fisher (1938) and use has been made of it in the following manner. A number of measurements (n) are taken on two known species or varieties and from these n measurements ($x_1, x_2 \ldots x_n$) the coefficients ($c_1, c_2 \ldots c_n$) of each measurement are computed and a single discriminating function X is set up:

$$X = c_1x_1 + c_2x_2 + c_3x_3 \ldots + c_nx_n.$$

The coefficients ($c_1, c_2 \ldots c_n$) are calculated from the means, variations, and correlations of the measurements within both species and in order to keep the groups as separate as possible the coefficients are chosen so as to minimise the variation within each group and maximise that between them. When the coefficients have been calculated, the measurements of each species are substituted for $x_1, x_2 \ldots x_n$ in the function and a value of the discriminant X obtained for each species. Then, if any further specimens are obtained whose classification is uncertain, the discriminant X is calculated using the coefficients from the two control groups together with the measurements of the new specimens. The difference between the discriminant of the new specimens and those of the control groups can be

determined and the new specimens assigned to whichever control group is indicated by significant comparison.

The discriminant function is thus essentially a comparative test. From it, a second multivariate function, the generalised distance, may be calculated. The generalised distance (D^2) was first proposed by Mahalanobis (1936), and it sums up in one quantity the divergence between the means of the complete set of measurements in one group and those of the group with which it is being compared (making allowances for the variances of the measurements and the correlations between them). It is thus a mathematical measure of the absolute resemblance between two groups and the larger D^2 is, the more difference exists between the groups in terms of the characters used. Generalised distances have been used to separate populations of Apodemus sylvaticus (Delany and Healy 1964) and Crocidura spp. (Delany and Healy 1966), and they have also been used to provide a concise geometrical presentation of the relationships of morphometrics in locusts with various environmental factors (Stower et al 1960).

In the present study, discriminant functions between each pair of populations were calculated using a step-wise multiple regression analysis following that described by Efroymson in Ralston and Wilf (1960). In this case the discriminant coefficients are the same as the regression coefficients. The

program was written by M. Garside of the London School of Economics and was run on the I.C.T. 1909 computer at the University of Southampton. From these results the generalised distance (D^2) was calculated by hand for each pair of populations using the formula:-

$$D^2 = \frac{R(n_1 + n_2 - 2)}{K(K-R)}$$

where n_1 and n_2 are the numbers of animals in each population, R is the sum of squares of differences from the means, and $K = \frac{n_1 n_2}{n_1+n_2}$.

The multivariate analysis of data does not provide new information; it merely enables the data to be handled so that general underlying patterns of variation can be seen. It does not necessarily follow that the results will have any biological meaning, but they will provide a guide to the similarities of the groups studied and, as such, may lead to the erection of hypotheses concerning the nature of the processes accounting for the variation.

Multivariate analysis is a better indicator of the main similarities of the populations than univariate analysis, but the latter method permits more detailed examination of the characters responsible for the differences. Consequently, as well as the multivariate analysis, the populations were compared on the basis of two linear measurements: Condylo-incisive length and cranial width. These two characters were

chosen because they were not highly correlated (r = 0.48) and give a guide to the overall size of the skull. Condylo-incisive length is preferred to other the measures of length taken because it suffers least from damage to the skull. The greatest length measurement is not so reliable because the projections of the nasal bones in front of the incisors were occasionally damaged. The means, standard errors and ranges of condylo-incisive length and cranial width were calculated, and comparisons between populations made on the basis of these. The means of the other characters used in the multivariate analysis were also computed, as were the correlations between all pairs of characters.

2. Methods based on Epigenetic variants.

Each character was scored as present or absent in every skull from all populations, and the percentage incidence of the characters in each population was calculated. A percentage is determined to different degrees of accuracy according to the size of the sample on which it is based. Consequently, when working with percentages it is necessary to transform them into values whose variance does not depend on the percentage itself. The transformation used here was one described by Grewal (1962). The percentages are transformed into angular values, which has the desired effect of making

that part of the variance which is due to errors of sampling independent of the incidence of the character. In this study, the angular value θ was calculated from the percentage p using the formula:

$$\theta = \sin^{-1} (1 - 2p),$$

θ being measured in radians.

When θ_1 and θ_2 are the angular transformations of the percentage incidence of a particular character in two populations, then a measure of divergence D between the populations can be found by:

$$D = (\theta_1 - \theta_2)^2$$

This raw measure of divergence requires correcting for random sampling fluctuations and this is done by subtracting $(\frac{1}{n_1} + \frac{1}{n_2})$ from $(\theta_1 - \theta_2)^2$ for any pair of populations when n_1 and n_2 are the number of mice in each population. Therefore, the measure of divergence between two populations based on one epigenetic character is now given by:-

$$D = (\theta_1 - \theta_2)^2 - (\frac{1}{n_1} + \frac{1}{n_2})$$

When x epigenetic characters are used, the measure of divergence between two populations is found by computing D for each character, adding all the values of D together and

dividing by the number of characters used,

$$\text{i.e. } D = \frac{1}{x} \cdot \sum \left[(\theta_1 - \theta_2)^2 - \left(\frac{1}{n_1} + \frac{1}{n_2}\right) \right]$$

In the present work, 12 characters were used and the measures of divergence between 12 populations calculated. The program for these calculations was written by Mr. N. Davies and run on the University of Southampton's I.C.T. 1909 computer.

D. Results.

(i) Linear analysis.

The means of all measurements on all the populations are shown in Table 21.

Correlation coefficients were calculated for all combinations of two characters (Table 22). As might be expected, greatest length is highly correlated with condylo-incisive and basal lengths and also with mandibular length. Length of the diastema is correlated with all these measurements. The measurements of tooth row length are not correlated with length.

