Population dynamics of clethrionomys glareolus and apodemus sylvaticus in relation to aggressive behaviour and genetic variation

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by

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(Graduate Society).

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ABSTRACT

The population dynamics, aggressive behaviour, population genetics and plasma testosterone levels of two populations of bank voles, Clethrionomys glareolus and the population dynamics and plasma testosterone levels of wood mice, Apodemus sylvaticus have been studied in mixed woodland in Castle Eden Dene and Houghall Woods, County Durham. Numbers of Clethrionomys, determined by live trapping, declined to a minimum in late winter and in three cases out of four rose to a maximum during the autumn. At Houghall, numbers of Apodemus were apparently markedly influenced by migration across the woodland edge but this was not so at Castle Eden. A distribution analysis confirmed that restriction of Clethrionomys to areas of suitable cover may be a proximate density-linked factor for this species. The distribution of Apodemus was relatively independent of cover, though dense areas were avoided during the summer. Social interaction between male Clethrionomys, studied by neutral cage encounters in the laboratory, though infrequent, was always aggressive. The number of aggressive acts per encounter was maximal during the spring, then declined to a winter minimum. Overwintered adults were dominant over individuals which matured in the year of their birth, and were more aggressive. An electrophoretically detectable esterase polymorphism of Clethrionomys showed significant variation in allele frequencies at Houghall but not at Castle Eden. At the former site the change took place during the exceptionally dry summer of 1975 and may have been a localised temporary response to environmental conditions, similar to those recorded for some other species of rodents. A radioimmunoassay for testosterone was developed for small samples of rodent plasma. In breeding males of both species the mean level was about 5ng/ml. Levels in non-breeding individuals were below the sensitivity of the assay of 0.65ng/ml. The spring increase in testosterone level is coincident with an increase in aggressiveness, and it is suggested that a high level of testosterone acts to initiate behaviours associated with breeding.

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CHAPTER 1

GENERAL INTRODUCTION

The concept of the regulation of population density by social behaviour has been in existence for two decades (Wynne - Edwards 1959), yet despite much experimental work, evidence for the behavioural regulation of small mammal populations is sparse and mainly inferential.

Many populations of small rodents living at high latitude show characteristic three to four year cycles of abundance (Krebs and Myers 1974) but this does not appear to be the case with either Clethrionomys glareolus or Apodemus sylvaticus in north east England (Crawley 1965; 1970). Ashby (1967) recorded rather poorly defined cycles in Clethrionomys during the 1950's but in recent years this pattern seems to have disappeared and been replaced by a rather variable annual cycle of abundance (Ashby unpubl.) typical of British populations of this species (Corbet and Southern 1977). Apodemus, by contrast, shows much more regular annual cycles of abundance with relatively little variation in peak numbers from year to year (Crawley 1965, 1970; Ashby 1967; Flowerdew 1978).

Two main regulatory mechanisms have been proposed for these annually varying species, one intrinsic, the other extrinsic. It has been suggested that during the winter survival of these species is related to the availability of suitable foods (Watts 1969 for Apodemus; Flowerdew and Gardner 1978 for Clethrionomys) whilst during the summer the rate of population increase is limited by the poor survival of juveniles which is, to some extent, density dependent in both species (Watts 1969; Flowerdew 1971). Juvenile mortality may be the result of the antagonistic behaviour of adults during the greater part of the breeding season (Sadleir 1965) but evidence for this is limited in all species and almost non-existent for Clethrionomys.

There are a number of ways in which Sadleir's (1965) hypothesis

might be tested on natural populations. Several authors (Smyth 1968; Watts 1970; Myers and Krebs 1971) have attempted to improve juvenile survival on an area by the selective removal of adults. Others have examined social interactions in the wild (Christian 1971), or in the laboratory (Sadleir 1965; Healey 1967; Krebs 1971). In all cases the degree of success has been limited (see Introduction to Chapter 3) and further study is required.

Mice and voles are not distributed at random in a uniform environment but show strong environmental preferences which may be modified by seasonal, social or other factors. Whilst the general habitat preferences of the two species have been studied, seasonal changes in habitat utilisation and movements between different areas are not well documented. In particular, the genetic consequences of inhabiting a patchy and variable environment, though the subject of a large body of theory (Weins 1976), have received little practical attention.

