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Handley, Roger

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A SUMMERTIME STUDY OF WOOD MICE AND BANK VOLES IN CASTLE EDEN DENE

by

Roger Handley

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degree of Master of Science
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SECTION A

INTRODUCTION AND GENERAL

INTRODUCTION

The original intention of this study was an investigation, by tracking methods, of the movements of two common small rodents, the bank vole, *Clethrionomys glareolus* Schr. and the wood mouse *Apodemus sylvaticus* (L) in mixed woodland. Furthermore, it was hoped to compare the movement patterns and home ranges of the two species as revealed by tracking methods, with those obtained by live trapping. The tracking procedure adopted, however, produced no results (see Appendix) and so the study was based entirely on results obtained by live trapping. Movement and home range continued to be the main factors for investigation but data were also collected on numbers of individuals, sex ratios and age composition of the populations trapped.

A considerable amount of work on these topics and involving these species has been done by various workers, including notably, Evans (1942) working in mixed woodland in Berkshire and more recently Hacker and Pearson (1952), Brown (1954 and 1956), Miller (1958), Kikkawa (1964), Tanton (1965), Ashby (1967) and Crawley (1965) (1969). Brown (1966, 1969) studied home range and movement using tracking methods with a population marked by toe clipping.

The current study was undertaken in Castle Eden Dene. This area was chosen partly because it provided large areas of natural and semi-natural woodland with little danger of any interference with the trapping grids and partly because Crawley (1965, 1969) studied *Clethrionomys* and *Apodemus* in this area over the two year period from 1963 to 1965, thus providing data with which those obtained in the present study might be compared.

THE STUDY AREA

1. General

The Dene is a local nature reserve and lies between the villages at Castle Eden and Shotton (Nat. Grid. Ref. NZ4138 and NZ4139). The A.19 Sunderland to Hartlepool trunk road forms the western boundary of the Dene. Roadworks, currently in progress, and involving the building of a completely new stretch of road, have removed some three hectares of woodland from the western extremity of the Dene. This western portion of the Dene, in which all the trapping areas were situated, is bordered to the south by the Castle Eden Golf course and to the north by arable farmland. To the east, the Dene continues until it opens into the North Sea. The area was surveyed generally by Ashby and Crawley (1967, 1969).

A shallow burn flows along the valley floor. It is polluted by coal washings and by considerable quantities of earth disturbed by the new roadworks. During most of the study period, however, the stream was quite clean and because of the unusually light rainfall, very low.

The bed-rock of the Dene is Magnesium limestone overlain by 200 feet of boulder clay. As the stream flows eastwards it cuts down into the limestone forming a steep sided gorge over a not inconsiderable stretch of the central Dene. When not so exposed the limestone is overlain with boulder clay. This has resulted in certain parts of the region in a high level of ground water which produces soft, marshy areas even during comparatively dry weather.

The western section of the Dene is entirely covered by boulder clay but the steep sides of the valley prevent the ground from becoming waterlogged except in a few places. The vegetation of this section

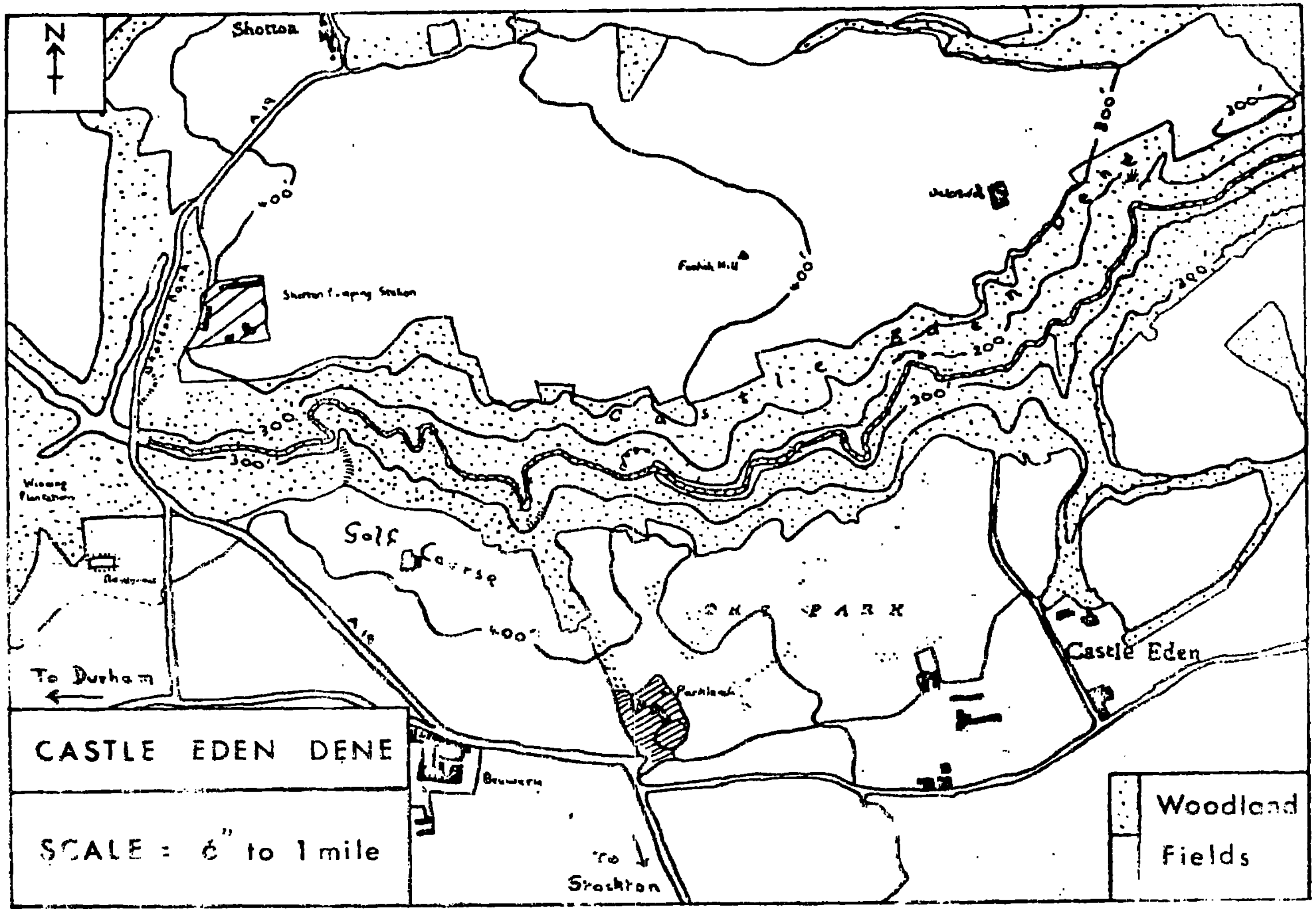

FIGURE 1. Map of Castle Eden Dene showing the woodland, surrounding fields, and the 200', 300', and 400' contours. National Ordnance Survey Map (1923. Durham, Sheet XXVIII).

is divisible into several discrete units of which the main types are:-

(a) Areas lacking a tree cover.

In these areas the ground cover consists primarily of tall grass, mainly *Deschampsia caespitosa* and *Arrhenatherum elatus* and *Dactylis glomerata*.

(b) Areas dominated by planted conifers, *Pinus nigra* and *Larix sp*.

(c) Areas dominated by sycamore *Acer pseudoplatanus*, mainly planted but some naturally regenerating.

(d) Areas with ash *Fraxinus excelsior* dominant

(e) Areas with scattered beech *Fagus sylvaticus* and yew *Taxus baccata* dominant.

(f) Areas with a tree cover of mixed hardwoods, e.g. wych elm, *Ulnus glabra*, oak *Quercus petraea* and *Q. robur*, yew and alder *Alnus glutinosa*.

Over most of the area the ground cover is formed by the same species or their dead remains, throughout the year but in some areas there are plants dominant in spring, e.g. anemone, *Anemone nemorosa*, bluebell, *Endymion non-scripta* and garlic, *Allium ursineum* which have died away by summer.

2. The Trapping Grids and Traplines

Three grids were marked out in the area (see Fig.2). The two most easterly grids originally consisted of thirty six traps laid out in a square with a grid interval at 16 m, while the third grid was rectangular with six traps along the long side and four along the short (the grid interval was the same as in the other grids). This grid had to be smaller than the others because of lack of traps. After the first trapping session all the grids were altered to rectangles with ten traps on one side and five along

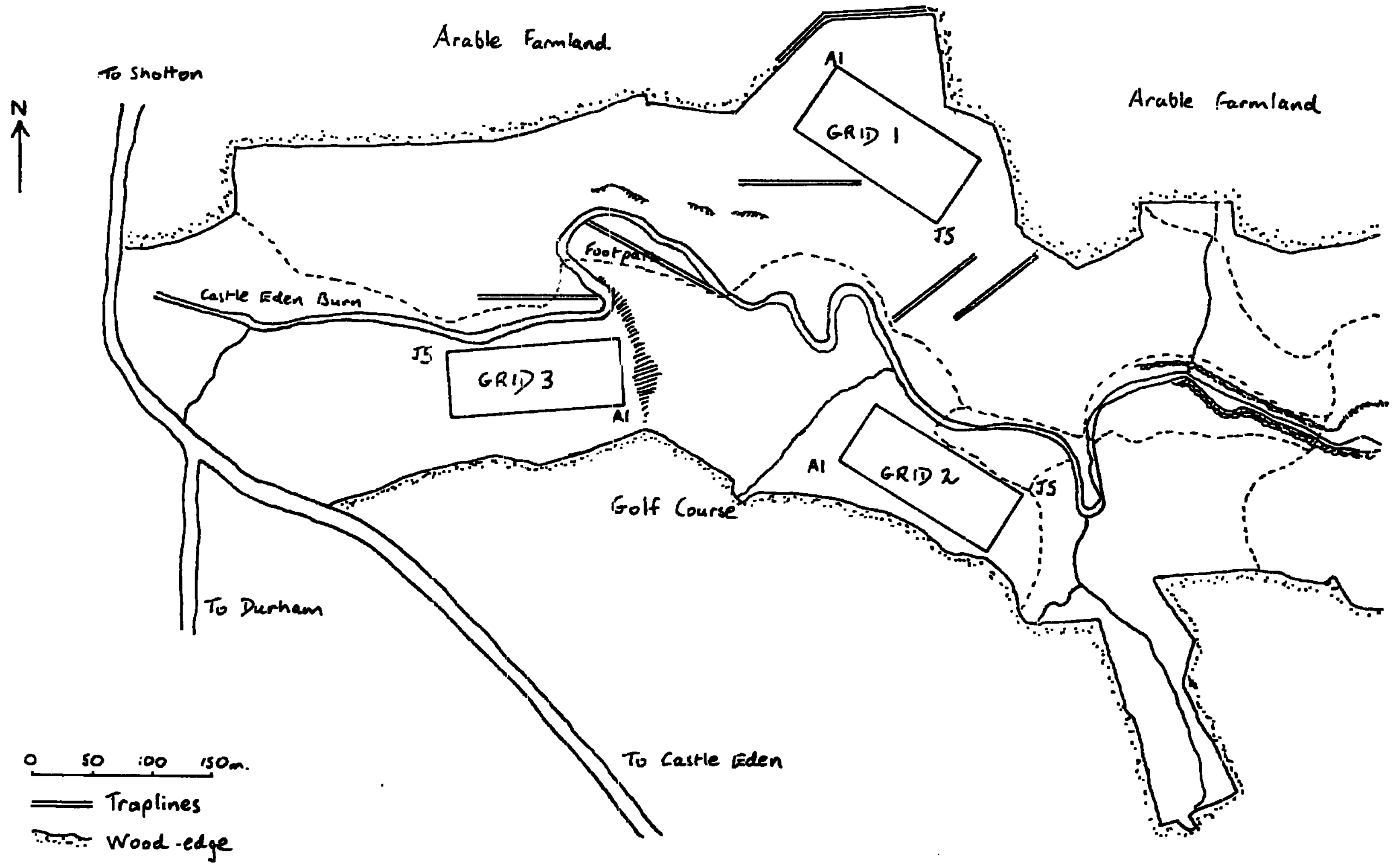

Figure 2 Map of the study area in Castle Eden Dene showing details of the pattern of the trapping grids and the traplines.

the other, again using the 16 m. grid interval. Although this adjustment complicated the handling of results, it was thought necessary, given tracking problems, for three reasons. Firstly, the original grids were too small to reveal adequately the home ranges of the animals by trapping. Secondly, the increased number of animals handled on the larger grids would make results more meaningful. Thirdly, by extending Grids 1 and 2 they came to coincide approximately both in position and area with Crawley's Grids A and B of his 1963 to 1965 study period and so direct comparison of results would be legitimate. Grid 3 was so positioned because Ashby and Crawley (1967), Ashby (unpublished) in their studies in the Dene, found that in late summer and autumn, certain Apodemus individuals were regularly commuting between the area of Grid 1 and that of Grid 3. As the journey involved the crossing of much damp ground and also the vegetation and nature of the soil at Grid 3 was apparently unfavourable for Apodemus, the reason for this commuting was obscure. Hence it was hoped that it might be observed again and some light shed on the subject.

Because of shortage of labour, only one trap was set at each grid point. Ideally, to thoroughly sample a population, an infinite number of traps should be placed at each point, but Tanton has shown that, provided catches are low, say less than 60 per cent of the traps are occupied each night, then over a period of five days, the population can be adequately sampled, provided trap shy and other aberrant individuals are absent or present at only low frequencies.

Grid 1 (Figure 2)

This grid was situated to the north of the burn. The thirty six traps laid out at first were in the lines A to F (see Fig.2), with an additional line above line 1. The ground was gently sloping. The western portion of the grid (traplines A to C) was situated in larch wood. Adjoining the larch, *Larix decidua* was a narrow belt of spruce *Picea abies*. Trapline D was partially situated in this. Further east was a stand of sycamore in which the other traplines of the grid were set. At the very eastern end of the grid the woodland was mixed sycamore and spruce.

The vegetation in the larch wood differed considerably from that in the sycamore. The former had a very sparse ground cover. In May there was little else apart from larch litter and quiescent bramble, *Rubus fruticosus* and even in July only small patches of bramble, bracken, *Pteridium aquilinum*, dog's mercury, *Mercurialis perennis*, nettle, *Urtica dioica* and wood sorrel, *Oxalis acetosella* broke the monotony of larch needles. The spruce was growing on very damp ground and here the vegetation consisted almost entirely of horsetail, *Equisetum arvense*. In the sycamore, the ground vegetation in May was predominantly the tussock grass *Deschampsia caespitosa*, with much bare earth between tussocks though patches of bramble and dead bracken fronds provided some cover. In June dog's mercury had grown up and completely covered the ground and hidden the grass. By July, bramble had assumed more prominence and an assortment of plants had grown. These included rose-bay willow herb, *Chamaenerium angustifolium*, enchanter's nightshade, *Circaea lutetiana*, and lords and ladies, *Arum maculatum*. On the western most part of the grid the ground cover was less dense because of the presence of the mature spruce.

Grid 2 (Figure 2)

This grid was situated to the south of the burn, about due south of Grid 1 and on sloping ground, steep in places. The thirty six traps originally laid down were in rows E to J with an additional line above line 1. Once the grid had been extended to fifty positions rows A to C were situated in an Ash plantation and rows D to J were in an immature larch plantation.

In May the ground cover in the larch was litter and dead fern, *Dryopteris dilatata*. In June wild garlic, *Allium ursineum*, and dog's mercury were locally abundant. In July the garlic had died away while the fern had grown to provide a moderately dense cover in most places. Tufted hair grass, *Deschampsia caespitosa* further increased the ground cover, especially toward the western limit of the larch plantation.

In the Ash plantation the ground cover in May was provided by dead bracken and bramble and by dominant wild raspberry *Rubus idaeus*. In June because of the late spring, bluebell dominated the ground layer but by July it had died away and willowherb, hogweed, *Heracleum sphondylium* and tufted hair grass were the dominant cover producers. Dog's mercury and rose bay willowherb were locally abundant. Nearer the burn, the ground was very broken and hazel *Croylus avellana*, was the dominant canopy producer. The ash and hazel section of Grid 2 had the most dense cover of any region studied, for in addition to the thick vegetation, there were many felled trees and lopped branches on the ground.