The two measurements used in the univariate analysis were condylo-incisive length and cranial width. Length of mandible was considered as well, but was not used because it was quite highly correlated with condylo-incisive length ($r = 0.89$) and therefore would probably have given similar results. The means,

POPULATION	GL	CW	IC	CIL	BL	DM	PFL	LD	MXT	WFM	LM	HC	MNT
M.m.soricinus													
Studland	17.1	8.7	3.1	15.5	13.8	1.76	3.36	4.11	2.86	3.7	10.1	4.7	2.93
Odiham	17.7	8.8	3.2	16.1	14.5	1.79	3.45	4.30	2.85	3.8	10.5	4.9	2.90
Belgium	17.5	8.9	3.1	15.9	14.4	1.81	3.24	4.15	2.81	3.4	10.4	4.5	2.74
France	17.7	8.7	3.1	15.9	14.3	1.82	3.38	4.29	2.75	3.6	10.3	4.6	2.77
Berlin	17.8	8.9	3.2	16.2	14.5	1.79	3.40	4.33	2.84	3.7	10.5	4.9	2.88
Halle	17.8	8.8	3.2	16.1	14.4	1.85	3.35	4.30	2.81	3.7	10.4	4.7	2.89
Ukraine	18.2	9.1	3.2	16.6	14.9	1.91	3.41	4.45	2.94	3.6	10.7	4.8	2.89
M.m.subobscurus	17.4	8.8	3.1	16.0	14.4	1.81	3.38	4.32	2.81	3.6	10.3	4.8	2.83
M.m.pratensis	18.7	9.1	3.2	17.1	15.2	1.86	3.47	4.51	2.86	3.8	11.0	5.1	2.97
M.m.minutus	17.5	8.9	3.2	16.1	14.4	1.88	3.36	4.26	2.91	3.6	10.5	4.6	2.83
M.m.batarovi	17.5	8.8	3.1	16.2	14.5	1.84	3.19	4.29	2.88	3.5	10.5	4.6	2.80
M.m.ussuricus	17.4	8.8	3.1	16.0	14.4	1.79	3.32	4.22	2.86	3.6	10.3	4.8	2.92
M.m.erythrotis	19.3	9.2	3.3	17.2	15.5	2.20	3.79	4.78	3.14	3.8	11.3	5.3	3.11

Table 21: Means of linear measurements of skulls used in the multivariate analysis.

CHARACTER	GL	CW	IC	CIL	BL	DM	PFL	LD	MXT	WFM	LM	HC	MNT
Greatest l.(GL)	1.00												
Cranial width(CW)	0.51	1.00											
Interorbital con.(IC)	0.41	0.45	1.00										
Cond.-incisive l.(CIL)	0.91	0.48	0.37	1.00									
Basal l.(BL)	0.91	0.48	0.36	0.96	1.00								
Dist. between molars(DM)	0.51	0.45	0.29	0.50	0.49	1.00							
L. pal. foramen(PFL)	0.65	0.33	0.27	0.66	0.65	0.41	1.00						
L. diastema(LD)	0.85	0.44	0.33	0.88	0.87	0.56	0.72	1.00					
L. max. tooth row(MXT)	0.47	0.37	0.37	0.45	0.42	0.26	0.39	0.40	1.00				
Width foramen mag.(WFM)	0.30	0.26	0.34	0.23	0.20	0.03	0.24	0.19	0.23	1.00			
L. mandible(LM)	0.89	0.51	0.37	0.89	0.89	0.53	0.64	0.87	0.47	0.28	1.00		
Height mandible(HC)	0.69	0.34	0.29	0.69	0.69	0.36	0.53	0.67	0.27	0.30	0.70	1.00	
L. mand. tooth row(MNT)	0.46	0.32	0.41	0.40	0.36	0.24	0.45	0.38	0.68	0.46	0.49	0.34	1.00

Table 22: Correlation coefficients between the linear characters.

POPULATION	CHARACTER					
	CIL			CW		
	Mean	S.E.	Range	Mean	S.E.	Range
M.m.soricinus						
Studland	15.5	0.3	14.7-15.9	8.7	0.2	8.3-9.2
Odiham	16.1	0.4	15.4-17.0	8.8	0.1	8.5-9.1
Belgium	15.9	0.7	15.2-17.2	8.9	0.2	8.4-9.2
France	15.9	0.5	15.1-17.0	8.7	0.2	8.2-9.0
Berlin	16.2	0.6	15.7-17.3	8.9	0.3	8.4-9.4
Halle	16.1	0.6	14.9-17.3	8.8	0.3	8.2-9.2
Ukraine	16.6	0.7	15.4-17.6	9.1	0.3	8.6-9.4
M.m.subobscurus	16.0	0.5	15.1-17.2	8.8	0.2	8.3-9.1
M.m.pratensis	17.1	0.8	16.2-18.2	9.1	0.2	8.7-9.1
M.m.minutus	16.1	0.9	14.5-17.2	8.9	0.1	8.8-9.1
M.m.batarovi	16.2	0.8	15.3-17.1	8.8	0.1	8.7-8.8
M.m.ussuricus	16.0	0.6	15.4-16.7	8.8	0.3	8.3-9.1
M.m.erythrotis	17.2	0.7	16.6-18.4	9.2	0.2	9.0-9.6

Table 23: Means, standard errors and ranges of the characters used in the univariate analyses.