This thesis presents the results of a project which has combined ecological, behavioural, genetic and physiological techniques to study the population biology of these two species of small rodent. The project has primarily been concerned with Clethrionomys glareolus but ecological data on Apodemus sylvaticus have been included for comparative purposes, as there are numerous differences between the ecology of the two species. Two areas of woodland in County Durham, which differ in soil texture and vegetation were studied by live trapping with particular emphasis on seasonal changes in the distribution of the two species. The two populations of voles have been examined for seasonal changes in the level of aggressive behaviour as measured by laboratory behavioural tests. In addition the genetic response of this species to seasonal and perennial changes in environmental conditions has been studied by following the frequency of a genetic marker using starch-gel electrophoresis. The practicality

of applying a sensitive steroid assay to the study of the hormonal background to breeding has been investigated and measurements of the breeding and non-breeding levels of plasma testosterone in males of the two species are presented.

Some of the terms used in the demographic analysis require definition. As in all live-trapping studies, it is not usually possible to distinguish between death and dispersal or birth and immigration. Survival is therefore defined as residence in the trappable population rather than vital survival and recruitment refers to the addition to the marked population of a group of animals first captured in the same trapping session. Such a group may therefore contain individuals of a diversity of ages. The term cohort refers to a group of animals of a similar age and thus differs from the recruitment at a trapping session as the latter generally contained a number of older animals as well as individuals which had become independent since the previous trapping session.

CHAPTER 2

POPULATION ECOLOGY.

A. The Study Areas.

1. Castle Eden Dene

a) General

Castle Eden Dene (Figure 2.1), a local nature reserve situated about 18km. east of Durham, is a long narrow locally precipitous valley running in an east-west direction and open to the sea at its eastern end. The Dene is about 4.5km. long from the western end, where it is bounded by the A19 trunk road, to the sea. Its width varies from 250-600m. A stream, which may disappear into the underlying limestone in summer, runs down the centre.

The bedrock is boulder clay which has not been resorted by water. This overlies magnesian limestone which can be seen where the stream has eroded through the boulder clay. Drainage is rather poor on the clay, particularly at the western end where the trapping grid was located, and there is a high level of ground water.

The vegetation is semi-natural woodland although there are some open heath-like areas, possibly the result of tree felling during the 1914-18 war. In some areas there are small conifer or sycamore plantations and there are a number of large beech trees (Fagus sylvatica) which appear to have been planted about 150 years ago. Although oak (Quercus petraea x Quercus pedunculata) is the expected dominant on boulder clay, this is common only locally and is not regenerating well. The most frequent dominants on the clay are -

a) Sycamore (Acer pseudoplatanus L.), which is regenerating freely.

b) Elm (Ulmus glabra L.)

c) Birch (Betula pubescens Ehrl.)

and on the limestone

Ash (Fraxinus excelsior L.)