Grid 3 (Figure 2)

Like Grid 2, this was situated south of the burn but was 200 m. to the west of it. Apart from the northernmost line of traps, the area was one of steeply sloping ground. The original 24 traps were in rows E to J and lines one to four. When the number was increased, rows A to D were added onto the eastern edge of the grid and an additional line (line 5) was added along the north of the grid.

Rows G to J were situated in mature sycamore woodland. Nearer the burn pine and elder, Sambucus nigra, were present. The ground cover was provided predominantly by wild garlic with patches of fern. Other ground layer plants were wood anemone, bluebell, bramble, dog's mercury, buttercup, Ranunculus repens, and early purple orchid, Orchis mascula. As on Grid 2, the garlic died away by July and left large areas of almost bare earth. Elsewhere the fern provided moderate cover. Rows C to F were in a mixed sycamore, pine woodland with pine dominant on the lower slopes. In the sycamore the wild garlic was again dominant but in the pine the ground was mostly bare though a considerable number of regenerating sycamore and patches of nettle, buttercup and wood anemone provided some cover. Rows A and B were in an area of mixed grasses and herbs including water avens, Geum rivale, early purple orchid, violet Viola sp, wild strawberry, Fragaria vesca, marsh thistle, Cirsium palustre, slender false broom, Brachipodium sylvaticum, dog's mercury, wood sorrel, buttercup and rose bay willow herb. Tufted hair grass is the main grass present. Here the ground sloped very steeply and only a few trees were present of which Birch, Betula pubescens, sycamore and hawthorn, Crataegus monogyna, were the commonest.

It will be seen from Figure 2 that the trap spacing on Grids 2 and 3 appears on the map, to be less than 16 m. This is because the grid distances were measured over the ground and where it sloped steeply this resulted in these distances appearing shorter than they were, when projected onto the map.

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PLATE 1

UPPER - The larchwood of Grid 1 in mid-June

LOWER - The sycamore wood of Grid 1 in mid-June

PLATE 2

UPPER - The western end of the immature larchwood of Grid 2 in mid-June

LOWER - The ash plantation of Grid 2 in Mid-June

PLATE 3

UPPER - The mature sycamore woodland of Grid 3 in mid-June

LOWER - The border between the spruce and sycamore woodland, and the open ground of Grid 3.

Additional Trapping Areas

Traplines U to Z were positioned as shown on Figure 2. The trap spacing along these lines was 8 metres. Line X was in open woodland with a thick ground cover of bracken and grasses. Line W was in open ground with a varied and rich ground flora including herb paris, *Paris quadrifolia*, and fragrant orchid *Gymnodoena conopsea*. Line V was in mixed deciduous conifer woodland with a good ground cover of bracken and bramble while line U was positioned along the boundary fence between the woodland and arable farmland. Lines Y and Z were in mature sycamore woodland which contained some pine.

The purpose of the traplines was to try to detect movement of marked animals away frmm grid areas and possibly their commuting between grid areas, as had been noticed by Ashby (unpublished). Crawley (1965, 1969) had similarly found some individuals of both *Clethrionomys* and *Apodemus* wandering between grids and so traplines were placed in positions, as suitable as the nature of the ground permitted, for in many places it was too steep and overgrown.

METHODS OF STUDY

1. Trapping Procedure

The three grids were trapped for five nights in May, June and July, approximately at monthly intervals. The trapping of the grids was simultaneous and they were visited in the same order once each day, that order being Grid 2, Grid 1, Grid 3.

The trapping was carried out using Longworth live traps (Chitty and Kempson, 1949) of which one was placed at each position. In his study in the Dene, Crawley (1965, 1969) used a minimum of three traps at each position but as mentioned previously (page) insufficient labour was available to permit more than one trap at each position during the current work.

No pre-baiting was done as it was considered that the five day period was long enough to offset the effect of any initial trap shyness which pre-baiting procedures were designed to avoid (Chitty and Kempson, 1949).

During May, when a total of only 96 traps wer set and catches were low, the traps were visited in the morning, beginning at about 09.30 and again in the late afternoon beginning at about 07.30. In June and July however, the increased number of traps and difficulty of the terrain prevented more than one visit per day. This began at Grid 2 at about 09.30 and ended at Grid 3 at about 14.30, depending on the number of animals caught.

The traps were removed at the end of the trapping sessions in May and June in the case of Grids 2 and 3. After the July session, the traps on these two grids were left in position for Miss Duckworth to continue her work on the fleas of the two species. In Grid 1, the traps were left in position throughout the period as Miss Duckworth required them for her studies. The traplines were not established until July when it became obvious that the attempt at tracking animals was not going to prove successful. Lines Y and Z were trapped for the same period as the grids in July, and all the traplines were operated for three days, from July 17 to 19th inclusive.

2. Marking Procedure

Animals captured on the three grids and on traplines Y andZ were marked by the removal of toes using sharp scissors. On the other traplines animals were not marked as they were used merely to determine movements of animals previously marked in the grids.

No animal had more than three toes removed and never more than one toe from any foot. As the original intention was to track the animals, the marks given were individually specific though duplicated between species as it was thought that *Apodemus* prints would easily be distinguishable from those of *Clethrionomys* by the large back feet possessed by the former.

3. Data Recorded

For each animal handled, as well as the position of capture and identification mark, the following data were recorded:-

I. The sex and sexual condition

As the animals were in breeding condition throughout the study period, sexing was straightforward with adults. In *Apodemus* the testes in the male are very obvious when descended. In *Clethrionomys* they are less so, but this feature combined with the greater distance between penis and anus compared with the distance between clitoris and anus makes sexing quite simple. Juveniles of both species are more difficult to sex, but with the distance between anus and either clitoris or penis, as the main criteria, little difficulty is encountered. Below are listed the various categories of sexual condition for both sexes and the criteria for defining them, as used by Crawley (1965).

(a) Males

Males were considered to be fecund when the testes are scrotal in position. They were generally regarded as adult (Crawley, 1965) if they weighed more than 14 gms, *Clethrionomys* or 15 gms, *Apodemus*, though some of Ashby's data (personal communication) suggests that not all individuals become fully adult at these weights. Juveniles were identifiable by their fluffy grey pelage and abdominal position of the testes which were retained up to a weight of about 10gms.

Animals between 10 and 14 gms were considered sub-adult.

(b) Females

(i) Perforate

Females in which the vaginal orifice had no covering membrane were classed as perforate. If they weighed over 14 gms in the case of Clethrionomys or over 15 gms in the case of Apodemus (Baker, 1930) they were considered adult. If they weighed less than the stated weights but were not juvenile they were considered to be sub-adult.

(ii) Imperforate

Females were considered imperforate when the vaginal orifice was not visible. Such females may have been adults, sub-adults in non-breeding condition, juveniles or pregnant adults or sub-adults. As the study was undertaken entirely during the height of the breeding season it is unlikely that any of the imperforate adults were in non-breeding condition. Hence they were classed as pregnant. In autumn however, the differentiation of females in early pregnancy and those coming out of breeding condition, can be difficult. Using the criteria listed below it was possible to differentiate most classes of imperforate female leaving only immature animals in the 'imperforate' category.

(iii) Pregnant

Females were considered to be pregnant when they were adult and in an imperforate condition during the breeding season. The latter stages of pregnancy could be detected by the discovery of embryos in the uterus, determined by palpation of the female's abdomen. A valuable aid to this diagnosis was the change in body weight of marked females which were repeatedly captured over short intervals.

(iv) Lactating

Females were considered to be lactating when the mammary glands were swollen and easily visible. Lactating animals could also have been imperforate, pregnant or perforate.

(v) Juvenile

Any female which were imperforate, with a fluffy grey pelage, and a weight of under 10 gms were classed as juveniles.

(vi) Sub-adult

Females which did not possess the fluffy grey pelage and weighed less than 14 gms. were classed as sub-adult. Some were perforate some imperforate.

II. Weight

All animals on the grids and traplines Y and Z were weighed each time they were caught. Weighing was achieved by suspending the individuals from a spring balance, in a polythene bag of known weight. The balance was frequently recalibrated and weighings were accurate to 0.5 gms. The weight was used to determine the approximate age of the animals.

III. Length

In the case of animals which had apparently ceased to grow, the length was determined at the first capture only. With growing animals the length was measured at each capture.

Other Information

Other animals captured were the short-tailed vole, *Microtus agrestis* (L) , common shrew, *Sorex araneus* L, water shrew, *Neomys fodiens* Pennant and the mole, *Talpa suropaea* L. The mole and all the shrews were dead in the trap.

SECTION B

THE POPULATION DYNAMICS OF APODEMUS AND CLETHRIONOMYS

THE TRAPPING RESULTS

1. Numbers of Animals Caught

The total number of Clethrionomys and Apodemus handled at each grid is shown in Tables 1 and 2 respectively. Details of the numbers of the two species handled in each trapping session at each grid are also shown.

The number of Clethrionomys caught in grids 1 and 3 was approximately equal, while on Grid 2 there were considerably more animals handled than on these two. Moreover, the number of animals handled per trapping session increased greatly on Grid 2 between May and June whereas on Grids 1 and 3 it increased much less. This is because the extension of the grids in the June session resulted in the inclusion, on Grid 2, of an area of ash plantation very favourable to Clethrionomys whereas previously the grid had been situated entirely in larch wood which supports a much less dense population. On Grid 1 the extension was into sycamore and sycamore/ spruce woodland. As the original grid had been partially sited in the sycamore, the increase in individuals handled, as might be expected, was approximately in proportion to the increase in grid area. On Grid 3 the extension resulted in the inclusion of pine wood and mixed grassland and only a little sycamore. Accordingly the increase in individuals handled was very small.

The numbers handled on the equivalent (see page 34) grids to the original ones are shown for July and June in Table 3. From this it can be seen that the number of Clethrionomys handled in May and June was approximately the same on all three grids. This is to be expected as only two juvenile Clethrionomys were handled in the June session, suggesting that breeding had not, as yet, caused a significant increase in the population size. In July, the

Grid	Trapping Session	No. of individuals ct.			No. of individuals ct.			Sex Ratio	No. of Deaths		
		♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂: ♀♀	♂♂	♀♀	Total
1	May	12	5	17	19	6	25	2·4 : 1	1	1	2
	June	17	6	24	31	15	47	2·83 : 1	0	0	0
	July	18	15	33	32	21	53	1·2 : 1	1	3	4
2	May	3	1	4	5	2	9	—	0	0	0
	June	20	9	29	34	19	54	2·22 : 1	0	1	1
	July	29	27	56	56	50	108	1·07 : 1	3	4	7
3	May	16	8	24	26	13	40	2 : 1	0	0	0
	June	16	10	26	35	22	57	1·6 : 1	0	0	0
	July	17	20	37	35	38	75	0·85 : 1	2	7	9
All	1	28	18	46	82	42	125	1·44 : 1	2	4	6
	2	35	30	65	95	71	171	1·16 : 1	3	5	8
	3	28	27	55	86	73	162	1·04 : 1	2	7	9
Totals		91	75	166	263	186	458	1·21 : 1	7	16	23

Table 1

The total number of Clethrionomys glareolus handled on all Grids, and the number handled on the three separate grids. Sex ratio in the tables refers to individuals, not captures. Escapees are included in the total of captures.

Grid	Trapping Session	No. of individuals ct.			No. of individuals ct.			Sex Ratio	No. of Deaths		
		♂♂	♀♀	Total	♂♂	♀♀	Total	♂♂ : ♀♀	♂♂	♀♀	Total
1	May	4	7	12	13	12	29	0·57 : 1	0	0	0
	June	4	5	9	8	12	23	0·80 : 1	0	0	0
	July	4	4	8	7	8	17	1 : 1	0	0	0
2	May	5	4	9	12	7	21	1·25 : 1	1	0	1
	June	2	1	3	4	3	7	—	0	0	0
	July	0	2	2	0	6	7	—	0	0	0
3	May	1	1	2	2	1	3	—	0	0	0
	June	2	0	2	2	0	2	—	0	0	0
	July	0	1	1	0	3	3	—	0	0	0
All.	1	9	9	18	28	32	69	1 : 1	1	0	1
	2	4	5	9	16	16	35	0·80 : 1	0	0	0
	3	2	2	4	4	4	8	1 : 1	0	0	0
Total		15	16	31	48	52	112	0·88 : 1	1	0	1

Table 2

The total number of Apodemus sylvaticus handled on all grids and the numbers handled on the three separate grids. Sex ratio in the tables refers to individu not captures. Escapees are included in the total of captures.

numbers handled on the original grids did not increase in Grid 1, although the observed ratio of the sexes altered; (the change was not significant though) increased considerably on Grid 2 and stayed about the same on Grid 3. The increase in numbers on a previously sparsely populated area of Grid 2 was ~~probably~~ possibly due to breeding pressures as discussed later (page 27). The failure of numbers to increase on Grids 1 and 3 is surprising. When the extended grids are considered (Table 1) it can be seen that on these, numbers did increase between June and July as a result of breeding. It is interesting to note, however, that the increase on these two grids is due almost entirely to an increase in the number of females caught and a similar trend is obvious on Grid 2. The age of these females caught for the first time varied between the grids. On Grid 1 almost 50 per cent of the new females were young adults or juveniles. On Grid 2 the proportion was about the same while on Grid 3, the whole of the increase could be accounted for by sub-adult and young adult animals.

Results for the extended grids show that by far the largest increase in individuals handled between June and July, both absolutely and proportionally, was on Grid 2. The number of captures on Grids 2 and 3 increased markedly, but on Grid 1 the increase was only slight even though the number of individuals handled increased by 35 per cent. The difference in recapture rate was not significant however ($p > 0.05$).

At all times the numbers of Apodemus caught were low. However, some information may be drawn from the results which appear in Table 2. The sycamore plantation (Grid 3) is not a favoured environment. The only four Apodemus captured on this grid were all in traps placed in the larch and pine. A few captures were made in the larch plantation of Grid 2 in May, but by July only two individuals could be captured.

GRID	MONTH	No. of individuals caught.			
		♂♂	♀♀	Total	
1	May	12	5	17	Clethrionomys
	June	13	4	17	
	July	8	8	16	
2	May	3	1	4	
	June	3	2	5	
	July	16	9	25	
3	May	16	8	24	
	June	12	8	20	
	July	13	10	23	
1	May	4	7	12	Apodemus
	June	2	5	7	
	July	4	3	7	

TABLE 3

Numbers of *Clethrionomys* caught on the original grids in May, June and July and the number of *Apodemus* caught on the original Grid 1 in May, June and July.

Grid 1 provided the majority of Apodemus captures and these were mainly in the larch and pine.

2. Estimation of Population Size from Numbers of Animals caught

(a) Introduction

The population sizes at each trapping session on both original and extended grids were estimated using Hayne's (1949b) method which is based on the 'Lincoln Index'. This index involves taking a random sample from a population, marking and releasing it and, after sufficient time has elapsed to allow the marked sample to distribute itself randomly in the population, another sample is taken and the proportion of marked animals in the sample is noted. The size of the total population is then given by:

$$\text{Total Population} = \text{No. marked at sample one} \times \frac{\text{No. caught in sample two}}{\text{No. marked in sample two}}$$

In using a 'Lincoln Index' method, the following assumptions are made:

(i) The marked animals are unaffected by the marking

(ii) The marked animals will become completely mixed with the population.

(iii) The population is sampled randomly with respect to its mark status. This assumes that all individuals of different age groups and of both sexes are sampled in the proportions in which they occur in the population, and that all individuals are equally available for capture.

It is difficult, if not impossible, to verify the assumption that sampling is completely random but Jolly (1965) has pointed out that the important thing is that the probability of capturing a marked animal is the same as that of capturing any member of the population. With small mammals, however, this may not be the case.

Animals may become 'trap addicted' and so be caught a disproportionate number of times while others may be 'trap shy' (that is of low hierarchical status) and either never be caught or be caught only once though present in the area throughout the study period.