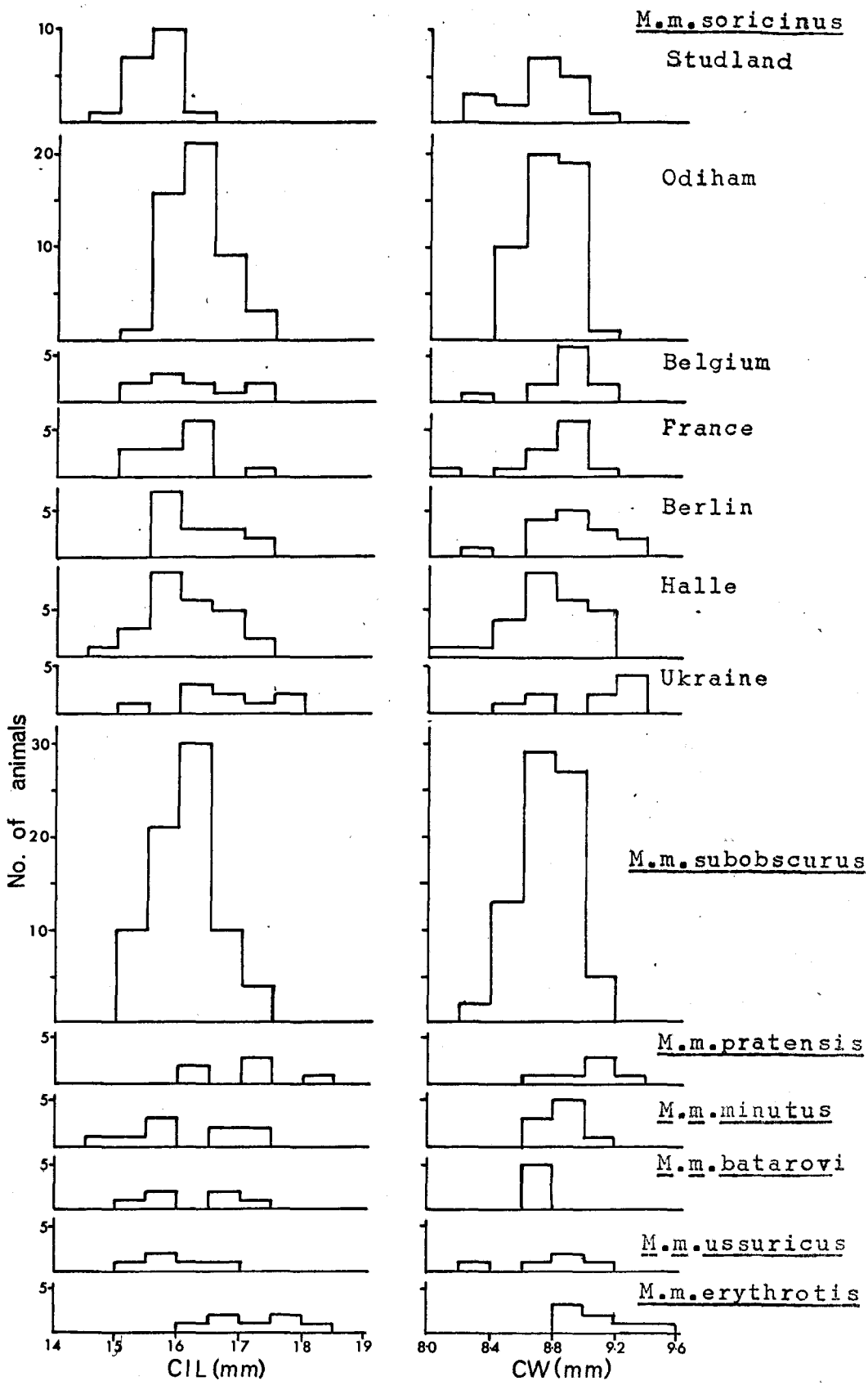


Fig.43: Frequency distribution of condylo-incisive length and cranial width.

standard errors and ranges of condylo-incisive length and cranial width are shown in Table 23. The frequency distribution of these two measurements for each locality is shown in Fig. 43. It will be seen that there is an appreciable spread about the means.

On the basis of condylo-incisive length, consideration of Table 23 and Fig. 43 shows that the smallest of all the populations is the Studland one and the largest are those of M.m. pratensis and M.m. erythrotis. On the basis that two populations are significantly different if both means are outside each others range of standard error, M.m. pratensis and M.m. erythrotis are significantly different from all other populations except that of M.m. soricinus from the Ukraine. This latter population, together with those from Berlin and Odiham, forms an intermediate group that is on the large side but significantly different only from the Studland population. The populations therefore fall into two main groups:-

1) M.m. pratensis and M.m. erythrotis.

2) The rest.

In addition, the Studland population differs significantly from the Odiham, Berlin, and Ukrainian populations of soricinus.

On the basis of cranial width there is not so much variation, and there is no significant difference between populations of M.m. pratensis, M.m. erythrotis, and populations

of M.m. soricinus from Berlin and the Ukraine, though the first two are still distinct from the majority.

The results of these two analyses suggest that the populations of the subspecies pratensis and erythrotis are larger than the majority of the other populations, and that the Ukrainian and Berlin populations of soricinus occupy an intermediate position. The Studland population of soricinus appears to be the smallest but is not significantly different from all the others. The Asiatic subspecies minutus, batarovi and ussuricus, together with the German subspecies subobscurus, show no signs of distinction from the populations of soricinus.

In the multivariate analysis all measurements were given equal weight and the result was dependent on simultaneous consideration of all of them. Nevertheless, it was interesting to see if any group of measurements were responsible for the bulk of the variation between all pairs of populations, as this could lead in future work to the use of fewer measurements with little loss of information concerning differences between populations. The number of pairs of populations between which each measurement was responsible for the largest single amount of variation is shown in Table 24. It will be seen that the width of the foramen magnum gave the best discrimination of any one character in 26 population comparisons. However, all the measurements except mandibular length possessed the best

MEASUREMENT	No.
Greatest length(GL)	6
Cranial width(CW)	3
Interorbital breadth(IC)	1
Condylo-incisive length(CIL)	3
Basal length(BL)	5
Dist. between 1st. molars(DM)	1
Length palatal foramen(PFL)	1
Length diastema(LD)	1
Length max. tooth row(MXT)	12
Width foramen magnum(WFM)	26
Length mandible(LM)	0
Length mand. tooth row(MNT)	8
Height mandible(HC)	3

Table 24: Number of population comparisons in which each measurement had the best discriminatory power.

discriminatory power in at least one population comparison. It is clear, therefore, that elimination of any of the measurements, with the possible exception of mandibular length, could lead to some loss of distinction between the populations.