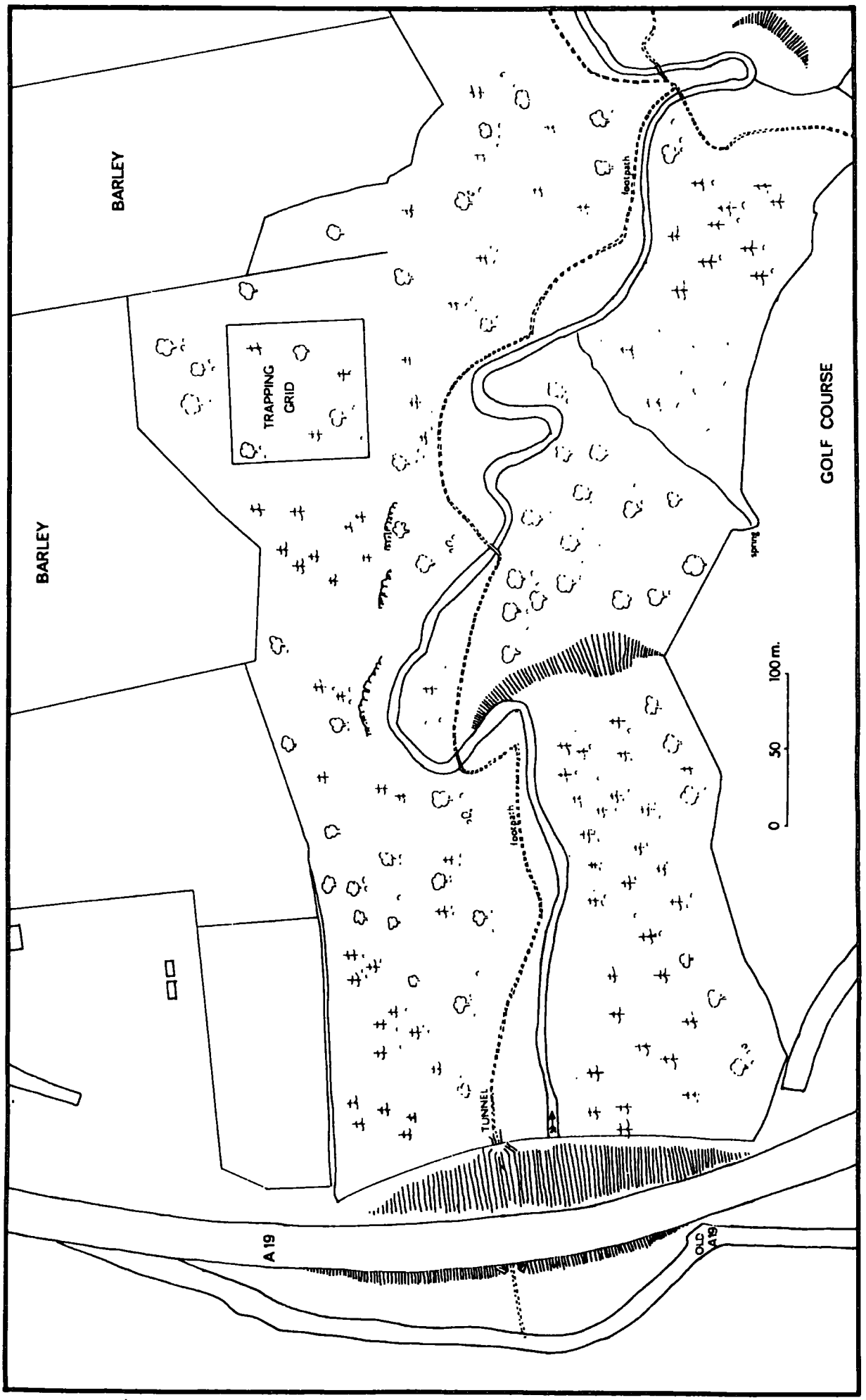


FIGURE 2.1 Castle Eden Dene, showing the trapping area and arable land

The ground vegetation is dominated in most areas by either -

a) Rough grass (Deschampsia caespitosa, Arrhenatherum elatius etc.)

b) Bracken (Pteridium aquilinum)

c) Bramble (Rubus fruticosus)

d) Dog's mercury (Mercurialis perennis)

or e) Rose bay willowherb (Chamaenerium angustifolium)

b) The trapping grid.

Suitable sites for a trapping grid were limited by the precipitous nature of much of the terrain and, on the flatter areas, by the proximity of public footpaths or difficulty of access because of the density of the vegetation. The area chosen was on the north side of the Dene overlapping the northern grid used by Crawley (1965; 1969) in his trapping study. The ground slopes to the south gently over most of the grid but steeply in the north eastern corner. The area is predominantly sycamore woodland bounded to the north by cultivated fields, to the south by a steep descending grassy slope, to the east partly by fields and partly by a steep ascending grassy slope, and to the west by a mature larch wood containing little ground vegetation. The grid was laid out as a square situated mainly in sycamore wood but including two small areas of Corsican pine (Pinus nigra) and several isolated elms. The ground vegetation was composed mainly of dog's mercury, wild garlic (Allium usinum), bramble and rough grasses, particularly Deschampsia caespitosa. There was a marked seasonal variation in both the composition and density of cover of the herb layer with an annual sequence of changes. In late winter the cover was rather sparse and was composed of areas of bramble and grasses together with isolated tussocks of dead bracken; in some areas fallen trees provided