Young et al (1952) found the frequencies of recapture of marked free living house mice showed large deviations from those expected if recaptures were random. Andrzejewski et al (1959) found a clear correlation between trap proneness and social dominance in males of confined laboratory house mice, but no difference in response of females to traps. Crowcroft and Jeffers (1961) found individual differences in both sexes of wild house mice in their response to live traps, when kept in controlled colonies. Moreover, they found that with limited numbers of traps, trap prone inviduals excluded other mice from capture and so population estimates based on the 'Lincoln Index' were too low. They suggested that the differences in trap-response were partially due to inherent differences in temperament but may be influenced by social strife which their experimental conditions could have accentuated. Tanaka (1963) classes Clethrionomys glareolus as a response type III or $\pi = p$ (π being the probability of recapture of marked animals and p that of unmarked animals). This means the chance of an unmarked animal being capture is the same as that for amarked one. The two species of Apodemus which he evaluates, A.speciosus and A.argenteus both fall into response type I, $\pi > p$, or previously captured animals (marked individuals) have a greater chance of capture than umarked. On this basis, he would rule out 'Lincoln Index' methods as a means of estimating Apodemus populations . Similarly, Krebs (1964) working on Microtus californicus arrived at the conclusion that 'Lincoln Index' methods were invalidated by differential trap response of individuals. Ashby (1967) considered that live trapping with closely spaced traps could gave a reliable estimate of not only the population size, but also the proportion of different classes of individuals in the population. He considered grid trapping tended to ruin juveniles.

(b) Hayne's (1949b) Method of Estimation

This method was designed to make use of serial recaptures over a short period. For long term studies, the 'Maximum Likelihood' method of Leslie and Chitty and Chitty (1953) and the stochastic method of Jolly (1965) is to be preferred, but insufficient trapping was carried out in the present study to permit its use.

Hayne's method consists of measuring the increase in the proportion of marked animals which is observed in succeeding catches as more animals become marked in the course of the experiment. The method can only be applied when catches from day to day are approximately equal. In the present study, this was the case with the five days of each session and so all the capture and recapture data was used in estimating the population size.

When 'x' animals have been marked and released into the population 'p' from which they are drawn, the proportion of the carch marked 'y' will be:

$$y = \frac{x}{p} \quad \text{or} \quad y = \frac{1}{p}x \text{ .... (1)}$$

Each sample will estimate the proportion of the population marked at the different stages of the process. Equation (1) is that of a straight line passing through the origin with a gradient of $\frac{1}{p}$ i.e. the reciprocal of the population size. As the experiment proceeds the proportion of marked animals will increase. Marking one additional animal will cause the proportion marked to increase by a certain amount, the increase is inversely proportional to the population number. After finding the average amount by which marking one further animal changes the proportion marked, it is then possible to estimate the total population size. The formula used is :

$$P = \frac{wx^2}{wxy} \quad \ldots\ldots\ldots\ldots(2)$$

where

P = population size

w = the total number in each catch

x = the number of marked individuals in the population

y = the proportion of 'x' (recaptures) in 'w'.

Using formula (2) data from short trapping periods may be used separately as though each period were a whole trapping experiment. The data for the July trapping session on Grid 2 for Clethrionomys females are set out below (Table 4), in the form necessary for an estimation of population size using Hayne's method.

TABLE 4. The arrangement of data for the estimation of population size by Hayne's method.

R = animal previously handled. Superscripts denote dead animals

Day	Total Captures (w)	New ans.	(R) (y)	Propn.R.	Total R (x)	wxy	wx^2
1	12	12	0	0	0	0	0
2	8	7'	1	0.125	12	12	1152
3	9	3	6'	0.67	18	108	2916
4	10	2	8	0.80	20	160	4000
5	10	2	8	0.80	22	176	4840
				TOTALS		456	12,908

$$P = \frac{wx^2}{wxy} = \frac{12908}{456} = 28 \text{ Voles}$$

Results

The results obtained using this for Clethrionomys are set out in Table 5. Estimates for the total numbers of animals on the original grids are also given. In all cases except for the July session on Grid 1, the population as estimated using the totals of animals of both sexes gives a result close to the sum of the totals for each sex estimated separately. The anomaly of the July result is due to the

		ORIGINAL GRID			EXTENDED GRID		
GRID	MONTH	♂♂	♀♀	All animals	♂♂	♀♀	All animals
1	May	15	6	22	–	–	–
	June	–	–	18	19	6	23
	July	–	–	20	22	37	42
2	May	+	+	+	–	–	–
	June	–	–	+	25	9	33
	July	–	–	27	29	30	57
3	May	20	9	30	–	–	–
	June	–	–	22	17	10	25
	July	–	–	31	17	18	33

Table 5

Population estimates of Clethrionomys on original and extended grids. Only estimates of total number of individuals were made in June and July for original grids.

+ Too few captures for an estimate to be made.

large proportion (0.8) of unmarked females captured on the last day. When the female capture data are combined with those for the males, the proportion of unmarked animals drops to 0.55 and results in the estimate based on both sexes being much lower than the combined totals for each sex.

The populations on the three grids all behaved differently on Grid 3 the estimate population was as large in May as it was in June even though the grid size in May was only 70 per cent of that in June. By looking at the population estimate for the original grid (Table 5) it can be seen that this is because extension of the grid was over ground with very few <u>Clethrionomys</u> on it. The increase in July as juveniles and sub-adults enter the population, was concentrated in the area of the original grid. On Grid 1 the estimated population only increases after June in agreement with trap findings of no juveniles or sub-adults until July. The increase in July, howdver, is due almpst entirely to an increase in the population of the area not included by the original grid. This is probably because it is a preferred environment, the original grid containing much larch and pine wood. The very substantial increase in animals handled on Grid 2 between May and June is due to the extension of the grid. Catches in the original area were too low to allow an estimate of the population even in June. The further large increase between June and July was due mainly to the appearance of juveniles, sub-adults and young adults in the population although previously unmarked adults continued to be captured. In July, numbers of animals on the original grid were very much higher. Possible reasons for this are discussed later (page 27), when the density of animals in differ ent areas is considered.

On only four instances did the population estimate based on Hayne's method give a result which was lower than the number of individuals recorded during the trapping session. These cases were for the estimates based on all animals on Grids 1 and 2 in June, and for females and all animals on Grid 3 in July. The reason for the underestimations on Grid 3 was the high trap mortality of females. In fact, Hayne's estimation gives results so close to the actual numbers of individuals trapped, that in most cases, it is legitimate to consider that the total population has been trapped. Those instances where Hayne's method actually underestimated the population, are due to deaths being a high percentage of the number of individuals caught.

The numbers of Apodemus individuals caught were so small that estimates were only made for Grid 1 (all trapping sessions) and for the May session on Grid 2. The results are set out in Table 6. The population apparently declined slightly on Grid 1 throughout the period of study. Whether or not this summer decline in numbers ~~is~~ was indeed true will be discussed later (page). On Grid 2 the May population ~~is~~ was less than that of Grid 1 but still estimable except for the females for although four females were caught, only one recapture was made. In June and July, however, Apodemus numbers fell so low as to be useless for purposes of population estimation.

Separate population estimates were not made of for the original Grids as only two individuals did not occur on them, a fecund male in June and a pregnant female in July were recorded on the extended portion of Grid 1.

3. Trap Mortality

Results

The trap mortality as a percentage of the number of individuals and as a percentage of the total number of captures is expressed for each

		Males	Females	All animals.
GRID 1	May	4	9	12
	June	4	5	9
	July	4	4	8
GRID 2	May	6	3	8

Table 6

Population estimates of Apodemus on Grid 1 for May, June and July and on Grid 2 for May. Results are for the whole grids each time.

sex of *Clethrionomys* and for each trapping session in Table 7. Only one trap death occurred in *Apodemus*, this being a fecund male on Grid 2 in May. Trap mortality, expressed as the percentage of individuals trapped which were found dead on a grid over all three trapping sessions was 11 per cent on Grid 1, 13 per cent on Grid 2 and 24 per cent on Grid 3. The high value for Grid 3 is due mainly to six deaths on one day. Of these, four were sub-adults females and one a sub-adult male while the final one was a pregnant female. The weather was no more inclement on this night than the others of the July period and the high mortality is perhaps due to the individuals caught being of low resistance to adverse conditions. Ashby (1967) found the trap mortality of *Clethrionomys* to vary greatly from year to year.

Discussion

The percentage mortality found agrees with Crawley's (1965, 1969) findings on Grid 1 (his Grid A) but on Grid 2 (his Grid B) he obtained a value of 31 per cent of trapped individuals dead. His percentages, however, are based on many more results and his higher figure is due largely to high trap mortality in winter, especially in November and December. If his results for May, June and July only are considered, then his mortality on both Grids 1 and 2 is lower. As in Crawley's work, most deaths may be attributed to inclement weather causing soiling and dampening of the animals and their bedding, the animals then dying of heat loss. This is especially so when traps can only be visited once a day as in the present study.

Whereas Crawley found deaths of females and males to be about equal on Grid 1, but male mortality to be twice that of female on Grid 2, the present study revealed that on all grids female mortality was higher than male but on no occasion was it significantly so ($p \; 0.05$).

GRID	MONTH	Deaths as % of individuals handled			Deaths as % of total captures		
		♂♂	♀♀	All animals	♂♂	♀♀	All animals
1	May	8	20	11	5	16	8
	June	0	0	0	0	0	0
	July	6	20	11	3	14	7
2	May	0	0	0	0	0	0
	June	0	11	3	0	5	2
	July	10	15	13	5	8	7
3	May	0	0	0	0	0	0
	June	0	0	0	0	0	0
	July	12	35	24	6	18	12
All grids	May	3	7	4	2	10	3
	June	0	4	1	0	2	1
	July	9	24	16	5	13	9
All animals handled.		8	21	14	3	9	5

Table 7

Trap mortality of Clethrionomys expressed as a percentage of individuals caught and as a percentage of total captures, for all three grids and for the grids combined and for all captures.

In agreement with Evans (1942) and Crawley (1965, 1969) it was found that trap mortality of marked animals was no higher than that of unmarked. On Grid 1 about 50 per cent, on Grid 2 about 25 per cent and on Grid 3 about 75 per cent of trap deaths were of unmarked animals. These workers also found a great difference in the trap mortality of Clethrionomys and Apodemus, Apodemus reacting, as in this study, far more favourably to confinement. Morris (1955) similarly found trap mortality to be low in deermice, Peromyscus maniculatus abietorum (Bangs) but high in red-backed voles, Clethrionomys gapperi.

4. Trap-revealed Sex Ratio

Results

Clethrionomys males were consistently but usually not significantly more abundant, than females, as revealed by trap ratios, on all grids and on all occasions except for the July trapping session on Grid 3. Two results showed a sex ratio significantly different from 1:1 these being the June sessions on Grids 1 and 2 ($p < 0.05$). However, the possibility of differential trap response between the sexes due to difference in hierarchical position, must always be borne in mind. The overall sex ratios for each grid can be seen in Table 1 and in no instance were they significantly different from 1:1.

In contrast, with Clethrionomys, Apodemus showed a preponderance of females or an equality of sexes on Grids 1 and 3, but a preponderance of males on Grid 2. Numbers handled, however, were so small as to prevent the results having any significance.

Discussion

Crawley (1965, 1969) also found in Clethrionomys a sex ratio in favour of males in all months on his Grid B. On his Grid A males were more numerous in catches in all months except July and August of 1963. Comparison of present results with Crawley's probably have litle meaning but it is interesting to note that he found the sex ratio to favour females on Grid A in May and June of 1963 and July 1964 and on Grid B in May 1964. On most other occasions the ratio favoured males. Ashby (unpublished) however, has found his reanalysis of Crawley's work, in conjunction with other observations by himself in Castle Eden Dene, suggests equality in the numbers of the two sexes during the summer months. Elton et al (1931) found the sex ratio in *Apodemus* altered in a similar fashion each year over the two years of their study. The pattern of change was characterised by near equality of the sexes in winter, followed by an increase in males over females in early spring; the trend was reversed in May and June so that numbers again approached equality, but in late summer the ratio strongly favoured males again; trends which are similar to Crawley's.

Evans (1942) found for *Apodemus*, a sex ratio varying very little from unity at all seasons though he gave no results for July and August when males might be expected to be trapped more than females, according to the results of Elton et al and Crawley. His results for *Clethrionomys* show no recognisable pattern the ratio varying considerably throughout his study period. Millen (1958) found variations similar to those of Elton et al, whereas Tanton (1965) found that there was no seasonal trend in the sex ratio in 1962, but for most of the spring and summer of 1963 it did not differ significantly from 1:1, but became significant in October/November. He noted, however, that the proportion of males is consistently and generally significantly higher than that of females. The traps revealed sex ratios, however, ~~and have~~ may bear no close relation to those actually occurring in the field especially in the light of the previously mentioned work of Crowcroft and Jeffers (1961) when, in particular, they showed that all female colonies of wild house mice there was no division into trap shy and trap prone individuals, but the introduction of males caused such a division to appear and also more males tended to be caught.

Kikkawa (1964) found the sex ratio in *Apodemus* slightly in favour of females. In his study he considered all resident mice had been trapped and that the balance would be made up by transient males. In different areas he found a sex ratio of 1:5 males : 1 female (approx.) using more widely spaced traps and less trapping effort. From this he concluded that males are drawn from a larger area than females which agrees with Miller's view (1958) that males are more abundant than females in spring and summer.

Ashby (1967) found that results obtained by him over a period of trapping of 10 years at approximately three monthly intervals, showed a preponderance of males, in both *Clethrionomys* and *Apodemus* the proportion being 56 per cent males in the former and nearly 60 per cent in the latter. The sex ratio of individual trapping sessions varied considerably. In *Clethrionomys* the ratio was generally 1:1 but there were periods of marked excess of males and values for χ^2 indicated the sex ratio did not remain constant. In *Apodemus* the sex ratio rarely approached 1:1. χ^2 for the sex ratio of animals caught from October 1955 to February 1966 compared with the sum of the figures of the remaining generations up to October 1969 inclusive gave a probability of homogeneity of $P=0.001$.

Ashby considered the variations in sex ratio during autumn and winter to be related to the degree of breeding success during the preceding summer. In years of good breeding success the ratio will approximate to 1:1 in others 2:1, but equality was always observed by him in spring.

5. Average Recapture Index

Introduction

The monthly total of individuals caught and total of captures for each grid is shown in Tables 1 and 2. If the number of recaptures is divided by the number of individual animals concerned, then an average recapture index per individual may be calculated. The calculated average recapture indices for Clethrionomys on each grid are shown in Table 8 and those for Apodemus in Table 9.

Results

In no instance are the recapture indices significantly different ($p \ngtr 0.05$) between sexes for a given trapping session on a given grid. For males, the chance of recapture appears to be lowest in May but the values of the indices are so close (none are significantly different, $p > 0.05$), as to make any valid generalizations difficult. The recapture indices for females are highest on all three grids in June but again there is no significance ($p > 0.05$).

Once again, the small number of Apodemus involved make it impracticable to calculate any parameters of real value. Although differences in average recapture index occur between sexes for the same trapping sessions and within sexes for different trapping sessions, none of them are significant ($p > 0.05$). From the figures it would appear that in May the males chance of recapture is highest while the females is lowest. The average recapture index for Apodemus is high when compared with that for Clethrionomys.

Kikkawa (1964) suggested that male Apodemus are more likely to escape recapture than are females but the present study does not support this and neither does that of Crawley (1965, 1969).

Grid	Trapping Session	Males	Females
1	May	1·58	1·20
	June	1·82	2·50
	July	1·78	1·40
2	May	1·67	2·00
	June	1·70	2·11
	July	1·93	1·85
3	May	1·625	1·625
	June	2·19	2·20
	July	2·06	1·90
Grid Totals	1	2·93	2·33
	2	2·71	2·37
	3	3·08	2·70
All animals		2·89	2·48

Table 8

Recapture indices on the average number of recaptures per individual, for Clethrionomys for each trapping session on each grid; for all captures of all individuals on each grid (all trapping sessions combined); and for all captures of all individuals on all the grids (all trapping sessions combined).