The generalised distances D^2 between each pair of populations, calculated as a result of the multivariate analysis, are shown in Table 25 in the form of D. The 13 characters used in the analysis together with the mean gave a total of 14 degrees of freedom. This meant that the analysis could not be performed on any pair of populations in which the sum of the individuals was 14 or less. In practice, it was also found that the distance between pairs of populations whose sum was 15 was infinity. Consequently, there are a few gaps in the table.

The main feature which is immediately apparent from examination of the results of the linear analysis is the large amount of variation between most of the populations. It is rather surprising to find this between the various European populations of M.m. soricinus, most of which are fairly close geographically. Although the two populations of soricinus from Germany resemble the two from Britain (Odiham and Studland), the French and Belgian groups, particularly the latter, are remarkably distinct from the other populations of soricinus. The most geographically remote population of soricinus, that from the Ukraine, is separated by large generalised distances

from the majority of the other populations of this subspecies.

The appreciable variation between the different soricinus populations can be highlighted by comparison with the results of similar methods on other small mammals. For example, Delany and Healy (1967) found the greatest generalised distance (D) between Apodemus sylvaticus populations on the Channel Islands and mainland Britain using 10 skull characters was 4.35.

The subspecies M.m. subobscurus is found only in the neighbourhood of Oldenburg, W. Germany. It is thus completely surrounded by the chief European subspecies M.m. soricinus. In view of this, it is not surprising to find that the subobscurus sample is separated by relatively small generalised distances from all other populations of soricinus and is particularly close to the Berlin population, its nearest geographic neighbour. The results of the condylo-incisive length and cranial width comparisons also indicate that subobscurus is very similar to soricinus. There is thus no evidence from the study of the univariate or multivariate linear analyses that subobscurus is distinct from the populations of soricinus that surround it. In fact, the generalised distances between subobscurus and soricinus populations are generally smaller than those between the different soricinus populations.

The considerable variation demonstrated in the present study between the various western European populations of Micromys

POPULATION	M.m.soricinus Studland	Odiham	Belgium	France	Berlin	Halle	Ukraine	M.m.subobscurus	M.m.pratensis	M.m.minutus	M.m.batarovi	M.m.ussuricus
M.m.soricinus												
Odiham	3.09											
Belgium	13.10	7.38										
France	4.98	4.13	4.61									
Berlin	2.99	2.91	9.44	4.99								
Halle	3.45	2.44	5.82	2.37	2.15							
Ukraine	9.63	4.67	7.50	25.72	8.45	3.42						
M.m.subobscurus	3.01	2.63	4.41	2.31	1.79	3.29	2.92					
M.m.pratensis	7.39	5.39	19.12	16.45	4.52	3.84	17.93	3.17				
M.m.minutus	7.27	4.61	5.01	4.65	5.80	4.06	4.21	3.08	-			
M.m.batarovi	6.35	5.84	10.28	15.45	5.73	5.10	-	2.92	-	25.43		
M.m.ussuricus	4.16	3.17	36.00	6.15	4.98	4.33	-	2.00	-	-	-	
M.m.erythrotis	8.94	6.21	21.23	15.16	12.28	5.20	9.75	5.94	-	-	-	-

Table 25: Generalised distances (D) between populations of Micromys .

may partly explain why so many synonyms for the mouse in this area were described during the 19th century. Miller (1912) lists 19 names synonymous with M.m. soricinus and it would seem that the variation between the mice in different areas led earlier workers to believe that they were describing different species.

The third European subspecies considered in this study was the one inhabiting Hungary and Roumania, M.m. pratensis. Although only a small sample was available, this subspecies has comparatively large generalised distances from the other European populations and appears to be a fairly distinct, rather large, form.

Although it was not possible to undertake multivariate linear analysis between the Asiatic subspecies, comparison of the results between them and the western European groups shows no regular pattern. Some of the generalised distances between the Asiatic and European groups are smaller than those between the different European populations, while in other cases the Asiatic subspecies are clearly distinct (particularly from France and Belgium). Thus, no definite trend can be distinguished as far as the subspecies minutus, batarovi and ussuricus are concerned. The mean measurements (Tables 21 and 23) certainly do not indicate that ussuricus is larger than the others, and it was on this basis, together with colour

differences, that it was first defined. M.m. batarovi was described as rather smaller than the other subspecies and with different coloration. There is no evidence from this study that it is different in size from any of the other subspecies, except pratensis and erythrotis.

The generalised distance analysis reveals that the Chinese population of M.m. erythrotis is very distinct from all the other populations. Inspection of the mean measurements of this subspecies show that it is significantly larger than any of the others, with the exception of the Hungarian pratensis. As pointed out earlier, M.m. erythrotis is the most distinct subspecies to have been described, since it is the only one in which the tail is generally longer than the head and body.

The results of the linear analyses may be summarised as follows. There is a considerable amount of variation on the basis of the multivariate analysis between the different subspecies, but this variation is also present between different populations of one subspecies. In general, the results of the univariate analysis do not indicate that size would provide a measure of distinction between the subspecies. However, the subspecies erythrotis appears to be distinctly larger than the rest on the univariate analysis, and is also distinct on the multivariate abalysis. To try and find some character on which this subspecies could be distinguished from the rest,

the results were re-examined.

Comparison of the means in Table 21 shows that the following characters might form a basis for distinguishing erythrotis from the other subspecies: greatest length (GL), condylo-incisive length (CIL), basal length (BL), length of palatal foramen (PFL), length of diastema (LD) and length of mandible (LM). However, the ranges of the length of palatal foramen and length of diastena for erythrotis (Table 26) are such that they include the mean of these characters in most of the other populations. Thus, these two characters would quite clearly not provide the necessary distinction and were omitted from further analysis. The ranges of the other characters were examined for all populations and the proportion of the population that lay in overlap between its range and that of erythrotis was calculated for each character. The results are shown in Table 26. Compared with the multivariate analysis, the numbers used in this analysis were generally larger for some populations, especially erythrotis itself, since skulls on which all measurements could not be taken because of damage, could be included for the individual measurements presented here. Pimentel (1959) suggests that 84% of the individuals from one population should be separated from 84 of another for the two populations to be referred to separate subspecies. However, other workers have used 75%

Table 26: Comparison of M.m.erythrotis with the other populations on the basis of the following characters:- greatest length(GL); condylo-incisive length(CIL); basal length (BL); length of mandible(LM). (% overlap I = the percentage of the other population that overlaps with M.m.erythrotis; % overlap II = the percentage of the M.m.erythrotis population that overlaps with the other.)