cover and there was a certain amount of conifer needle and sycamore leaf litter. In early spring the wild garlic grew rapidly and soon provided moderately dense but shallow cover over much of the previously bare ground. In May and June the garlic died back and was replaced by dog's mercury, which provided cover of similar density. The dog's mercury persisted until mid autumn (October - November) when it died back leaving large areas bare once more. Elsewhere grass tussocks and bramble provided cover throughout the year. Thus there were small areas of permanent cover supplemented by large areas of seasonally available cover. The seasonal variation had important consequences for the small mammal populations.

2. Houghall Woods

a) General

Houghall Woods, (Figure 2.2) situated about 0.5km. from the Zoology Department, are owned by the University. They are situated on sloping ground to the west of the flood plain of the river Wear. The parent rock is subglacial boulder clay with a substantial sandy fraction owing to resorting by water. A proportion of the vegetation is natural with naturally regenerating oak (*Quercus petraea*) as the dominant tree. At the southern end, however, nearly all the oak has been removed and its place taken by a mixture of naturally regenerating and planted sycamore interspersed with trees of other species, notably beech, elm and larch (*Larix decidua*).

b) The trapping transects

Three trapping transects were already in existence at the start of this project. These were laid out in 1954 (Ashby 1967) and are still trapped twice a year to provide a long term monitoring of small