		Males	Females
1	May	3·25	1·71
	June	2·00	2·40
	July	1·75	2·00
2	May	2·40	1·75
	June	2·00⁺	3·00⁺
	July	—	3·00⁺
3	May	2·00⁺	1·00⁺
	June	1·00⁺	—
	July	—	3·00⁺
Grid Totals	1	3·11	3·55
	2	4·00	3·20
	3	2·00	2·00
All animals.		3·20	3·25

Table 9

Recapture indices for Apodemus for each trapping session on each grid; for all captures of all individuals on each grid (all trapping sessions combined); and for all captures of all individuals on all the grids (all trapping sessions combined).

+ Estimate based on very few results

6. Distribution of Populations within the grids

Introduction

After the extension of the trapping grids in June, it became apparent from the results that Clethrionomys was unequally distributed over Grids 2 and 3. To test this, the returns from all grids were studied with respect to location of each individual captured. The number of individuals recorded in each half was then tested (by χ^2) to see if there existed any significant difference between them on the hypothesis that the number of individuals on each half of the grid should be equal. Sexes were tested individually and together the results are set out in Table 10. Animals which occurred on both halves of the grid were not used in these calculations. However, as this category did not include more than two animals on any one grid, it did not seriously affect the results.

Results

On Grid 1 no significant differences occurred for either sex or the sexes combined. On Grid 2 the difference in numbers of individuals on the halves of the grid was highly significant in June, when all animals were considered even when Yates' correction factor for small sample numbers was applied. In July the difference was significant but less so when Yates correction was used. When the sexes were considered separately it was found that the males had significant differences in distribution, on the half grids in June, but not in July. The females were significantly unequally distributed in June (but not when Yates correction was applied) and again, though at a higher level, in July. When Yates correction factor was applied, the results were significant but only at the $p < 0.05$ level.

TABLE 10 Levels of significance between differences in population on the two halves of each grid for the June and July trapping sessions (NS = Not Significant)

		Significance level			Sig.level using Yates c.f.		
Grid	Month	Males	Females	All Animals	Males	Females	All Animals
1	June	NS	NS	NS	NS	NS	NS
	July	NS	NS	NS	NS	NS	NS
2	June	0.01	0.05	0.001	0.01	NS	0.001
	July	NS	0.01	0.01	NS	0.05	0.05
3	June	0.01	0.02	0.001	0.02	NS	0.01
	July	NS	NS	0.02	NS	NS	0.05

The very different population densities on the two halves of the grid can be explained in terms of the vegetation cover. The high numbers occurred in the ash plantation with its dense ground cover of bluebell, bracken, bramble, wild raspberry, willowherb and grasses (plus fallen trees and branches) while the low numbers occurred in the larch plantation where much of the ground was covered with larch litter only and the vegetation, of ferns and patches of wild garlic and dog's mercury was comparatively thin.

The difference between sexes in the degree of significance of their inequality of distribution may be due to breeding activities and the data would be explained if, in July, when breeding, as judged from the number of females and young, was more intense than in June, the increased territoriality of the females associated with breeding (Brown (1966, 1969)), caused a dispersal of males out of the more favourable habitat, which presumably the females would occupy for breeding. In June, when territories are less fiercely defended and demand on food resources is less both males and females would occupy the optimum habitat. Hence the significant inequality of distribution of both sexes in June, but only of females (and at a higher level than that for June) in July. This is only a tentative suggestion and would need more trapping data combined with direct observation before anything definite could be said.

On Grid 3 neither sex was significant in the inequality of its distribution in July though both were in June. It may be that the death of the wild garlic which occurred between June and July reduced the favourability of the western half of the grid which it occupied and the distribution of animals then became more uniform though still biased towards the western end as shown by the significance values for disparity of distribution when all animals were considered.

Discussion

In his study in Bagley Wood, Berkshire, Evans (19~~6~~42) found Clethrionomys to be significantly more abundant in areas of bracken. Ashby (1967) considers that Evan's results are due to the fact that bracken was providing the densest cover, and he found, in his studies in Houghall Wood, Durham, that Clethrionomys was associated with dense cover but was indifferent to its nature, and that cover above, as well as at, ground level might also be important. Brown (1954) also noticed a correlation between the amount of cover, as provided by undergrowth, and the distribution of rodents. Delany (1957)working on Clethrionomys and Apodemus in oakwoods found many more captures of both species occured in areas with cover provided by rhododendrons and bramble than in less densely covered areas. He emphasised however, that there was no indication of either species preference for a particular habitat excluding or causing a significant reduction in the number of the other. Ashby (1967) supports the view that one species does not influence the distribution of the other by its habitat preference and states that local anomalies in density are usually caused independently in the two species.

Morris (1955) also emphasised the importance of protective cover in the ecology of *Clethrionomys gapperi* (the red backed vole) of North America. Of particular interest to the present study is his observation that the voles are especially dependent on the type of cover provided by debris, such as fallen trees, decaying log and slash from cutting and thinning. This is just the type of cover found on part of the densely populated section of Grid 2. He noted also that a ground cover of tall bracken was less effective than debris in encouraging vole populations, again a fact which ties in closely with observations on Grid 2. Morris considered the protective function of cover to be more important than the food supply it might provide, basing his arguments on the omnivorous diet of rodents. Whether this is true in the case of *Clethrionomys glareolus* with its predominantly vegetable diet with a fairly high proportion of green plants and their succulent parts (Southern, 1964, Drozdz, 1966, 1967; Watts, 1968), is doubtful. Miller (1958) concluded that cover was important in *Clethrionomys glareolus* and Newson (1960) also found a correlation between density of cover and numbers of this species. Crawley (1965, 1969) found in his work in the same area as the current study that the graphs of mean numbers of Clethrionomys caught at positions with a given cover index against the density of cover gave a good regression line with a highly significant correlation coefficient. This was the case for all four seasons and on both of his grids. Ashby (unpublished) found the same phenomenon for a parallel study over 90 acres at Castle Eden Dene on the basis of a 50 m. grid. Getz (1961) found the amount of cover to be important in the local distribution of the bog lemming *Synaptomys cooperi* and *Microtus pennsylvanicus* but as both rely on gramminoids for their food, the nature of the cover, rather than the mere abundance was the governing factor. For instance, *Microtus* avoided areas of *Potentilla fruticosa* even though the cover was as high there as in old field stations where the vole was common; Getz attributes this avoidance to the woody nature of P.fruticosa. Evans (1942) with regard to his results for Apodemus came to the conclusion that it was impossible to associate the distribution of this species with any known habitat factor and Millen (1958) and Newson (1960) also found the distribution of Apodemus to be at random with respect to cover as did Crawley (1965, 1969), but Crawley did find that the majority of individuals were caught in larch and spruce areas which have more open spaces than sycamore areas. Delany (1961) considered Apodemus to positively prefer habitats with a firm dry substrate and little ground cover, associating this with the preference of Apodemus of run quickly over clear areas whilst being slowed down by dense vegetation. Ashby (1967) also found Apodemus captures to be unrelated to the degree of cover and the variation was that to be expected from random variability affecting the capture of a species uniformly distributed over the area. He also found, like Delany, that they generally have a preference for dry and well drained grounds and avoid wetter localities. However, Ashby (unpublished) did find Apodemus commuting to an area of wet sycamore woodland in Castle Eden Dene in late summer. The reason for this is uncertain, but it is possible some preferred food may have been abundant in the sycamore wood.

The studies of Fullager et al (1963) on Clethrionomys glareolus skomeri and Apodemus sylvaticus on Skomer were carried out on habitats different from those normally used for the study of these small mammals, for the island is covered variously by bracken, well-grazed turf and rank-grown grasses. There are patches of heathland, patches of marsh in the stream valleys and large areas of bare rock, which form an important feature of the island. They found, unlike other workers, that a single species may be dominant in a particular habitat, but it is a situation where, at the extremes of dense bracken and bare rock, the habitats are in sharp contrast. On Skomer the association of Clethrionomys with bracken ~~is~~ was very close. Areas with a hig density of Clethrionomys were shunned by Apodemus and they conclude that the vole is excluding the mouse. Brown (1954) similarly found that high densities of Microtus agrestis will restrict the range of Apodemus. An opposite effect cannot be suggested for areas where the field mouse alone abounded as they were unsuitable for the vole, being either open or of sparse vegetation. The nocturnal mouse was able to exploit these areas and the authors state that debris scattered by gulls on the rock outcrops was attractive to the mice. In areas of scattered bracken, both species occurred.

Thus it has been shown by several workers that Clethrionomys has a dependence upon upon adequate vegetational cover whereas Apodemus tends to have a preference for more open drier ground. Klein (1960) suggests that the amount of illumination reaching the forest floor at night, when the animals are active, is an important factor in influencing the distribution of Peromyscus maniculatus gracilis and P.leucopus noveboracensis. Blair (1943a) found that the desert mouse P.m.blandus was most active in total darkness. Apodemus being a nocturnal animal and the ecological counterpart of Peromyscus in this country, light penetration could have a similar effect on its distribution and activity. Hacker and Pearson (1944) and Tanton (1965) have observed it to be less active on moonlit nights. Crawley (1965, 1969) found it more common in larchwood than in sycamore. In the former, the high density of trees and the dense growth of needles in summer causes light to be largely excluded. In contrast, on losing of their leaves, the sycamore intercept very little light.

Thus he concludes "that the preference of *Apodemus* for the dark open areas, of the larch wood may be a continuation of their preference for open areas for tree movement, and a necessity for a cloaking darkness for protection." Ovington (personal communication) has pointed out that in conifer plantations, only about 60 per cent of precipitation penetrates the ground level, the rest being retained in the branches and evaporating off. In deciduous woodland, up to 95 per cent of precipitation penetrates. This will lead to drier ground beneath the conifers and may be another reason for the greater abundance of *Apodemus* in this type of habitat.

In the present study, Apodemus captures on Grid 1 were divided in a 1:1 ratio level between larch and sycamore in May when the sycamore were still bare and giving no protection from light, but in July were confined entirely to larch wood. At this time the sycamore canopy was dense and intercepted much of the incident light. This change in distribution would appear to be the opposite of that expected in the hypothesis that the abundance of light penetrating to the forest floor. It must be remembered, however, that catches of *Apodemus* in July were much lower than in May and if this reflects a drop in population size, all individuals may in July be recurring in their preferred habitat, larch wood. Moreover, the ground cover in May in the sycamore is quite sparse, consisting almost exclusively of tussocks of *Deschampsia caespitosa*. In July it is much thicker with a heavy carpet of dog's mercury, campion and willowherb. This lack of open space may be a causal factor in the drop in numbers in the sycamore in summer, though it is possible that the animals have migrated into the surrounding arable farmland.

The distribution of Clethrionomys found in the present study agrees with that found by other workers. On Grid 3, however, by July the wild garlic had died back and the ground cover ~~is~~ was very poor so much so that in places the traps were difficult to conceal and yet catches of Clethrionomys remained high. The area was bounded by the new road works to the west, the golf course to the south and and patch of rough grassland some 30 m. wide to the south. To the north was the stream which was only very narrow in July and yet no animals appeared to cross it from Grid 3 as trapline X, placed close to the stream (Figure 2) but on the opposite side to Grid 3 failed to catch any animals marked on the grid. Hence it appears that movement from the area was prevented on all four sides, by the unfavourable habitat to the south and populations of other voles elsewhere, and the voles may have had no alternative but to remain in the area and make the best of a bad job with regard to loss of cover. Some ferns and wood sorrel provided better cover but this was only patchy and many catches were made in traps placed in particularly poorly covered areas.

7. Densities of Apodemus and Clethrionomys on the three grids

Introduction

The area ~~at~~ of both Grids 1 and Grid 2 in May was 6400 m^2 while that at Grid 3 was 3840 m^2. In June the area of all three grids was extended to 9216 m^2. The increase in area of the grids was made on the recommendation of Dr. Ashby who suggested that numbers caught on the smaller grids might prove inadequate for any kind of reasonable analysis. Moreover, the extension of Grids 1 and 2 made them roughly comparable with Crawley's Grids A and B which he trapped from 1963 to 1965.

Using these figures and the population estimates derived by Hayne's method, that is, assuming all animals are resident within the area of the grid 'hypothetical' densities of both species can be worked out. If the area occupied by the estimated population is considered to be that of the grid plus a border strip of width equal to half the calculated observed range length (which was 51.7 m for *Clethrionomys* and 55.7 for *Apodemus*), then the resulting 'adjusted' density will be considerably lower. 'Hypothetical' and 'adjusted' densities for *Clethrionomys* and *Apodemus* on all grids are given in Table 11. In calculating 'adjusted' densities, allowance was made for situations where the grid bordered on habitats unsuitable for the animals. Densities on the original size of grids are also calculated for June and July to see how these compared with densities on the whole grids. Though in June and July one trapline of the original grids 1 and 2 had been removed, on Grid 2 the trapline removed caught no animals in May and on Grid 1, all of the animals caught in the trapline, subsequently removed, were caught elsewhere too. Thus, in order to be able to compare densities on the original size of grid for the three trapping periods, the original grids on areas 1 and 2 were considered to consist of six traplines by five traplines i.e. they covered an area of 5120 m^2 or 0.512 hectares

Even with this alteration, the results will not be strictly comparable because of the presence of the additional range of traps which may have restricted animals which would otherwise have been caught on the original grid.

Results

The results obtained (Table 11) further emphasise the unequal distribution, i.e. the preponderance on animals on one half of the grid, of *Clethrionomys* within Grids 2 and 3. On area 2 the original

AREA (ha.)		Original Grids			Extended Grids		
		1	2	3	1	2	3
Hypothetical.		0·512	0·512	0·384	0·9216	0·9216	0·9216
Adjusted.		1·524	1·524	1·296	2·263	2·263	2·263
Adjusted minus area unsuitable for animals		1·524	1·371	1·264	2·239	2·053	2·018
DENSITY – Clethrionomys (Animals/hectare)							
Hypothetical :	May	44	8	78	–	–	–
	June	36	10	58	25	36	27
	July	40	53	81	46	62	36
Adjusted : minus area unsuitable for animals	May	15	3	24	–	–	–
	June	12	4	18	11	16	13
	July	14	20	25	19	28	17
DENSITY – Apodemus (Animals/hectare)							
Hypothetical :	May	24	16	–	–	–	–
	June	18	–	–	10	–	–
	July	16	–	–	9	–	–
Adjusted : minus area unsuitable for animals	May	8	6	–	–	–	–
	June	6	–	–	4	–	–
	July	5	–	–	3·5	–	–

Table 11

Actual and adjusted areas of the original grids and the expanded grids; and densities of Clethrionomys and Apodemus based on population estimates obtained by Hayne's method.

grid was situated in the unfavourable environment, larchwood, and the density here when compared with the density for the whole grid is markedly less in June. In July the difference in densities between original and extended grids is less, a possible reason for which has been advanced earlier (page). On Area 3, the original grid was situated in the favourable area and so densities calculated for it are considerably higher than the densities for the grid as a whole, again the difference being most pronounced in June.

The variation in density of the *Clethrionomys* raises the question of whether it is meaningful to talk of population densities of ~~and~~ this vole in mixed woodland. It would seem that unless a very detailed and exact description of aspect, position and especially vegetation cover is given together with figures for density, it is of little value to compare results obtained in different areas. Results for *Apodemus* may be more easily compared between areas as this rodent appears to range further and occupy more widely differing types of habitat, though a marked preference for larchwood as opposed to sycamore or ash plantations, was noted in this study. Densities of *Apodemus* were only calculated for Grid 1 and Grid 2 in May as these were the only times when sufficient captures were made.