Population	Character	N	Range(mm)	% overlap I	% overlap II
erythrotis	GL	13	18.0-20.9		
	CIL	7	16.3-18.4		
	BL	7	14.5-16.8		
	PFL	22	3.26-4.29		
	LD	22	4.29-5.33		
	LM	22	10.6-12.3		
soricinus	GL	18	16.6-17.6	0.0	0.0
Studland	CIL	18	14.7-15.9	0.0	0.0
	BL	18	13.3-14.7	5.5	28.5
	LM	18	9.5-10.5	0.0	0.0
Odiham	GL	49	16.7-18.8	30.6	46.2
	CIL	49	15.4-17.2	30.6	57.1
	BL	49	13.9-15.4	57.1	57.1
	LM	49	10.0-11.2	42.9	36.4

continued

Table 26: contd.

Population	Character	N	Range(mm)	% overlap I	% overlap II
soricinus	GL	25	16.2-18.0	4.0	7.7
Belgium	CIL	22	14.9-17.2	27.3	57.1
	BL	18	13.4-15.7	38.9	57.1
	LM	25	9.8-11.0	20.0	36.4
France	GL	14	15.6-18.4	28.6	23.1
	CIL	14	14.1-17.0	14.3	57.1
	BL	14	12.5-15.3	50.0	57.1
	LM	14	9.4-11.0	25.0	36.4
Halle	GL	31	16.5-19.0	45.1	46.2
	CIL	31	14.9-17.0	38.7	57.1
	BL	30	13.4-15.6	50.0	57.1
	LM	30	9.8-11.3	30.0	50.0
Berlin	GL	18	17.0-19.1	55.5	46.2
	CIL	18	15.7-17.3	38.9	57.1
	BL	17	13.9-15.6	41.2	57.1
	LM	21	10.0-11.6	47.6	81.8
Ukraine	GL	9	17.3-19.4	55.5	61.6
	CIL	9	15.4-17.6	66.6	85.7
	BL	9	14.0-15.9	77.8	57.1
	LM	9	10.4-11.5	77.8	68.2
subobscurus	GL	73	16.2-18.8	13.7	46.2
	CIL	73	15.1-17.2	26.0	57.1
	BL	73	13.5-15.7	36.9	57.1
	LM	73	9.7-11.2	19.1	36.4

continued

Table 26: contd.

Population	Character	N	Range(mm)	% overlap I	% overlap II
pratensis	GL	6	17.8-19.9	83.3	76.9
	CIL	6	16.2-18.2	66.6	85.7
	BL	6	14.4-16.4	66.6	85.7
	LM	6	10.3-11.7	66.6	81.8
minutus	GL	9	16.5-18.6	55.6	38.5
	CIL	9	14.5-17.2	44.4	57.1
	BL	9	12.7-15.5	44.4	57.1
	LM	9	9.4-11.5	33.3	68.2
batarovi	GL	6	16.6-18.8	33.3	46.2
	CIL	6	15.3-17.1	50.0	57.1
	BL	6	13.6-15.6	50.0	57.1
	LM	6	10.4-11.2	33.3	36.4
ussuricus	GL	7	16.7-19.5	42.8	69.2
	CIL	5	15.4-16.7	40.0	28.5
	BL	5	13.7-15.5	40.0	57.1
	LM	8	10.0-10.8	37.5	31.8

(Amadon 1949) and 90% (Corbet 1964).

Table 26 shows that, even at the 75% level, the erythrotis population can be distinguished from only two others: Studland (soricinus) on three of the four characters used, and Belgium (soricinus) on one. It cannot be separated at this level from any other population.

Thus M.m. erythrotis, which is the most distinct subspecies on both linear analyses, cannot in fact be separated from any of the other subspecies used on the basis of any one character, though it can be separated from two populations of the subspecies soricinus. However, it may be possible to separate erythrotis from the rest on the basis of tail-length. Allen (1940) gives 11 measurements, in nine of which the tail is longer than the head and body, in one it is equal, and in one subequal to the head and body length. For any firm decision to be taken, however, a larger sample is necessary.

(ii) Results of the epigenetic analysis.

The percentage incidences of the epigenetic variants studied in each population are given in Table 27. It will be seen that the percentage incidence of some characters varies widely in different populations, while that of others is fairly constant. Six characters are generally rare. These are:- interfrontal present, parted frontals, fused frontals, foramen

hypoglossus double, mandibular foramen double, and accessory mental foramen present. Fused frontals are absent in all populations, parted frontals are present in only three, and accessory mental foramina and interfrontals are present in four. Of the other characters, double preorbital and frontal foramina have a generally low incidence but are present in the majority of populations. Most of the variation between the populations resides in four characters:- maxillary foramen I present/absent, foramen palatinum majus double/single, foramen palatinum minus anterius present/absent, and processus pterygoideus present/absent. These characters are found in all populations and vary considerably. The presence of the foramen palatinum minus anterius appears to have become fixed in the Dutch population where it has an incidence of 100%.

The variability of the epigenetic characters themselves is summarised in Table 28. It will be seen that the foramen palatinum minus anterius present has the highest average percentage incidence and is found in all populations.