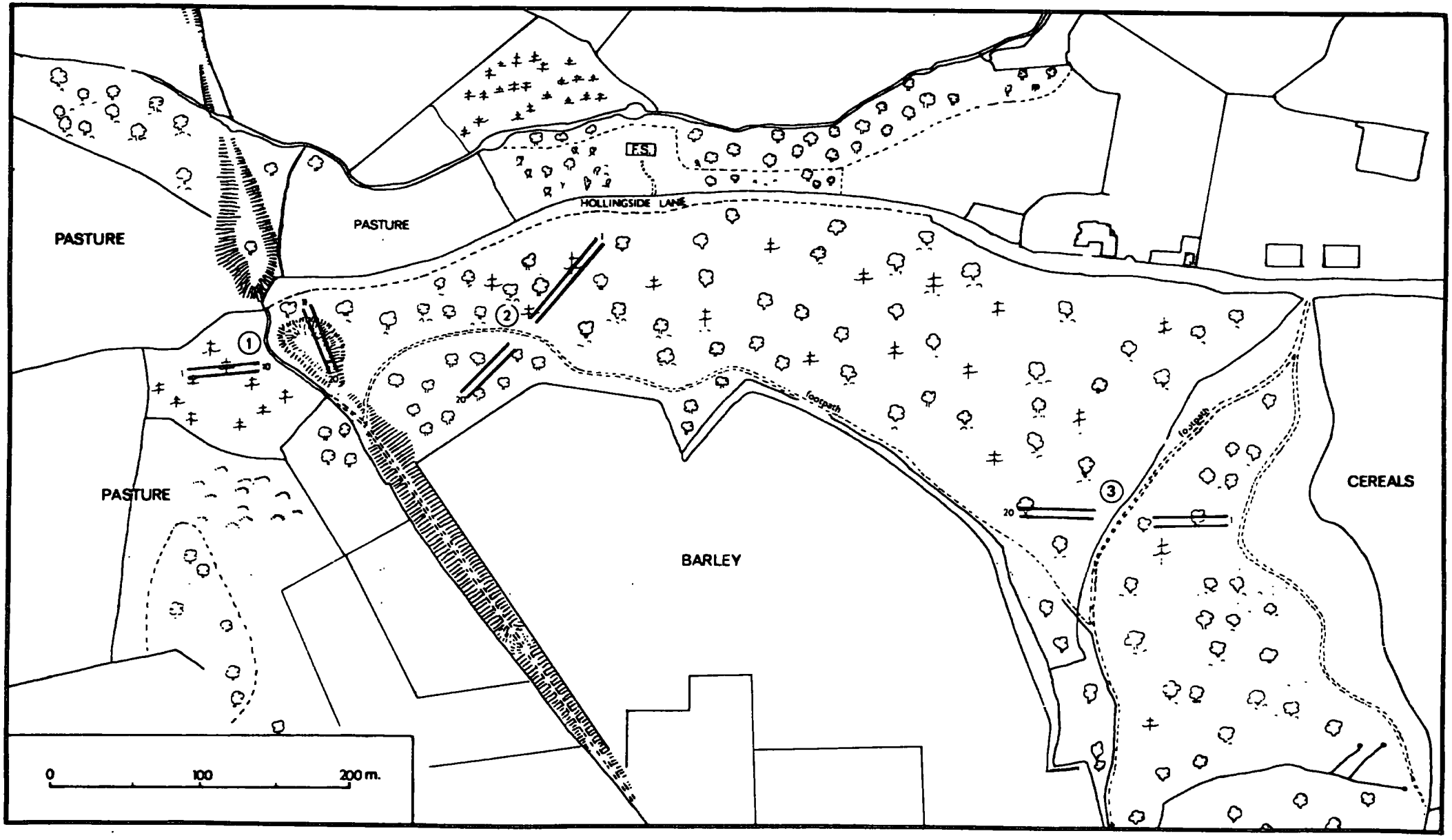


FIGURE 2.2 Houghall Woods, showing the three trapping transects

mammal abundance. Rather than lay out a new grid it was decided to use these transects for which a large amount of trapping data already exists.

When originally planned the three transects were designed to cover the maximum possible range of habitats. Each transect ran from the top edge of the wood, where drainage is good and exposure relatively great, towards the lower edge where conditions are less well drained but more sheltered. Each transect was in two parts with a gap of about 30m. necessitated by the presence of public footpaths. For the first and third transects this gap was at the halfway point but for the second it was two thirds of the way down.

Since the laying out of these transects, there have been considerable changes in the vegetation as a result of woodland management policies and the maturation of trees planted since 1950. Details of these changes are given in the sections dealing with each transect.

i) Transect 1

This transect slopes unevenly down towards the north-east; the soil is generally a heavy loam although lighter and sandy in parts. During the last century the area was the site of digging operations for an extension to a mineral railway which was abandoned before completion. The area including the transect was planted in about 1950 with a mixture of larch and sycamore, although few of the larch have survived on the upper half. The sycamore are now approaching maturity and the transect is much more shaded and less exposed than formerly. The present ground cover is mainly a rather thin turf of Holcus species which provides poor cover. Locally bracken and bramble provide patches of denser cover. The lower half of the transect slopes steeply into a small gully, one of the trap lines running along the north-west side, the

other along the bottom. On this half the vegetation is much more dense, with bramble and bracken providing moderately dense cover over much of the area. Further cover is provided by piles of old branches interspersed with grasses whilst at the bottom of the gully there is a considerable amount of leaf litter. The last trap position along the side of the gully was situated outside a badger sett.

ii) Transect 2

The land slopes towards the south-east with the transect being slightly oblique to the slope. The trees are mainly a mixture of planted and naturally regenerated sycamore but include a number of beech and a few birch. The top third of the transect slopes steeply and has little cover except beech leaf litter and occasional tussocks of grass and bracken. Further down, the slope moderates and the cover becomes dense, consisting mainly of bramble with some bracken. The lowest third of this transect, below the public footpath, provides moderate cover consisting of patches of leaf litter, bramble, bracken and bluebell (Endymion non-scriptus). There has been a considerable increase in the amount of bramble in the central portion since thinning operations in 1958 as Ashby (1967) reported fairly poor cover even in summer. This increase in cover will have produced a more favourable habitat for Clethrionomys in compensation for the decrease in cover on transect 1 since 1965.