As Crawley's (1965,1969) Grids A and B were situated in very similar positions to Grids 1 and 2, of this study, it would seem reasonable to compare the results of the two authors for the months of June and July. In June 1963 he obtained a population density for *Clethrionomys* of 58.5 to the hectare on Grid 1 and 63.75 per

per hectare on Grid 2 compared with 25 and 36 per hectare respectively in the current study. These are for 'hypothetical' densities. For 'adjusted' densities his figures are 20.5 and 22.5 compared with 11 and 16. In July his 'hypothetical' density figures are 72.75 and 90.25 compared with 46 and 62 respectively. 'Adjusted' densities are 22.5 and 31.5 compared with 19 and 28. For 1964 he has no results or only doubtful estimates except for Grid 1 in July, when the 'hypothetical' density is calculated as 79.95 and 'adjusted' as 22.75. Thus his estimates are higher. Ashby and Crawley (1967), trapping on a 50 m grid over a much larger area obtained results similar to those in the current work. However, in view of Crawley's (1965, 1969) results it may be that in the present study, all the animals in the population were not sampled, as there was only one trap per grid intersection compared with Crawley's minimum of three. Tanton, however, has argued that with catches which are not high (less than 60 per cent of the traps occupied per night) then over a five day period, the population will be adequately sampled to allow an accurate estimate of its size. In this study, the number of traps occupied never exceeded 50 per cent on Grid 1 or Grid 2. If the latter were considered in sections, though, the capture rate in rows A, B and C, the three most westerly ones, often exceeded 70 per cent in July and here the population estimates and hence, densities, may be too low. The calculated densities (actual) for Apodemus in Grid 1 were 24, 18 and 16 animals per hectare in May, June and July respectively. Crawley's figure for the same months and the same grid area are, for 1963, 8.5, 5 and 30 (the last is a doubtful estimate) and for 1964, 36.25, no figure for June and 7.25. The current results are at the same order of magnitude but the data from the three different years vary considerbly. This may reflect actual population differences or the unreliability of live trapping as a method of estimating Apodemus numbers in summer (see page 62-64)

8. THE AGE STRUCTURE OF THE POPULATIONS AS REVEALED BY WEIGHT MEASUREMENTS

Introduction

The weights of each individual to the nearest half gram was recorded each time it was handled and graphs were plotted of weight against number per weight class for half gram intervals. Separate graphs were drawn for each sex at each trapping session on each grid and for totals for each sex on the three grids at each trapping session. Where an animal was caught more than once in a session, the weight used was the mean. The results may be seen in Figures 3 & 4.

Results

Numbers of animals handled on the separate grids were too small to be analysed, so only the combined grid totals will be considered in detail (see Figs. 3 & 4)

For *Clethrionomys* males the weights in May and June followed an approximately normal distribution though the one juvenile recorded in June would be outside a normal distribution curve based on the other weight records. In July, a skewed distribution was apparent with a tail at the lower weights because of the influx of juveniles, sub-adults and adults into the populations. The means for the three months are set out in Table 12a

TABLE 12a Mean body weights of *Clethrionomys* and *Apodemus* for each trapping session (Totals pooled for each grid)

Clethrionomys	May	June	July
Males	20.63±0.28	20.52±0.31	19.53±0.41
Females	19.38±0.47	20.50±0.68	19.97± 0.57
Apodemus			
Males	21.45±0.50	22.75±0.49	24.33
Females	21.25±0.90	22.42±0.59	23.64±1.45

37a

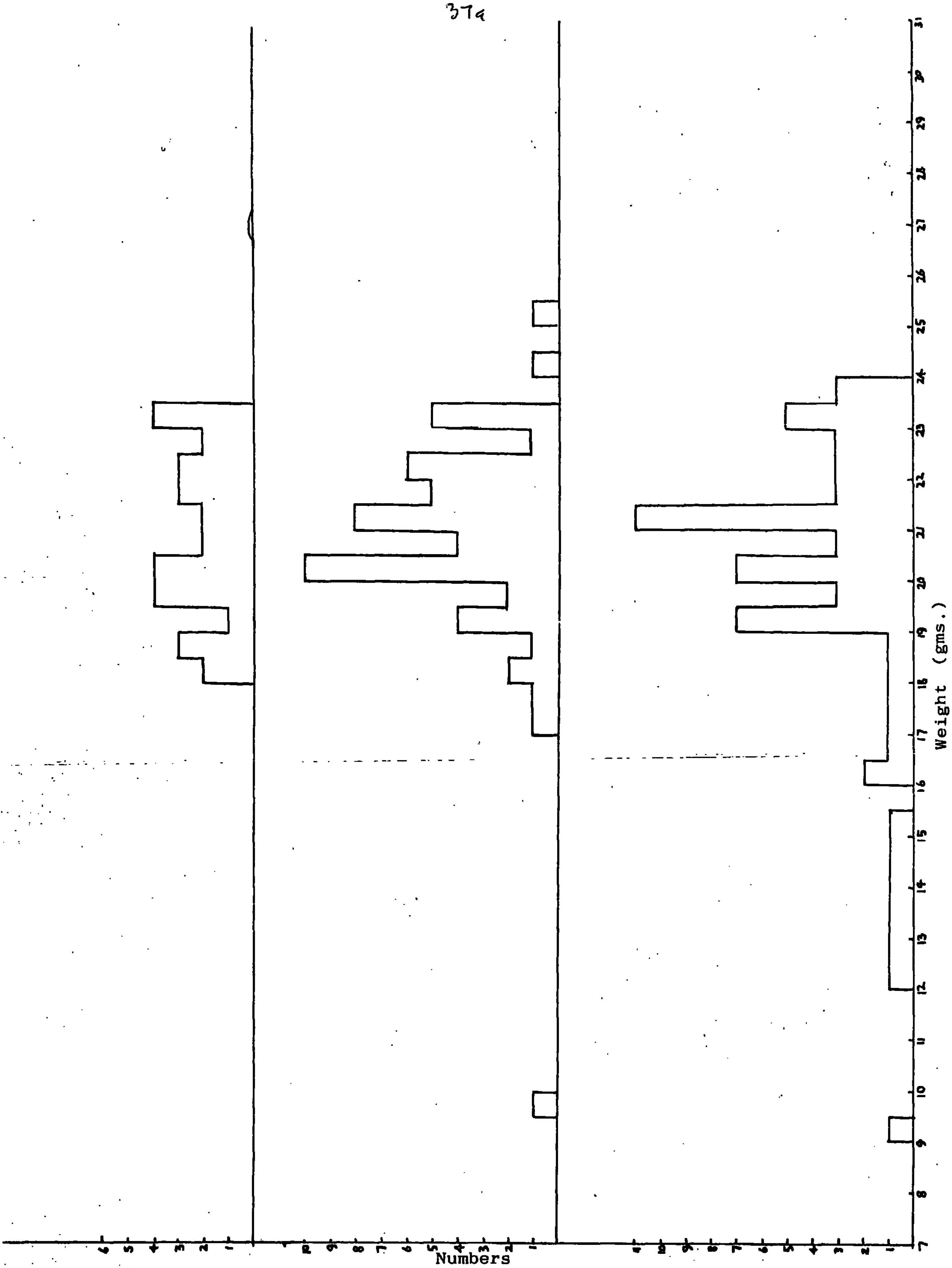

Figure 3

Weight classes of *Clethrionomys* males in May, June and July (All Grids)

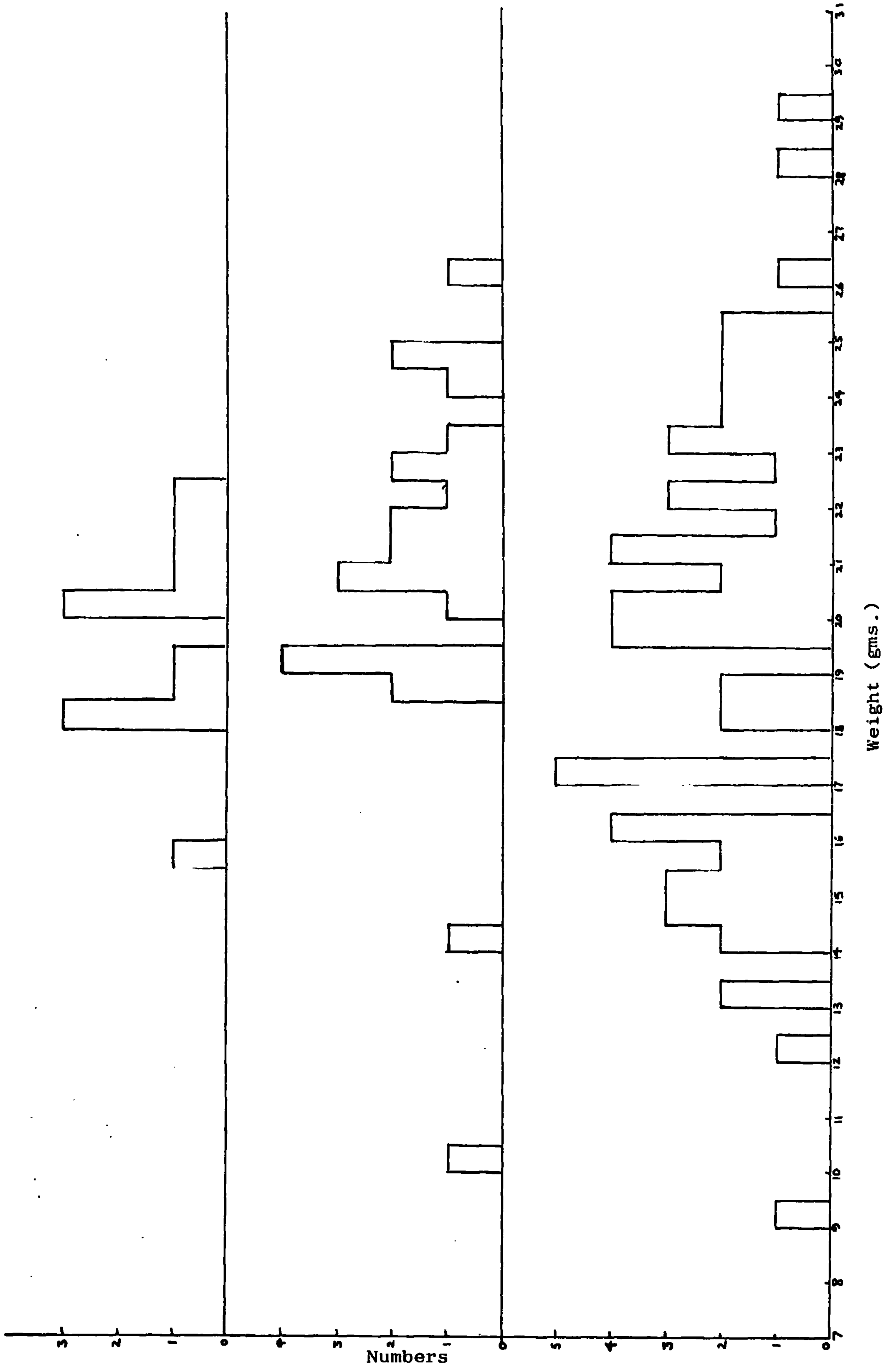

Figure 4
Weight classes of Clethrionomys females in May, June & July
(All Grids)

For Clethrionomys comparing means within sexes, the mean for males in May is significantly greater than the July mean ($p < 0.05$). None of the means for females are significantly different. Comparing means between sexes, only in May are males significantly ($p < 0.05$) heavier than females. Pregnancy of females probably prevented any significant differences in mean weight in June or July. In Apodemus there is no significant difference in mean weight either within or between sexes.

The gradual decrease in mean weight of Clethrionomys males can be accounted for by the influx into the population of juveniles, sub-adults and young adults in June and more especially in July. The animals caught in May were all overwintered individuals and none was caught weighing less than 18 gms. In the females, the influx of juveniles was offset by increase in weight due to pregnancy, of some of the fecund adults. This more heterogeneous distribution of weight in the females is reflected in the greater standard errors of the mean weights. The highest mean weight occurred in June when several individuals were pregnant, but only two animals (both sub-adult) were recorded weighing less than 18.5 gms. In July, 20 out of a total of 52animals weighed less than 18.5 gms.

Assessing the age of individuals caught in July using their weight and length as guiding factors, it was found that about forty individuals were either juvenile, sub-adult or young adult and could reasonably be considered to be animals born in the current breeding season. This is about 50 per cent of the number of adults in breeding condition earlier in the season, that is in the May and June trapping sessions. According to Southern (1964), the mean number of young per litter is 4.4. By July, the animals in breeding condition in May and June should have produced at least one litter per female which would of trappable size by July. If survival were high, then it is reasonable to expect that for every two adults present early on, there should be four juveniles produced, and that the trapping results should reflect this. That such a ratio does not exist is clearly obvious and an explanation must be sought to account for this discrepancy.

The supposition that discrete pairs of adults produce offspring may be wrong. One male may father several families as may be the case in the house mouse (Crowcroft 1966), or there may be a large imbalance in the sex ratio and for instance, three males may be present for every one female in the population, in which case, four young would be produced for every four adults present. In the present study, the sex ratio in May and June as revealed by trapping, was two male to every female. If this was indeed the case, and not merely an artifact of the method, then the maximum number of young expected would be one litter per three adults. Even taking this into account, the number of juveniles trapped is still smaller than expected. Other explanations must therefore be advanced of which the most likely are:

(a) Poor sampling - the young animals are trap shy or they have a small home range and do not come into contact with traps.

(b) The young scatter from their area at birth. But if this were so it seems reasonable to expect that they would be compensated for by young of other areas 'scattering' into the one being trapped.

(c) Mortality either direct by predation or disease, or as a consequence of failing to get a home range.

In May, no females were captured at an advanced stage of pregnancy and several were imperforate. However, in his study in the Dene, Crawley found in both his years that breeding began in April and was well underway by May. Thus it seems likely that most, if not all of the imperforate females were in fact in early pregnancy, especially as all males captured were fecund though the very late spring may have resulted in some females being in non-breeding condition.

A female *Apodemus* was captured in late pregnancy on Grid 1 in May, indicating an earlier onset of breeding than in *Clethrionomys*. Further pregnant females were captured in June and July but no juveniles were ever trapped on the grids though one sub-adult female weighing 13.5 gms. was taken on trapline 2 in July. This failure to capture any young *Apodemus* resulted in a gradual increase in body weight of females as pregnancy became more prevalent. The male *Apodemus* also increased in weight which is at variance with Crawley's observations. He found much higher mean body weights for males in May and June of 1963 but an average of only 17.90 gms. in July. His July reading, however, was based on only five animals which were, he suggested, all quickly matured young of that year. The pattern for 1964 was similar. In the present study, only three males were captured in July but they had an average body weight of 23.64 gms. and were males of the previous year.

Discussion

The absence of young *Apodemus* from the traps is interesting. Brown (1966, 1969) came to the conclusion, from results obtained in tracking animals, that adult, fecund males are very agressive in spring and early summer. As a result of this, recruitment of juveniles into the population is low and those that survive only have a very small home range. This small home range, low hierarchical position and low numbers of young *Apodemus* would account for their lack of trappability. Sadleir (1965) showed that in *Peromyscus maniculatus* the summer populations were low and a comparison of the number of pregnancies with the number of juveniles showed a large juvenile mortality. He found sudden population drops to be associated with the presence of highly agressive males and that removal of adults from an area increased juvenile survival.

Healey (1967) extended the studies on agression in this species and showed that male aggression increased in spring and summer. In controlled experiments he showed that juveniles grew much more slowly in the presence of adults, especially if the adults had an established territory before the young were introduced. The male adults were the most aggressive, juvenile survival being one hundred per cent when they were released into cages of adult females only. He also found that in the field aggressive males hade a significantly greater effect on juvenile growth than did docile males. However, poor juvenile survival was also noted in areas containing docile adults and Healey suggested some other factor may be involved in addition to male aggression.

In his studies in Clethrionomys based on a 50 m grid trapping system, Ashby (unpublished) found that a graph of number in each weight class against weight class, of very large samples in the latter part of the breeding season, gave two overlapping normal distributions. When plotted out on probability paper, the results gave two straight lines with an inflexion between 15 and 17.5 gms. There are a number of possible explanations (Ashby personal communication) but the total data collected suggested that this reflected an increase in trappability of individuals on the attainment of sexual maturity. With traps closely spaced in lines, Ashby believed this effect was much reduced (Ashby 1967). No such increase in trappability of animals reaching maturity can be inferred from the present study, but Ashby was dealing with higher numbers of individuals and it is possible that with greater numbers of results, the present study might have shown a similar distribution of captures per weight class though the grid system used could account for the difference.