The measures of divergence between all pairs of populations, described as "measures of distinctiveness," are shown in Table 29. The populations from Norfolk and Hungary (seven and six mice respectively) are so small that they can be neglected in this analysis, but they do show a broadly similar pattern of variation to the others. The measure of uniqueness, included

POPULATION	Preorb. for. double	Interfrontal pres.	Parted frontals	Fused frontals	Frontal for. double	Max. for. I pres.	For. pal. majus double	For. pal. min. ant. pres.	Proc. pterygoid. pres.	For. hypoglossus double	Mandibular for. double	Acc. mental for. pres.
M.m.soricinus												
Studland	9.5	9.5	0.0	0.0	2.4	64.3	28.6	95.2	45.0	4.6	2.4	0.0
Odiham	3.8	0.0	0.0	0.0	2.8	33.3	11.3	72.6	26.4	0.9	0.9	0.9
Norfolk	0.0	0.0	0.0	0.0	0.0	42.9	28.5	78.5	28.5	0.0	0.0	0.0
Belgium	8.9	0.0	7.5	0.0	1.3	21.6	12.9	77.7	20.0	5.5	3.2	1.5
Holland	9.1	0.0	0.0	0.0	0.0	47.2	15.9	100.0	16.7	0.0	2.3	0.0
France	7.9	5.6	0.0	0.0	0.0	44.7	13.2	92.1	25.0	0.0	6.2	0.0
Berlin	2.0	0.0	0.0	0.0	4.2	47.9	26.0	92.0	19.5	2.3	6.0	0.0
Halle	2.8	2.8	0.0	0.0	4.1	10.9	28.9	89.4	19.1	3.0	1.4	1.4
Ukraine	5.0	0.0	0.0	0.0	0.0	35.0	40.0	55.5	37.5	0.0	0.0	0.0
M.m.subobscurus	1.2	1.2	2.4	0.0	1.8	30.0	15.3	87.5	22.8	2.5	2.4	0.0
M.m.pratensis	0.0	0.0	0.0	0.0	8.3	58.3	25.0	91.7	16.6	0.0	0.0	0.0
M.m.erythrotis	8.7	0.0	8.7	0.0	2.1	86.9	6.5	95.6	30.0	0.0	0.0	4.3

Table 27: Percentage incidence of epigenetic characters.

CHARACTER	Av.% inc.	Range	No.popns. with char.
Preorbital for. double	4.9	0.0-9.5	10
Interfrontal present	1.5	0.0-9.5	4
Parted frontals	1.9	0.0-8.7	3
Fused frontals	0.0	0	0
Frontal for. double	2.3	0.0-8.3	8
Max. for.I present	43.6	10.9-86.9	12
For. pal. majus double	21.0	6.5-40.0	12
For. pal. min. ant. pres.	85.7	55.5-100.0	12
Proc. pterygoid. pres.	25.6	16.6-45.0	12
For. hypoglossus double	1.6	0.0-5.5	6
Mandibular for. double	2.1	0.0-6.2	8
Acc. mental for. pres.	0.7	0.0-4.3	4

Table 28: Variability of the epigenetic characters.

M.m.soricinus	Odiham	Norfolk	Belgium	Holland	France	Berlin	Halle	Ukraine	M.m.subobscurus	M.m.pratensis	M.m.erythrotis	M.of U.
Studland	0.238	0.361	0.290	0.265	0.163	0.029	0.145	0.377	0.133	0.213	0.453	0.242
Odiham		0.579	0.054	0.486	0.503	0.154	0.144	0.526	0.432	0.452	0.384	0.359
Norfolk			0.538	0.101	0.099	0.314	0.675	-0.121	0.707	-0.209	0.294	0.303
Belgium				0.495	0.522	0.220	0.189	0.530	0.280	0.378	0.166	0.333
Holland					0.013	0.190	0.536	0.190	0.554	0.099	0.419	0.305
France						0.260	0.375	0.129	0.360	0.142	0.447	0.274
Berlin							0.274	0.282	0.256	0.165	0.410	0.232
Halle								0.621	0.274	0.528	0.439	0.382
Ukraine									0.649	-0.001	0.327	0.319
M.m.subobscurus										0.543	0.502	0.426
M.m.pratensis											0.117	0.221
M.m.erythrotis												0.360

Table 29: Measures of Distinctiveness between the populations of Micromys.
(M.of U. = Measure of Uniqueness)

in the last column of Table 29, is the mean of the measures of distinctiveness of that population, and is therefore an estimate of the overall distinctiveness of each population.

The two British populations (Norfolk omitted) and the two German ones of the same subspecies (soricinus), together with the German subobscurus population, stand out as the closest group, having generally low measures of distinctiveness between each other and high ones against other populations. Apart from this group, the other populations do not form any patterns, having some small and rather more large measures of distinctiveness with each other.

The subspecies erythrotis has one of the largest measures of uniqueness. Thus, this subspecies, which is distinct on the basis of genetic characters (but not on any particular one), is also fairly different when epigenetic characters are used. In general, however, the measures of uniqueness are not large. Berry (1963), examining populations of Mus musculus from different parts of the world, obtained a largest measure of uniqueness of 0.656; the largest measure between the Micromys populations is 0.426. This greatest measure of uniqueness belongs to the subspecies which was least distinct in the linear analysis, namely subobscurus, and these two results may well provide a clue to the position of this subspecies. It has already been mentioned that subobscurus is distinguished from the neighbouring populations of soricinus mainly on the basis of coat coloration.

These differences in coat colour may be due to a mutation affecting only the genes responsible for coat colour and this change has had no effect on any of the other measured characters. The differences in coat colour may, however, be brought about by some peculiarity of the environment affecting the expression of a gene complex essentially similar to that in soricinus. In view of the distinction of subobscurus on the basis of the epigenetic characters, the expression of which are known to be affected by environmental conditions, this latter hypothesis seems a possibility. However, owing to the lack of information concerning the habitat from which the subobscurus population was collected, it is not possible to speculate as to the nature of the environmental factor(s) which cause these differences in epigenetic characters and, possibly, coat coloration.