iii) Transect 3

This transect shows greater variation in vegetation than the other two. The ground slopes towards the south although at the upper and lower ends the slope is not steep. The upper five trap positions are situated partly in a clump of young birch and partly among mature

oak trees. Ground cover consists mainly of grasses, some forming a turf, others in tussocks. Cover is moderate throughout the year. The second quarter of the transect is steeply sloping, the trees being mainly oak and the ground cover a thick continuous carpet of Vaccinum myrtillus interspersed with oak leaf litter. There is little variation in cover here between summer and winter. Below the footpath which divides the transect, the nature of the woodland changes. The lower half is situated in rather open mixed woodland consisting of a mixture of sycamore, beech and birch. The ground cover on the third quarter of the transect consists of grasses together with small patches of bramble and rather bare mossy areas. The lowest quarter, where there is little slope contains grasses, mainly Holcus species with patches of bluebells in spring. Grasses of this type appear to provide rather poor cover for Clethrionomys.

3. Comparison of the two study areas.

There is a considerable difference between the vegetation of the two study areas. Castle Eden Dene contains large areas of perennial herbs which appear for only a limited period of the year. Permanent cover is restricted to a small part of the trapping grid. In Houghall Woods the situation is reversed. Much of the area of the three transects contains cover which is present throughout the year, and only small areas are covered by seasonal herbs. As the density of Clethrionomys has been shown to be closely related to the density of ground cover (Kikkawa 1964; Crawley 1965; Ashby 1967) it is clear that any seasonal differences in the availability of cover could have important consequences for the population dynamics of this species. A more detailed account of seasonal vegetation changes and their consequences is given in section 2D.

B. The Trapping Methods

1. Trap spacing.

In Castle Eden Dene the size and shape of the trapping area was determined to a large extent by the nature of the terrain. The area chosen was such that it could be covered by a square grid 90m. x 90m. giving an internal grid area of 0.81 hectares.

The trap spacing used on such a grid is an important variable as it may influence the estimate of population density. Spacing must be such that there is a high probability of animals encountering an empty trap during their normal daily movements. This probability is influenced both by the activity of the animals concerned and their ability to recognise the trap at some distance, often termed the 'recognition distance'. There are few data on individual species recognition distances but a figure of about 3m. has been suggested for common North American species (Gentry, Golley and Smith 1971) and a trap spacing of about one sixth of the average diameter of the home range of the dominant species has been suggested by Smith, Gentry and Golley (1969-70). Crawley (1965; 1969) obtained the following estimates of home range in Castle Eden Dene; the diameter has been calculated on the assumption that the home range is circular.

Species and sex	Home Range ($m.^2$)	Diameter (m.)
Clethrionomys ♂	1970	50
Clethrionomys ♀	1354	42
Apodemus ♂	2250	56
Apodemus ♀	1817	48

Apodemus males have the largest home range with a mean diameter of 56m, although that of Clethrionomys males is not much smaller. One sixth of 56m. gives a suggested trap spacing of approximately 10m. This

spacing, giving a total of 100 trapping points on the grid was therefore adopted. This is rather closer than the spacing of 15m. used by many other investigators (Smith et al 1969-70) but a close trap spacing should sample a high proportion of the population even if only one trap is used at each position.

In Houghall Woods the trapping positions marked out by Ashby (1967) were used. Each transect consisted of two parallel lines of twenty trapping positions 10 yards (9.14m.) apart. Except at the gap dividing the transect into two parts (see page 9) adjacent trapping positions within a line were 6.5 yards (5.94m.) apart, giving a total length of 58.5 yards (53.6m.) for each half transect. The minimum separation between transects one and two was 80m. whilst transect three was about 400m. from transect two. Ashby (1967) has recorded very limited movement of animals from transect one to transect two. During the present study only one animal was found to have moved in this fashion.

In the course of the study an attempt was made to estimate the catchment area of each transect by using a similar trapping scheme superimposed on the grid area at Castle Eden. The results of this experiment, together with a survey of previous comparisons will be presented in section C6.

2. Length of the trapping period

The length of the trapping period used in censusing is a compromise between attempting to catch all the rodents present on the trapping area and avoiding attracting non-residents onto the grid. The longer the traps are left in position the greater the possibility of non-residents becoming aware of this extra source of food.