SECTION C

MOVEMENT AND HOME RANGE

Introduction

Although many aspects of the ecology of Clethrionomys and Apodemus have been studied in detail, the problem of movement ~~of~~ and home range though arousing considerable interest, has only been studied in detail in these species by a few workers. Most notable among these are Evans (1942), Hacker and Pearson (1951, 1952), Brown (1956, 1962, 1966, 1969), Miller (1958) for Apodemus only, Kikkawa (1964), Tanton (1965) again on Apodemus, Crawley (1965, 1969), Watts (1966, 1970) and Ashby (1967).

The brevity of the present period of study prevented an assessment of seasonal variation in activity but sufficient results were obtained to investigate the following:

(a) Movement patterns of the two species.

(b) The size of the home range area

(c) Inter and intra specific differences in movement patterns

(d) The influence of sex, number of recaptures and method of estimation on estimates of home range size.

Methods used to assess movement and Home Range

When estimating the home range, from an individual, all captures for that animal were considered. With an interval of approximately a month between trapping sessions, it was hoped that this might allow animals to be captured in different parts of their home range, especially if they tended to concentrate their activity in small areas for short periods of time, for between trapping periods they could move around uninhabited by traps. On Grid 1, however, Miss Duckworth trapped for eight days in between May and June and ten days between June and July and it was hoped that sufficient trap free periods occurred to permit free movement over the home range.

In studying the movement patterns the maximum distance moved between successive captures in any one trapping period was noted for each animal. On Grid 1, the results from the trapping periods undertaken by Miss Duckworth were also used. One advantage in using this method is that data from animals captured only a few times may be used, and as these animals form the bulk of individuals handled, this is very useful.

Results obtained on traplines Y and Z and movements from grids to traplines, are also included.

MAXIMUM MOVEMENTS

Introduction

In his study of maximum movements, Crawley divided the year into three seasons which were spring (February to May), summer (June to September) and winter (October ~~September~~ to January). May was included in spring while June and July were included in his summer category. Thus, present results should be most nearly correlated with his summer results.

Movement categories were defined on a 16 m, that is one trap, interval, The number of maximum movements occurring in each distance category for all the trapping sessions are set out in Table 13.

Maximum movements between successive captures

It will be seen from the histograms in Figure 5 that the majority of animals with Clethrionomys and Apodemus make only short movements between successive captures over 50 per cent of the results being in the category of two trap distances or less. In Apodemus the category with highest numbers of animals in is the 0-16 m for females and the 16-32 m for males. In both sexes of Clethrionomys the 0-16 m category has most animals, though in the females this is much more pronounced with over 50 per cent of the results being in this grouping. Long distance movements were rarely observed within trapping sessions the only animal which was observed to move further than 176 metres was a female Clethrionomys. This animal was first marked as a perforate female on Grid 3 on 10 July. On 11 July, a perforate female of similar weight of the same mark was taken on trapline Z. On the 12th. the animal was back on Grid 3 but on the 13th. was recaptured on trapline Z. It was taken twice more, on the 19th and 20th of July on Grid 3.

It is possible of course that two different animals were being dealt with, one having lost a toe (only one toe was clipped on this animal) naturally. However, the fact that the animal captured on the grid and the trapline was perforate in all four instances between 10 July and 13th inclusive, and weighed approximately the same, would indicate that it was one and the same animal. If this is so then the animal was commuting over a distance of some 500 metres, as measured on the map. The actual distance travelled must have been considerably more. This is indeed an extraordinarily long journey for such an animal to make, but to make it on three successive days is astounding. The factors which might cause such behaviour are hard to imagine. If other Clethrionomys could find everything they needed on Grid 3 or close to, why should this animal move such distances? Alternatively, such movements might be quite common, but rarely detected. Ashby (unpublished) found Apodemus commuting from the area of Grid 1 to that of Grid 3, a distance pf some 300 metres or more but Apddemus is generally recognised to move over greater distances than Clethrionomys. Crawley did however find some Clethrionomys individuals both male and female, which wandered between his grids, a distance of over two hundred metres.

If movements between trapping sessions are considered, then a male Clethrionomys captured in June on Grid 2, moved from there to trapline Y. This movement was only of 100 metres but is unusual in that the animal involved crossed the burn. With the exception of the female mentioned above this was the only one to do so in the present study. Trapline X, placed close to Grid 3, but on the opposite side of the burn, failed to catch any animals marked on Grid 3. However, it did catch a fecund male in July (13th) and again on the 19th, which had been marked on the eastern end of Grid 1 on 11th July. Unfortunately this animal escaped on Grid 1 before it could

Distance moved (m)	Clethrionomys				Apodemus			
	Males		Females		Males		Females	
	No.	%	No.	%	No.	%.	No.	%.
0-16	26	29	21	54	3	18	6	40
16-32	22	24	12	31	8	47	5	33
32-48	17	19	3	7·5	5	29	2	14
48-64	15	17	1	2·5	0	0	1	7
64-80	7	8	0	0	0	0	0	0
80-96	2	2	1	2·5	1	6	1	7
96-112	0	0	1	2·5	0	0	0	0
112-128	1	1	0	0	0	0	0	0
Total	90	100	39	100	17	100	15	100

Table 13

The distribution of maximum movements between successive captures for Apodemus and Clethrionomys (Totals for all three grids and all trapping sessions are combined) and the average range lengths for both species.

	Average Range Maximum Length (m)
Clethrionomys males	57·3
Clethrionomys females	37·0
Apodemus males	54·6
Apodemus females	56·6

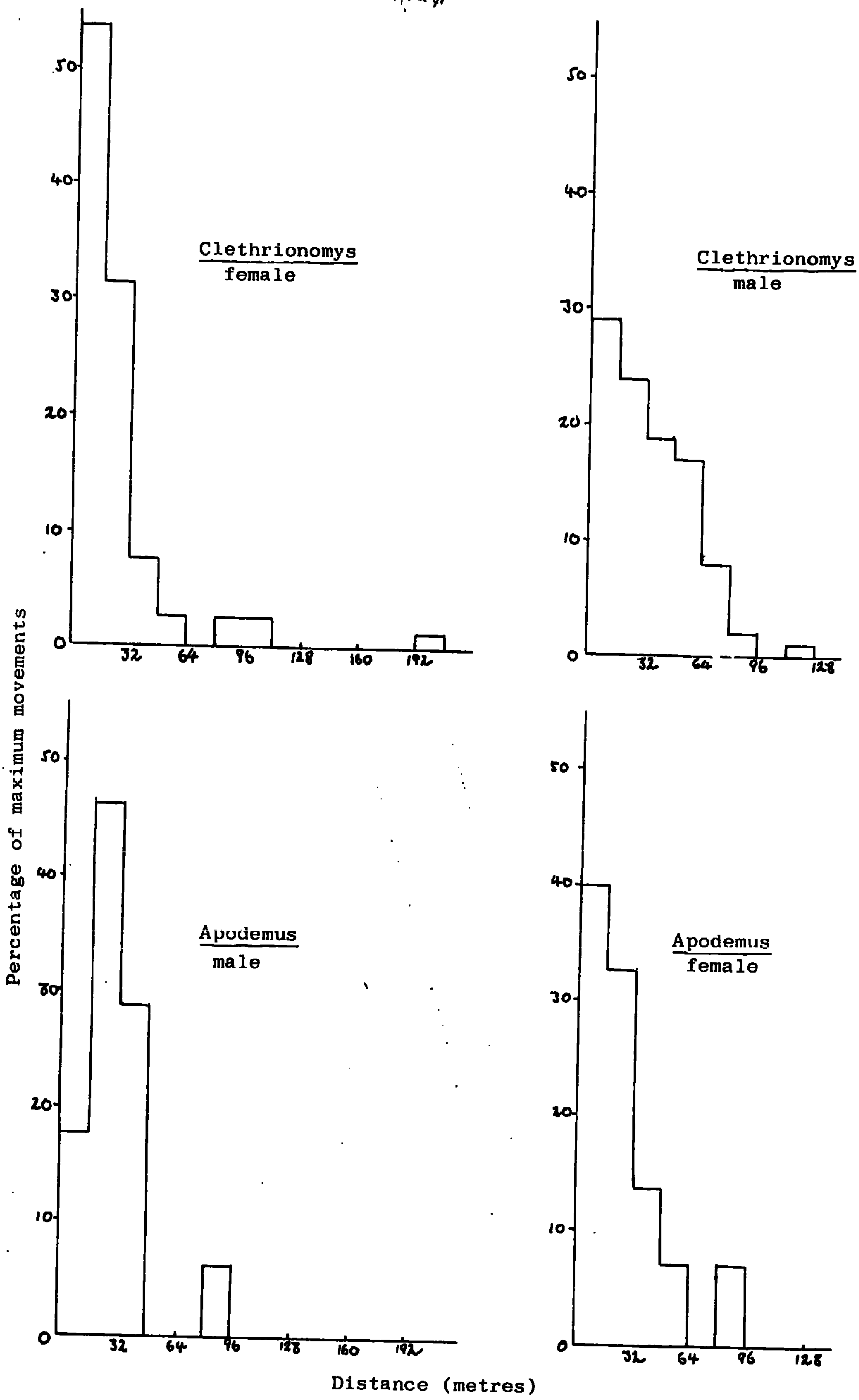

Figure 5

The frequency distribution of maximum movements of Apodemus and Clethrionomys be weighed and so only the mark (again only one toe removed) and sex can be used to identify it. However, this should be quite reliable. Assuming it is the same animal which is being dealt with then it moved about the same distance and covered approximately the same ground as the female discussed above. This animal may or may not have crossed the stream.

Why so few animals crossed the stream is not immediately apparent, as for much of the study period, especially in June and July, the water level was very low and could not have prevented a serious barrier to movement, especially not in the case of Apodemus which could easily have jumped the stream in several places.

Maximum Range Lengths

Table 13 shows the maximum range lengths for both sexes of each species. The average maximum range length was used earlier (page 34) in computing 'adjusted' densities of animals on the three grids. Only animals caught three or more times were used in these estimations.

The results obtained here are lower than those of Crawley (1965, 1969), especially for Apodemus males. In his study, he estimated the range length for animals caught three or more, five or more, seven or more and ten or more times and found that, with the exception of Clethrionomys females, the range length increased markedly with increased number of captures. This probably accounts for the low estimate for Apodemus males in the current study when only five results were used in the estimation of range length. With estimates based on large numbers of animals he found the ascending order of range length to be Clethrionomys females Apodemus females and Clethrionomys males and Apodemus males.

Discussion

In estimating range length and in determining the pattern of movements of the two sexes of both species, the number of individuals which provided data was limited because to be of use, an animal had to be trapped three or more times. In the current study, the number of animals, caught only once, or in one trapping session only, was quite high. These animals may be called 'transients' after Evans (1942) or alternatively they may be ephemeral and die before they have a chance of being recaptured. Animals caught once only will be referred to as transients for the sake of brevity. As trapping was continued on Grids 1 and 3, after the July session, it is legitimate to consider animals which were caught only on this session as belonging to the 'transient' category. On Grid 2, no trapping after July occurred and so animals caught in July only may or may not have been transient. Thus in computing the percentage of transients in the populations, Grid 2 results from May and June only would be used. The results are shown for *Clethrionomys* in Table 12b. *Apodemus* catches were too low to allow any assessment of numbers of transients.

TABLE 12b Individuals caught only once expressed as a percentage of total individuals caught on each grid for *Clethrionomys*.

	Grid 1	Grid 2	Grid 3
Males	31	22	33
Females	33	45	25

These figures are lower than Crawley's (1965, 1969) and Evans (1942) who found the percenrage of transients to be about 45 per cent for males and females. Other workers have considered their results to show high percentages of transient individuals e.g. Youngman (1946), Getz (1960) and Tanton (1965). Trojan and Wojciechorska (1964) working on *Clethrionomys glareolus*, *Apodemus agrarius* and *Apodemus* *flavicollis* have analysed the residency and disappearance of rodents in a population more thoroughly. These workers found that there were three stages in the average time of occurrence of an animal in an area, these stages being 'settling', 'real residency' and 'disappearance'. They found the 'settling' phase to last, depending on the species, up to nine days. With *Clethrionomys* they noted that attachment to a small home range area was firm and characterised by high trappability. 'Real residency' was discovered to last up to 21 days depending upon the species. Al the species showed high trappability in this phase. *Clethrionomys* movements were more wide ranging in the 'real residency' phase than in the 'settling' phase. The 'disappearance' phase occurred after the 'real residency' and was characterised by a considerable decreased capture rate, indicating a less rigid attachment to a home range area. With *Clethrionomys* and *A.flavicollis* an enlargement of the area penetrated was observed during this phase. The analysis of the distribution of maximum movements has shown that the majority are of less than 32 m. When all movements between successive captures are considered, the percentage of small movements (less than 32 m) becomes even higher. Evans (1942), Brown (1956), Kikkawa (1964) and Tanton (1965) together with Crawley (1965, 1969) all noted this. This raises the question of the individuals response to traps and whether these short movements are really only artefacts caused by the close grid spacing. Results from the traplines Y and Z which were situated 50 m apart on ground very similar to that of Grid 1 showed that in this instance, out of a total of eight *Clethrionomys* providing data, (4 males and 1 female), five made maximum movements of greater than 50 metres. Thus it would appear that within trapping sessions, traps severely limit the movement of individuals. Sheppe (1968) studied the movement of *Peromyscus leucopus* by smoked paper tracking supplemented by occasional live trapping. He found that the mice left enough track records on nights when trapped to show that they often did not enter the first trap encountered and usually moved through their home ranges for sometime before being trapped. He suggests that in live trapping these may be little or no bias in favour of traps located near the nest. However, the movements of mice for several nights after being trapped were markedly altered. There were many more track records than usual probably partly due to increased activity and partly to an altered response to the tracking shelters. Animals sometimes travelled far outside their home ranges on nights after being trapped, sometimes resulting in a permanent shift of range. Because of these results, it would appear that live trapping could give erroneous results when used to estimate activity and home range.

Assuming however, that trapping affects all animals equally, the present results show that female *Clethrionomys* have a smaller range length and a greater proportion of small movements than the males. Results from other workers show this is true for *Apodemus* also. The restriction of females to the nest in the breeding season is probably one of the major factors in producing this result.

The present study revealed very few dispersal or wandering movements although many workers have found them to be quite common. (Evans, 1942; Hacken and Pearson 1951, 1952; Kikkawa 1964) and Crawley (1965, 1969). However, in view of the interpretation put on her tracking results by Brown (1966, 1969), care must be exercised in differentiating wandering animals from those dominant males which are patrolling their range which may be as large as three and a half acres in *Apodemus*.

HOME RANGE

1. The Concept of Home Range in Small Mammals

Early work on rodents by many people including Elton et al (1931); Chitty (1937); Dice (1941); and Evans (1942) revealed a tendency for these animals to remain in a localized area ~~and~~ after they had attained sexual maturity. However, because of the difficulty in observing and recording the movements of these mammals, little development was made in the assessment of the extent of this localized area of residence, or home range. It was clearly defined first by Burt (1940) as 'that area about its established home which is traversed by the animal in its normal activities of food gathering, mating, and caring for young. Occasional ~~studies~~ sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range'. Similar sallies were observed by Blair (1943b) and Storer, Evans and Palmer (1944). Stickel (1954) considered they may be important in orientation and at least partially explain the apparent familiarity with large areas that is shown in homing studies.

Burt's definition has since met with some criticism. Blair (1951) working on *Peromyscus polionotus leucocephalus* (the beach mouse) found the 'established home' of Burt's definition is not always permanent. Blair also ~~method~~ noted, as did Hayne (1949a) that some parts of the area may be subjected to more intensive use than others and that use patterns may change as conditions change, and the 'boundaries' may shift and vary from time to time. In fact like Yerger (1953), they considered boundaries of the range to be diffuse and general rather than sharply or definitely outlined.

Burt (1943) also considered animals to have a small defended area around the nest, which he called the 'territory' the aggressive defence of which could lead to the dispersal of young animals.