The results of the linear and epigenetic analyses can be summarised as follows: there is generally a considerable amount of variation between the different populations, within, as well as between, the standing subspecies. There is no recognisable trend in either analysis. No single character measured will differentiate between the most distinct subspecies, erythrotis, and all the others.

E. Discussion.

Geographic variation in mice is probably attributable to three chief factors: mutation, selection, and isolation or partial isolation of different populations of the same species (genus). Mutation provides the raw material on which selection can work and there is considerable evidence that mice can be closely adapted to their environment. For example, many species of Peromyscus show a good correlation between their pelage coloration and the colour of the soils in the area they inhabit. (Blair 1950). Isolation of a population restricts gene flow between it and neighbouring populations and this may either augment the effects of selection or allow the development of non-adaptive characters. Blair (1950) generalises that the species with the greatest geographic ranges have the greatest number of subspecies, and suggests that this may be caused by the great variety of habitats since local populations will be adapted to the particular habitat in which they live.

With these considerations in mind, it is surprising to find that Micromys, whose range stretches right across Eurasia, exhibits so little subspecific variation. Even the 13 currently valid subspecies are too many, since the present work has shown that no clearly definable characters have been found to separate seven of them. However, erythrotis may possibly be separated on tail length. This may be compared

with the situation in Apodemus. Over the same range as Micromys, though with the addition of parts of southern Europe and the Middle East, Apodemus has been divided into 15 species and 85 subspecies (Ellerman 1941), though the position of some subspecies has been revised by recent work (e.g. Delany and Healy 1964).

The ecological results presented in another section of this thesis indicate that Micromys is discontinuously distributed, and it is suggested that this is due to the discontinuity of the rather special habitat - that of tall grass-like vegetatio n. Bobrinskii et al (1965) show that, whereas the genus Apodemus is fairly evenly distributed over the U.S.S.R., Micromys is found chiefly in the vicinity of lakes, rivers and marshes. Near such places the principal habitat of Micromys is likely to occur. Because of this discontinuity of habitat, the populations of Micromys must be relatively isolated, with far less opportunity for gene flow between them than between populations of a fairly continuous genus such as Apodemus. One would expect, therefore, to find a greater amount of variation between the populations of Micromys than between those of Apodemus. While this may be so, in view of the large generalised distances obtained, between geographically close populations, it is not true over the animals' range as a whole, since the variation of Apodemus is such that 15 species have

been described whereas all specimens of Micromys are referable to a single species.

There is no clear trend of variation in Micromys. For example, the two British populations, which came from places no more than 70 miles apart, are separated by a larger generalised distance than one of them (Odiham) is from the German populations. The smallest generalised distance recorded is between two populations at the opposite ends of Eurasia (subobscurus and ussuricus).

Over all, then, there is little subspecific variation in Micromys, at least on the characters that have so far been used. Neverthless, the result of the generalised distance analysis, which gives a measure of distinction between populations based on all the characters, suggests that considerable minor variation does exist, not only between subspecies but also of a similar magnitude between populations of the same subspecies.

Subspecific names only serve a useful purpose if a population can be defined on the basis of certain characters, and if a high proportion (75-90%) of individuals can be assigned to a particular subspecies. With the exception already mentioned, there are no characters on which this can be done for the subspecies studied in the present work. More detailed work on larger samples might possibly uncover such characters, but the generalised distance analysis suggests that if distinguishing

characters were found to separate the standing subspecies, they could equally well be found to split up some of them. In fact, the variation is such that every population studied might be found to differ on some minor character. This would lead to such proliferation of subspecific names that the system would become unworkable.

There seems, therefore, to be a good case for abandoning subspecific nomenclature altogether for this genus, and referring all harvest mice to Micromys minutus. Details of variation could be appended if required as follows: Micromys minutus is highly variable on inconspicuous characters (if these can be named) but shows little overall variation; the chief variable is the length of the tail which, normally equal or subequal to the length of the head and body, is longer than the head and body in S.E. Asian forms. Apart from this, the species extends from the British Isles across central Eurasia to Japan exhibiting very little variation, though specimens found in Hungary and S.E. Asia tend to be slightly larger than the rest. It does, however, exhibit some variation in pelage coloration which cannot, in general, be ascribed to particular areas. (This could be followed, if necessary by a brief review of variations in colour so far described).

This system, if adopted in check-lists, would convey a considerable amount of information regarding the species,

without the burden of many subspecific names, which give little or no information regarding the detailed variation of the species and, furthermore, take up a considerable amount of space. However, the main conclusion of this study is that, with one possible exception, the seven subspecies dealt with cannot at present be distinguished from one another.

VII CONCLUDING REMARKS.

The Order Rodentia is a large and successful group of animals and within this Order the Muridae contains numerous and diverse forms. Out of the 71 genera comprising the subfamily Murinae, Micromys is highly unusual as regards its small size and peculiar habitat. These two features have profound effects on the ecology, physiology and variation of the species.

The small size and prehensile tail of Micromys adapt it for climbing among the stalks of tall grasses and reeds. The animal's distribution appears to be tied to the occurrence of this type of vegetation, for it has rarely if ever been found far from it. As a result, although the range of the mouse is wide, extending across the central band of the Palaeartic region, it is by no means uniform. This has been brought out especially in the work on the distribution of the mouse in England. The ecology of Micromys is associated with its unusual habitat, and in view of the failure of conventional trapping methods, it is evident that special methods are necessary to determine such aspects of the animal's ecology as home range and population dynamics.