While many individuals in populations of small woodland rodents thus appear to have a permanent, or in some cases semi-permanent home range, others appear to be transient animals with no permanent residence. Forty five per cent of *Apodemus sylvaticus* and forty eight per cent of *Clethrionomys glareolus* in Evans (1942) study and up to forty per cent in *Apodemus Agrarius coreae* in Youngman's study (1956) were transients. Within any population, the death of a resident will result in its place ~~result~~ being taken very rapidly ~~in~~ by a transient. Brown (1966) states that the small mammal cannot survive long as a wanderer, a thome is vital to its existence.

Howard (1949) working on *Peromyscus maniculatus* and Blair (1951) with *Peromyscus polionotus* studied tracks made by the mice. They interpreted their results as suggesting that the mice are purposeful in their movements and do not wander aimlessly. Blair's results on the question of a shift of established home received support from Curry-Lindahl's (1956) work on *Apodemus sylvaticus*. The latter worker emphasised that the 'concept of a single established home for each individual is too limited.' Such changes of home site within the home range have been observed by Howard (1949), and Brown (1956) and changes of home site to outside the original range have been observed by Miller (1958), Kikkawa (1964) for *Peromyscus*, *Apodemus* and *Clethrionomys*. Curry-Lindahl's (1956) also noted that *Clethrionomys glareolus* sometimes lived in one part of their home range but maintained direct poutes to food supplies in other regions and Ashby (unpublished) has found *Apodemus sylvaticus* commuting over 400 metres from their home range areas, perhaps presumably to a favoured food supply. The results of Brown (1966, 1969) based on tracking experiments on *Apodemus sylvaticus* led her to suggest a social hierarchy in this species which gave rise to different classes of individuals having very different sized home ranges. These ranged during the breeding season from a few tens of square metres for juveniles and sub-adults to over a hectare for dominant males. In winter, however, the social structure altered as male aggression subsided and all animals came to live as a clan with perhaps a largely communal territory. Within and on the periphery of the area of a dominant male, sub-dominants each possessed a home range and on the death of a dominant, extended their range to cover ground they did not previously occupy. Brown therefore concluded that mean home ranges for species or even for separate sexes of a species, had little meaning when considered in the light of the social system and Kikkawa (1964) pointed out that it was more important to know the proportion of animals in the population which show wandering and dispersal movements and how these vary with age, sex, season, habitat and density than to obtain a calculated size of the average of their ~~its~~ range.

2. The validity of trap-revealed home range size

Most estimates of home-range size have come from information supplied by live trapping. Mohr (1947), Hayne (1949a) and Stickel (1954) have reviewed some of the problems encountered in estimating home range size from such records. Davis (1953) specifically criticises the grid system on the grounds that the animals home range does not necessarily coincide with the distribution of traps and the home range may extend beyond the grid. Also The home range cannot be calculated for animals caught in traps that are in a straight line. Further disadvantages are the great labour in laying out the grids, the necessity of setting some traps in obviously unfavourable locations and the need to recapture a single animal many times to obtain adequate data. The observation (Mohr 1947) that most small mammals follow more or less definite pathways further complicates the issue as animals may fail to pass close to traps and the full range of their movements therefore goes unnoticed. Finally, the results of grid trapping give little idea of the intensity of use of the various parts of the home range.

The grid system receives support from the behaviour during poisoning experiments by Tevis (1956). Contrary to expectation, Peromyscus maniculatus and Peromyscus truei visited distant traps as regularly as they did the nearer ones. Tevis found that bait stations, in order to be effective, needed to be distributed evenly in a grid system. The behaviour of mice when they are aware of '~~goods~~ goals' in the form of bait may here explain the greater visits to the peripheral traps (Calhoun 1956).

An obvious limitation in trapping studies is the restriction of the individual, once trapped. The most ~~approximate~~ appropriate trap spacing has to be judged for each species. Stickel (1954) calculated a home range of 17,200 square feet for 19 feral house mice with a 60 foot grid and a range of 33,700 square feet for the same mice with a 120 foot grid. Too wide spacing gives bad results but traps should be far enough apart to avoid too many captures being necessary to show the extent of an animals home range. Hayne (1950) demonstrated for Microtus pennsylvanicus that there is a definite relationship between the spacing of the traps and the apparent size of the range.

In spite of the many difficulties in the method many workers, including Blair (1951), and Stickel (1954) believe that ranges revealed by live trapping are significantly related to the animals natural range. Comparing results from tracking with those from other methods gives a valuable index of reliability. Blair (1951) reported a similarly set of results from trapping and tra~~d~~cking.

In the present study it was hoped that the interval between trapping periods would allow individuals to move about freely within their home range and possibly be sampled in different parts of their home range during different trapping sessions. Animals with three or more recaptures were used in estimating mean home range value. Ideally, only animals showing a high number of recaptures would have been used, but the numbers of these were too small to allow this. Moreover, animals with captures at or near the edges of the grids had to be used. Because of these two factors, home ranges estimated may have been much too low. Natural barriers (e.g. the golf course) would reduce the error caused by using peripheral dwelling animals.

3. Methods used to estimate home range size (~~minimum area method~~)

Stickel (1954) compared the inclusive and exclusive boundary strip methods and the observed and adjusted range length methods of estimating home range. Studies on artificial populations showed that the boundary strip methods gave the best estimate of area and the adjusted range length gave the best estimates of range. Accordingly, the exclusive boundary strip method and adjusted range length methods were used in the current study together with Manville's method. The latter was used because it is considered to give fairly accurate results and is easy to use.

(a) The Exclusive Boundary Strip Method

This method is designed to compensate for lack of traps at a boundary, or to allow for movements beyond the traps in which the actual captures were made. The external points of capture are regarded as squares, the sides of which have a length equal to the trap spacing used on the grid. The internal edges of these squares are then joined and the area so included is considered to be a measure of the home range.

(b) Manville's (1949) Method

This is essentially a modification of thw Exclusive Boundary strip method. Manville based the home range on the area of quadrants which the animal was reasonably assumed to have entered or passed through in successive captures. Each capture point was considered as the centre of a square with sides equal in length to the trap spacing employed. The total area of squares with capture points, and those which the animal must have passed through to reach subsequent capture points was regarded as the home range.

(c) Adjusted Range Length

The maximum range length is a linear measure of the greatest distance between the most distant points of capture. The adjusted range length is calculated by adding half the distance to the next trapping point onto each end of the Observed Range Length to allow for the possibility of the animal having travelled beyond the last trap in which it was caught. The home range may be calculated from this measure by considering it to be the diameter of a circle the area of which is then calculated.

3. Results

(a) Variation of Home Range between sexes and species

The estimated home range (average) sizes of Clethrionomys and Apodemus on the three grids are given in Table 14 and the estimated ranges for all individuals of each sex and each species for 3+, 6+ and 9+ captures are given in Table 15. Because estimates are averages, the range is given also. The exclusive boundary and Manville's method gave very similar results while the area of the homerrange as calculated from the adjusted range length, was considerably higher because home ranges are very probably not circular.

Species & Sex	Grid	Exclusive Boundary Strip		Manville's Method		Adjusted Range Length		No. of
		Estimate (m²)	Range (m²)	Estimate (m²)	Range (m²)	Estimate (m²)	Range (m²)	Animals
Clethrionomys males	1	1706	768-3456	1757	768 - 3840	4429	1168-12870	15
	2	1260	768-2304	1536	768 -2304	4280	1168 - 8839	9
	3	1666	1024-4033	1720	1024-3072	4918	2059-9882	18
Clethrionomys females	1	1144	768-1536	1195	768-1536	2718	1168-5230	6
	2	896	768-1024	1024	768-1280	2158	1168-3497	3
	3	1134	768-1536	1169	768-1536	2085	1168-3463	7
Apodemus males	1	1528	1152-1664	1792	1536-2048	3109	2059-5209	3
	2	1536	1152-1920	1664	1280-2048	6089	2934-9244	2
	3	—	—	—	—	—	—	0
Apodemus females	1	1920	1024-3328	1855	1024-3072	5195	2059-10080	4
	2	1280	1280	1280	1280	2059	2059	1
	3	—	—	—	—	—	—	0

Table 14

The average home ranges, for animals caught three or more times, of Clethrionomys and Apodemus in each of the three grids.

Species & Sex	Exclusive Boundary Strip		Manville's Method		Adjusted Range Length		No. of Animal
	Estimate (m²)	Range (m²)	Estimate (m²)	Range (m²)	Estimate (m²)	Range (m²)	
	All animals caught 3 or more times						
Clethrionomys males	1156	768-4033	1676	768-3840	4607	1168-12870	42
Clethrionomys females	1104	768-1536	1152	768-1536	2336	1168-5230	16
Apodemus males	1531	1152-1920	1741	1280-2048	4301	2059-9244	5
Apodemus females	1792	1024-3328	1741	1024-3072	4566	2059-10080	5
	All animals caught 6 or more times						
Clethrionomys males	1940	768-4033	1936	768-3840	5054	1168-8893	23
Clethrionomys females	1294	768-1536	1365	768-1536	2816	1168-5230	9
Apodemus males	1370	1152-2048	1601	1280-1664	3066	2059-5210	4
Apodemus females	2176	1280-3328	2304	1280-3072	5783	2059-10080	3
	All animals caught 9 or more times						
Clethrionomys males	2306	1664-4033	2464	1536-3840	6230	4108-8134	8
Clethrionomys females	1334	1024-1536	1425	1280-1536	3043	1810-5230	7
Apodemus males	1664	1664	1536	1536	2054	2054	1
Apodemus females	3328	3328	3072	3072	5210	5210	1

Table 15

The average home range for all animals caught 3+, 6+ and 9+ times

Variation within one method of estimation when different classes of animals were concerned was less than when results for the same class were compared between the adjusted range length method and the other two methods. For example, the most widely divergent results for the adjusted range length estimate for animals caught three plus times are those for Clethrionomys males compared with Clethrionomys females. The results are 4607 and 2336 cm^2 respectively. However, when results for males are compared between methods, they are 4607, 1637 and 1520 m^2 for the Adjusted Range length, Manville's and the Exclusive Boundary Strip Methods respectively.

In the current study, the ranking of methods in terms of magnitude of estimate of home range size was, in ascending order, Exclusive Boundary Strip, Manville's and the Adjusted Range Length. In Clethrionomys, the males had considerably larger home ranges than the females. When estimated home ranges for animals caught three or more, six or more and nine or more times are compared it can be seen that the estimate of the size of the home range increases with the number of catches.

Males on Grids 1 and 3 have approximately the same size of home range, as do the females, but on Grid 2, both males and females have apparently smaller home ranges. This may be a result of the very good cover and favourable environment, which occurs on part of Grid 2, for it may enable the animals to obtain sufficient food within a smaller area. Alternatively, it could be a result of the estimate being based on a smaller number of animals especially as the number of animals caught six or more times was proportionately lower than on the other two grids. That the latter explanation is probably the correct one is indicated by Crawley's results when he found no significant difference in home range of Clethrionomys on the two grids.

The numbers of *Apodemus* used for home range studies were so small that results for this species are included only for the sake of completeness. As the figures appear in Table 14, it appears that the *Apodemus* males studied have a home range equal to that of *Clethrionomys* males, while *Apodemus* females have a home range greater than either. This is very doubtful perhaps a result of sampling males with only small home ranges,, as all other workers have found *Apodemus* males to have a greater home range than the females. Moreover, the males home range has been found to be greater than that of *Clethrionomys* males, while the females home range has been found to be intermediate between the estimates for female and male *Clethrionomys*. Crawley considered Manville's method to be probably the most accurate and his results for animals captured ten or more times were:-

	Size of Home Range (m^2)
Apodemus Males	3124
Apodemus Females	2143
Clethrionomys Males	2430
Clethrionomys Females	1521

These results compare quite closely with the current ones for *Clethrionomys* especially when animals captured nine or more times are considered. When *Apodemus* is considered, current estimates for females appear too high and those for males too low.

(b) Variation of Home Range with Number of Captures

As estimated size of home range increased with number of captures, the size of the home range after each capture was estimated for every animal caught nine or more times. The average value for the home range of these animals was then worked out for each capture number and the results plotted graphically (see Figure 6). Estimates of home ranges up to that for the ninth recapture are based on 7 individuals for females and 8 for males. Home range for the tenth recapture is based on 7 males and 5 females. From the figure it is readily seen that size of the home range increased with the number of captures up to six in the females, when it levelled off.

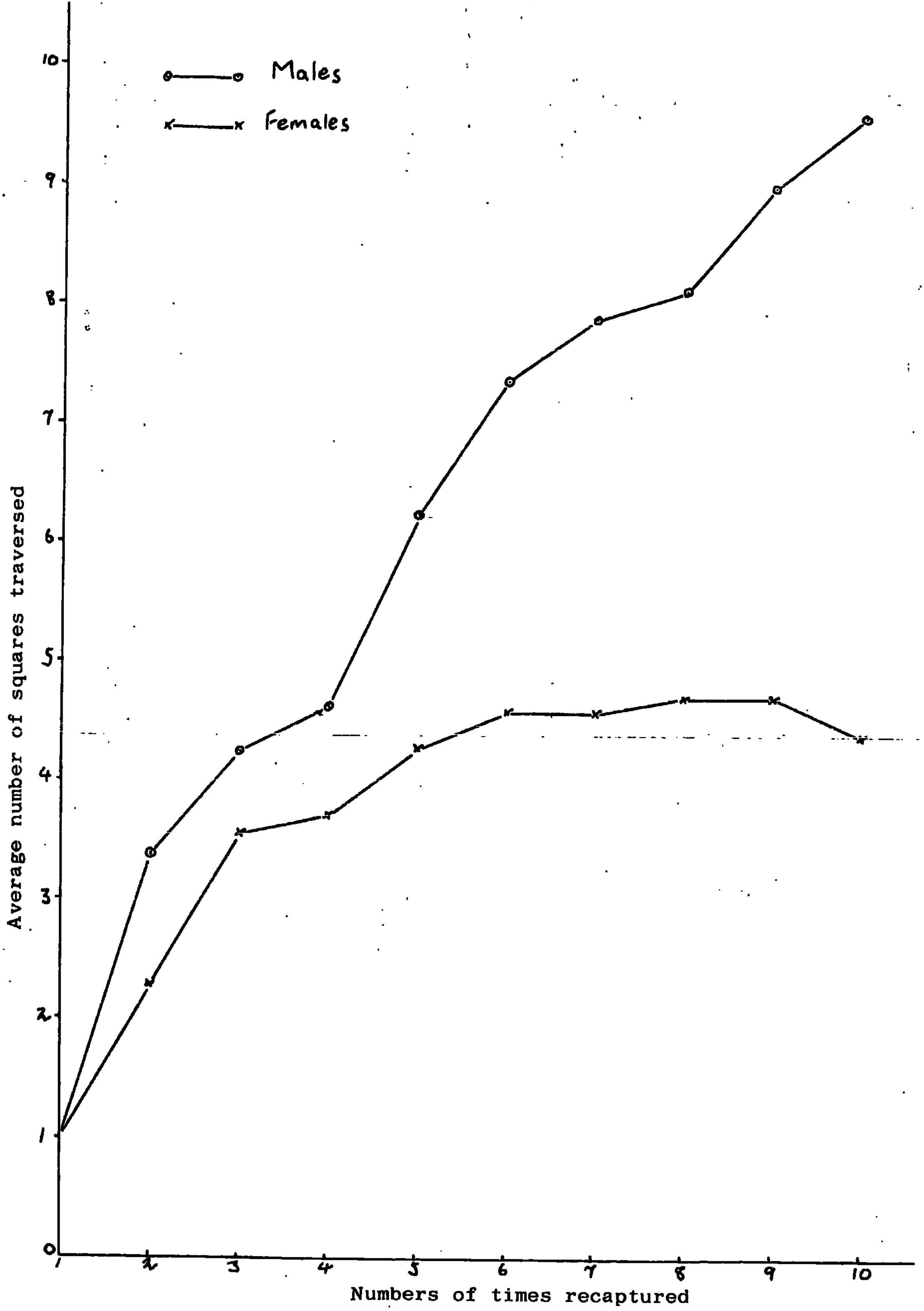

Figure 6

Graph showing the increase in apparent home range size with increased number of recaptures per animal for both sexes of Clethrionomys, in samples of animals which were eventually recaptured ten or more times.

For males the estimated range size increased right up to ten captures and showed little sign of levelling off. Thus it is probable that ten recaptures will in most cases adequately reveal the home range of a female, but not of a male.

Crawley found, using larger samples, very similar results for female Clethrionomys, but found that the home range estimate for his male Clethrionomys levelled off at about ten captures. Davis (1953) considered 15-20 captures were needed to fully reveal home range size. He did not however state to which size of grid this applies.

6. Discussion

Brown (1956) working in mixed woodland at Silwood found results for Clethrionomys similar to the current ones and those of Crawley when using Manville's method but she found, as in current work, that the home range of female Apodemus was greater than that of male Clethrionomys. Home ranges calculated by her after five or more recaptures again for Clethrionomys were similar to those for ten and more for the current work. More work has been done ~~at~~ on the home range of Apodemus than Clethrionomys. When these studies are considered, Tanton (1965) and Crawley (1966, 1969) have found the largest range lengths, larger than those of Brown (1956), Miller (1958) and Kikkawa (1965). Miller considered his and Brown's estimates to be too large, but Tanton considered the reverse to be true and that Brown's and Miller's estimates were too low because they included many animals captured only a few times and animals that were captured near the periphery of the grid.

Thus in spite of the limitations of live trapping, several workers have obtained results which agree, reasonably well, both between species and between sexes, and the concept of a trap revealed home range is thought to be valid. However, average values for species are of limited value because of the marked difference in home range size between the sexes and for trap-revealed home ranges to have most validity, the following data should be quoted along with the estimate of size:

(a) Method used e.g. trap-line, grid and the interval of trap spacing

(b) The number and length of trapping sessions and the time in between them.

(c) The season and the habitat in which data were collected.

(d) The sex and age and condition of the individuals concerned.

(e) The method of estimation of range size used.

(f) The estimated population density of the species.

(g) The importance of territorial behaviour and social hierarchy in the species, if known.

(h) The variation of behaviour of individuals in the population to traps, if known.

Only recently has the importance of the two latter criteria come to be regarded and it is probably worth examining them in a little more detail.

I. The importance of territorial behaviour and social hierarchy

Brown (1966) and (1969) discusses the results of tracking experiments and their interpretation in the light of results from the direct observation of *Apodemus*. Possibly her most interesting discovery is that of the dominant male which patrols a large territory, within which all other animals are subordinate, though some subordinate males probably exclude the dominant from the area around their home site, and within limits, all resident mice have freedom of movement within the territory. There are examples of ~~movement and~~ how the young are helped to learn the safe territorial limits by their parents. Howard (1949) recorded a male *Peromyscus maniculatus* and four of its young in a multiple catch trap 100 metres from their nest and Crowcroft (1966) described how a *Mus musculus* took her young out on their first main exploration of the territory.

Brown (1969) observed *Apodemus* of both sexes moving in groups to feed in favoured areas and concluded that group action ensured greater safety. Small mammals appear to know when an area outside their own range can be visited in safety. Brown found that one dominant knew when it was safe to invade the territory of another. Stickel (1946) depopulated a central area of one acre in a 17 acre plot and found Peromyscus leucopus readily entered this area. As depopulation of this area was continued, animals cameefrom progressively further away. All classes were present, but males outnumbered females two to one, possibly because they possess greater wandering tendencies. This raises the question of how small mammals know of each others presence. Sewell (1967) considers that ultrasounds are probably used and play an important part in social life. It is possible that tail drumming is used. Zapus is known to do this and Apodemus certainly has the tail for the purpose. Crowcroft (1966) reported rapid movements of the tip of the tail in excited Mus. Smell must be very important.

Dominant males, according to Brown (1969), were not usually directly aggressive and their dominance was made manifest by the submission of other individuals in the dominant's presence. She directly observed subordinates moving about in groups and keeping out of the way of dominants. Crowcroft (1966), found that in a colony of 48 Mus 33 subordinate individuals crowded with one nest box though others were untenanted. They were kept so by the aggressive patrolling of the dominant. In agreement with Mohr's (1947) observations, Brown (1969) found that Apodemus went out and back along a definite track on a particular night. She also found general exploration to be important.

Brant (1962) used the term 'movement pattern' for Peromyscus rather than home range and Brown (1966, 1969), found that after midsummer there were several Apodemus in the woods without established homes, ~~and~~ who carefully avoided resident mice.

Although little enough is known of the social life of Apodemus above ground, even less is known about its subterranean social scene.

Brown consideressthis latter is probably at least as important, if not more so, in the determination of social hierarchies. However, Ashby, Cleminson and Brooks (unpublished) found no extensive interlinking underground burrow system. The maximum movement which could be made in any direction was only two metres. Hence animals would have to spend a considerable time above ground when moving and it is therefore possible that underground encounteres are less important than Brown thought.

The presence of a structured community in Apodemus raises the question of its effect on population control. Some workers have found evidence in other small animals which suggests that females favoured by the dominant male may be the only ones breeding (Petruszewicz 1958, 1960)Lidicker, 1965; Crowcroft, 1966). In Peromyscus Sadleir (1965) reported that the old, dominant males severely affect in an adverse manner, juvenile survival and growth rate.

Failure of spring born to become sexually mature by autumn has been suggested as a possible explanation of density oscillation in some species. However, in Apodemus there is no evidence for it. Brown (1969) found only seasonal variations in numbers, but considered her studies had not extended over a long enough period to be conclusive.

In winter Brown (1966, 1969) considered that males accepted as part of super-families over winter in woodlands, but others will move nearer habitation e.g. barns. In spring, the social hierarchies are set up. From May to early July is a critical phase of numbers depending on the health of overwintered animals and the success of rearing new litters. By the end of July most unestablished males have dispersed and older males move to preferred feeding grounds which Brown considered were corn fields. Crawley (1965, 1969), however, caught very few animals in traps set in fields around Castle Eden Dene, but the ~~average~~ acreage of arable land around the Dene is considerable and his work is not conclusive. Even if Apodemus had moved out into the fields, they would be so thin on the ground as to be very difficult to trap. The trapline set along the edge of the wood in July in the current study(but again this is inconclusive) caught only one Apodemus. The animals, according to Brown, return from the fields after harvesting. Most dominants of the spring will now be dead and new hierarchies are established and a second breeding peak occurs.

This, then, may be the social pattern of life in Apodemus and it is doubtful if trapping results alone could ever have revealed its presence in any great detail. However, more ~~initial~~ critical reviews of trapping results in the light of these discoveries, may provide interesting results. Whether similar social patterns exist in Clethrionomys is not certain, but Brown thinks they probably do.

II. The Variation of Behaviour of individuals in the populations to traps.

Young, Ness and Emlen (1952) studied the results they obtained while trapping ~~and~~ large populations of wild house mice to see if the series of trapped samples conformed to a Poisson distribution, which would mean that the probability of being captured was the same for any individual on any night.What they found in fact, was that the distribution of recaptures of mice differed significantly in the very low recapture group and in the high recapture group. However, there was no change in the form of recapture distributions with time indicating that the difference in response for individuals was a relatively permanent characteristic of any one house ~~mice~~ mouse. They found, moreover, that males were less trap shy, or more trap addicted, than females, but this discrepancy could not account for the differences in traps response observed in the whole population. A further point they made was that a trapping programme such as theirs might only be studying a fraction of the population to begin with in that only individuals vulnerable to capture will be sampled.

Further evidence of heterogeneity of trap response in Mus musculus was found by Crowcroft and Jeffers (1961) as mentioned. Their results supported the findings of Young et al (1952) and ruled out the possibility that the heterogeneity of response was possibly due to trap spacing as Young et al tentatively suggested. They suggested that the innate differences in trap response may be inherited but also noted that much of the heterogeneity of trap response was due to social strife. Andrzejewski et al (1954) found a clear correlation between trap proneness and social dominance in males in confined colonies of laboratory mice.

Young et al (1952) considered that population estimates based on the assumption that all animals were equal with respect to trapping, could be severely misleading, but Crowcroft and Jeffors (1961) found the numbers of especially trap prone and trap shy individuals to be small and population estimates worked out from recapture data by means of the Lincoln Index were surprisingly accurate. However, samples were much larger in relation to the total population than samples taken in the field in many experiments. With trap limited catches, the proportion of trap prone animals was high and the population estimates accordingly low.

Tanton (1965) seriously doubts the validity of the use of live trapping in estimates of summer populations of <u>Apodemus.</u> He caught very low numbers in summer followed by a big influx into the traps in autumn. Only a few of these animals had been previously handled. Ashby (1962) postulated a high rate of summer breeding, to account for the autumn increase, but Tanton dis~~cussed~~missed this on the basis of the weight distribution on his animals. He advanced three possible explanations:

(a) Animals were migrating across the area in a certain direction.

(b) Immigration was occurring from all sides

(c) The animals were on the area throughout the summer although few had been caught for behavioural reasons.

The first two he dismissed after sensitive statistical tests and came to the conclusion that in <u>Apodemus</u> the summer population consisted of a trappable and a non-trappable p~~osi~~ortion. Evidence he cited to support this was the fact that the average range of movement revealed by recapture of new individuals was similar to that observed previously for Apodemus, and in several cases juveniles were caught in adjacent traps in central portions of the area (He presumed the juveniles came from the same families). Tanton estimated these juveniles must have left the nest at least two weeks before the capture and yet were not captured until the autumn influx began. If the juveniles had moved onto the area, he argues that a greater dispersion would be expected.

Applying tests to test the hypothesis of no dilution and random trapping as described by Leslie (1952) and Leslie et al (1953), Tanton found that more marked animals than expected were caught in early autumn but by November sampling of marked and unmarked animals was satisfactory and no dilution was occurring.

Tanton postulated that the response of Apodemus to traps changes during the summer and that food may be a possible cause for this. Miller (1954) and Kikkawa (1959) both found a high percentage of animal food in stomaches they examined and so Tanton suggests that because of the availability of alternative (and possibly preferable) food sources, the Apodemus lose interest in grain baited traps. Cleminson (unpublished), however, found that in food preference tests in the laboratory and in the field Apodemus favoured wheat, which is often used to bait traps (the current work was done dusing wheat). With the onset of colder weather, the interest of the Apodemus in the baited traps increases, according to Tanton and so catches increase. Watts (1968) however found animals food made up a significant proportion of the diet of Apodemus only when caterpillars were in abundance. At other times, seeds formed the main constituent, and these were still in abundance in autumn, the time of the sudden influx into the traps.

This failure to sample the summer population at all realistically and the heterogeneity of the trap response in the population generally led Tanton to the conclusion that live trapping as a means of population estimation was at best approximate and at most highly misleading, in Apodemus.

Ashby (1967) however, argued against many of Tanton's conclusions and deductions, basing his arguments largely on information he obtained by live trapping for a period of several years in Houghall Wood, Durham. He found only a few abnormalities in recapture proportions in Apodemus and these were attributable to changes in the behaviour of the population as a whole. However, the current work, that of Crawley (1966, 1969) and that of Kikkawa (1964), all substantially confirm Tanton's view of low catches in summer and in the current work at least, the animals captured showed high trappability.

There was a large discrepancy in the captures of juveniles in Ashby's and Tanton's work. The latter ~~regarded~~ reported an almost total failure to catch juveniles, while Ashby found the proportions of captures of juveniles quite sufficient to account for the subsequent recruitment. Thus Ashby found it unnecessary to involve Tanton's hypothesis in his work and attributed much of the difference in his and Tanton's work, to the difference in trapping methods employed. In trapping for four continuous days every fortnight on a 18 m grid with a single trap at each grid-point Ashby considered that Tanton may have significantly increased the food supply of Apodemus and hence lessened the mouse's interest in other food supplies e.g. bait in the traps. Ashby also considered the confinement im~~proved~~posed on the animals in Tanton's work ~~and~~ might lead to them developing a trap aversion, but Young et al (1952) and Crowcroft and Jeffers (1961) found no evidence for this. Ashby considered that Crawley's (1965, 1969) results, similar to Tanton's were again a possible result of the effect of the grid system used, though using his transect technique in Castle Eden Dene (the site of Crawley's work), he only achieved small catches, and concluded that in addition to difference in technique, difference in population size might account for the discrepancy in catches between the two workers.

As mentioned previously, Brown (1966, 1969) is of the opinion that agonistic behaviour of dominant males severely reduces the summer population in woodland, and the autumn increase is due to immigration from surrounding fields. Tanton refuted this on the basis of the statistical tests he applied, but Ashby (1967) considered that one possibility was that the animals did migrate but either did not enter traps until they had established a home range or were moving very quickly. In the latter case, if animals were moving at a speed which could carry them across the grid overnight, then captures would be random over the grid, provided animals did not actively search out and enter traps as soon as they were on the grid. Such a speed of movement in Apodemus is by no means impossible. Hence the distribution of new catches would show no orientation in a specific direction. The lack of an autumn immigration of any significance at Houghall is explained by Ashby, on the grounds that the surrounding farmland has proportionately much less arable land and so the animals do not concentrate on it.

Thus, the shortcomings of live trappings for small mammals are quite considerable. Some authors would go so far as to say that the results can provide very little information that is relevant to what actually happens in small mammal populations. However, the majority find that information from live trapping, if interpreted correctly, provides a valid and interesting insight into the inter-relations of small mammal communities.

SUMMARY

After failing to produce a suitable tracking medium, the study switched to one of a survey of the population dynamics movement and home range of Apodemus sylvaticus and Clethrionomys glareolus as revealed by live trapping.

The results obtained were in agreement with those of other workers in this field. Comparison of the present results with those of Crawley (1965, 1969) who also worked in the Dene, showed that current population estimates for Clethrionomys were lower than his though of the same order of magnitude. Results for trappability trap mortality, sex ratio, distribution in relation to cover and age structure of the populations were in general agreement with those of many other workers. A drop in numbers of Apodemus in summer was observed and possible reasons for its cause were reviewed in the light of the work of other authors, many of whom have observed a similar phenomenon.

Long range movements were observed in Clethrionomys and it is postulated that these are more common than often thought, but pass undetected (Watts, 1970). Similar movements for Apodemus have been shown in the same area by Ashby (unpublished) but were not detected in the present study, probably because of the low numbers of Apodemus caught.

Finally, the importance of social hierarchies and the heterogeneity of trap response between individuals were considered in the light of the effect that they might have on trapping results.

APPENDIX

The Attempt at Tracking

Materials

The tracking plates were made of tin foil which was dipped into a suspension of talcum powder in silicone water repellant solution, Romanite W.R. When the Romanite dried, a fine layer of talc was left on the tin foil.;

Plates so prepared were fixed into waxed cardboard milk cartons with metal skewers which also served to fix the cartons to the ground. Tracking plates were placed near the traps on Grid 1 to see what results might be obtained.

Although the cartons and contained plates were left in position for a week and visited regularly, no tracks could be discovered in the talc. The proportions of the talc and Romanite used in preparing the plating medium were as recommended by Brown (personal communication). However, when tested with Apodemus in the laboratory, they did not give identifiable foot marks. Thus the propoxtions were altered, but no satisfactory prints could be obtained. Another possible reason for the failure to obtain good impressions was the use of tin foil without a paper backing. In her studies Boown used paper-backed foil, but this could not be obtained for the present work and so ordinary baking foil was used. It was rather soft though and wrinkled easily, hence preventing the talc from being spread really smoothly over the foil.

However, the hardness of the talc surface, rather than its unevenness seemed to be the main reason for the failure to obtain good footprints.

Whether or not the animals would visit the milk cartons in the field is problematical for the smell of the Romanite was very strong and might very well have been repugnant to animals with such a highly developed sense of smell.

Hence, for mechanical reasons, or behavioural reasons or both, no prints were obtained and hence no tracking undertaken.

Smoked paper was considered as an alternative, but the inconvenience and labour involved each day in carrying sufficient smoked paper for 150+ tracking plates 10 miles by road and then into the Dene, was too great an obstacle.

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