The physiology and activity of Micromys present a situation in which two apparently opposing factors are combined. It has been shown that small size in mammals

results in comparatively high energy requirements. Furthermore, because of the lower temperatures prevailing at night, a nocturnal mammal requires more energy to maintain its body temperature than a diurnal one. Therefore, it would seem advantageous if a mammal as small as Micromys reduced its energy requirements by being wholly diurnal. However, as shown in the Activity Section, the harvest mouse is mainly nocturnal and it would appear that there is some advantage in being nocturnal which outweighs the extra energy cost. One such advantage is that the evaporative water loss from the mouse will be less under the lower night-time temperatures than during the day. However, the fact that the mouse is active to some extent during the day, and can evidently control its evaporative water loss under dry conditions rather better than the completely nocturnal Apodemus, suggests that the advantage of reduced water loss at night is not a very important one. The other advantages of nocturnal activity can only be surmised - perhaps predation by hawks during the day would be greater than that by owls at night. These results indicate that Micromys is not adapted to a single factor in its environment but to a combination of factors. In general, animals are adjusted in a complex way to their environment, and morphological, ecological, physiological and behavioural factors are combined in an integrated pattern. Such a complex

adjustment invariably involves compromise solutions (Allee et al 1949). In the present case, there is a compromise between the energy requirements of Micromys, which would be lowest during the day, and some other factor(s) which tend to make the mouse nocturnal.

It is possible that the adaptation of Micromys to a certain habitat is responsible for the comparative lack of variation over its wide range. As a result of this adaptation, no major alterations in its form would be of advantage to the mouse. In fact, only minor changes such as slight differences in size and coat colour have been observed. On the other hand, the sporadic distribution of the mouse and the comparative isolation of many populations as a result of the discontinuity of its habitat, appears to have led to a fair amount of variation in these minor differences.

It is evident, therefore, that all the aspects of the biology of the harvest mouse considered in this study are linked to a greater or lesser extent by its small size and habitat, and it is these attributes that separate this mouse from related species. The aims in the present study of Micromys have been twofold: firstly, to investigate those aspects in which it differs from related species, and secondly, to add to the basic knowledge of the ecology, activity and variation of the mouse.

VIII SUMMARY

1. All the Old World harvest mice are included in the species Micromys minutus and 13 subspecific divisions are currently recognised. Previous work on the harvest mouse has been mainly concerned with the breeding biology and development. In the present work the distribution, ecology, physiology and variation of the species has been studied.

2. Records of the animal's occurrence in Britain since 1950 were collected and show that its range has decreased since the turn of the century. It is now mainly confined to the south and east of a line from the River Severn to the River Humber. The mouse is by no means confined to agricultural land and occurs in a wide variety of habitats.

3. Ecological studies were carried out on populations of Micromys at Studland Heath National Nature Reserve in Dorset, and at Spursholt Farm, Romsey, Hampshire.

4. At Studland, it appeared that the mice lived on the heathland during the winter months but went into the marshes to breed between May and September. The maximum corrected density recorded on the heathland study area was 3.3 mice/acre.

5. At Spursholt Farm, it was found that Micromys was much less common than most of the other small mammals inhabiting the hedgerows. The presence of old breeding nests indicated that the animal's distribution was more widespread and uniform in the summer of 1965, than it was in February and March 1966 according

to trapping results.

6. It was found that 93% of the movements in a 24-hour period made by the mice at Studland, and all those at Spursholt Farm, were less than 60 yards.

7. The mice did not make burrows themselves but would use those made by Apodemus.

8. Micromys formed 3.9% of the catch in a collection of barn owl (Tyto alba) pellets.

9. The activity rhythm of four Micromys under a 12-hour day-length was investigated by direct observation. The activity of a further four mice under day-lengths of 9, 12 and 15 hours was recorded by time-lapse photography. No influence of changing day-length was detected on total activity. The mice were most active during the hours of darkness,but some activity took place during the day and this increased with increasing day-length. Activity peaks occurred at dawn and dusk.

10. 62% of the rest periods lasted up to 60 minutes. The usual interval between feeding during activity periods was 6-12 minutes.

11. The metabolic requirements in the form of food and oxygen consumption were determined for Micromys and Apodemus.

12. The maintenance energy requirement of Micromys under minimum activity conditions and fed on Diet 41B was 1.10 Kcals/g/day(based on three animals). The maintenance energy requirement of Apodemus under the same conditions of activity and diet was 0.58 Kcals/g/day(based on three animals).

13. Using a closed-circuit respirometer apparatus, the oxygen consumption of three Micromys was measured at 20°, 25°, and 30° - 35°C inclusive, and that of three Apodemus at these temperatures and at 27° - 29°C and 36°C. The zone of thermo-neutrality for Micromys was found to be approximately 1°C about 33°C. For Apodemus it extended from 30° - 34°C.

14. The average basal metabolic rate of five Micromys was 2.65 ml O_2/g/hr or 2.43 Kcals/day. The average basal metabolic rate of four Apodemus was 1.74 ml O_2/g/hr or 3.86 Kcals/day. Both these results agreed with the calculated values. The maximum oxygen consumption of one Micromys was 8.65 ml O_2/g/hr at 23°C, which was 44% above the calculated minimum metabolism at this temperature.

15. The minimum assimilation intake, measured in the food consumption studies, and the basal metabolic rate were compared as methods of estimating energy flow through populations. Because of the variable activity conditions in assimilation studies, determination of BMR is to be preferred where comparisons between the results of different workers are to be made.

16. The evaporative water loss of Micromys and Apodemus was measured under dry air conditions, and an absolute humidity of 13.6 mg H_2O/litre of air. It was found that whereas the water loss of Apodemus increased under dry air conditions, that of Micromys remained the same as it was under the humid conditions.

17. 367 skulls, representing seven subspecies of Micromys minutus from 15 localities,were examined. 13 measurements were made on each skull and 13 epigenetic variants were scored as present or absent.

18. The linear measurements were analysed using a multiple regression technique and calculating generalised distances (D^2) between populations. The percentage incidence of the epigenetic characters were also analysed using a multivariate method and calculating measures of distinctiveness between populations.

19. An appreciable amount of variation between populations was found in both analyses. No single linear measurement would separate M.m.erythrotis, which was the most distinct population in the generalised distance analysis, from the majority of the other populations. The variation between different subspecies was paralleled by variation of a similar magnitude between populations of the same subspecies, M.m. soricinus. In view of this, it is recommended that subspecific nomenclature be abandoned in this species and all Old World harvest mice referred only to Micromys minutus.

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