The total trapping time may be subdivided into a prebaiting period, when the baited traps are present but not set to catch, and a catching

period when the traps are set and emptied at regular intervals. Prebaiting allows the animals time to find and investigate the traps and increases the probability of capture on the first day the traps are set. It also increases the probability that the data will fit a regression model for population estimation. (Hayne 1949; Zippin 1956; Tanaka and Kanamori 1969). Previous studies have shown, however, that prebaiting does not eliminate bias due to the unequal catchability of marked and unmarked animals (Tanaka 1970; Grodzinski, Pucek and Ryskowski 1966).

In Houghall Woods population parameters have been studied in detail by Ashby (1967 and pers. comm.) who has concluded that transect trapping has given a reliable index of small mammal abundance over a period of 20 years. He was also able to relate the number of animals caught on these transects to absolute density by laying out a transect in an area already being studied by grid trapping. In view of the evidence of reliability of these transects it was decided to continue with this trapping scheme.

The trapping routine, shown in Table 2.1, consisted of two days prebaiting followed by two days catching. In Castle Eden Dene the same prebaiting period was used but the catching period was extended to three days. This permitted the use of a greater variety of statistical methods and increased the proportion of recaptures.

Day	Castle Eden	Houghall
1	Lay traps, prebait	Lay traps, prebait
2		
3	Set to catch	Set to catch
4	Empty, reset	Empty, reset
5	Empty, reset	Empty, remove traps
6	Empty, remove traps	

TABLE 2.1 Trapping routine at the two study areas.

	No. of Captures				No. of Individuals			Trap deaths		
	♂	♀	Escape	Total	♂	♀	Total	♂	♀	Total
Castle Eden Dene	217	194	14	425	140	132	272	10	14	24
Houghall Woods	197	136	4	337	161	118	279	25	20	45

TABLE 2.2 The total number of Clethrionomys handled on the two trapping areas

	No. of Captures				No. of Individuals			Trap deaths		
	♂	♀	Escape	Total	♂	♀	Total	♂	♀	Total
Castle Eden Dene	224	155	9	388	147	100	247	3	2	5
Houghall Woods	170	77	16	263	140	64	204	2	0	2

TABLE 2.3 The total numbers of Apodemus handled on the two trapping areas

C. Population Dynamics

1. Numbers caught

The total numbers of individuals captured at the two study areas are shown in Tables 2.2 and 2.3 for *Clethrionomys* and *Apodemus* respectively. Results for individual trapping sessions are shown in Tables 2.4 and 2.5. The figures for Houghall Woods include all three transects. As the organisation of the trapping routine and total trapping effort differed at the two sites the numbers are not directly comparable. *Clethrionomys* individuals outnumbered *Apodemus* at both study sites, at Houghall by 1.37:1 and at Castle Eden by 1.10:1

2. Trap mortality.

The number of individuals found dead at both sites are included in Tables 2.4 and 2.5. In this study trap mortality was calculated as $\frac{\text{number of dead}}{\text{number of captures}}$ as this gives a more realistic indication of the probability of trap death than $\frac{\text{number of dead}}{\text{number of individuals}}$ used by Crawley (1965; 1970) in his study at Castle Eden.

The mean trap mortality of *Clethrionomys* was 13.3% at Houghall and 5.6% at Castle Eden. The number of dead found at Houghall is considerably elevated by the high mortality in October 1975; when the filming of a television programme delayed the trapping routine and the weather was cold and wet. Given an allowance of 10 deaths for this upset, the mean mortality is reduced to 10.4%, a figure which is still significantly higher than that for Castle Eden ($\chi^2 = 13.5$, $p < 0.001$). It is difficult to account for this discrepancy as the trapping technique was the same at both sites. One possibility is that there is a difference in local weather conditions between the two sites, which are about 12 miles apart. During the course of the study the impression was formed, that heavy frosts were more frequent in Houghall Woods.

Date	Captures				Individuals			Dead			% of male individuals
	♂	♀	Escape	Total	♂	♀	Total	♂	♀	Total	
a Aug.'74	9	6	0	15	7	5	12	0	1	1	58
b Sept'74	37	40	3	80	17	18	35	1	0	1	48
Oct.'74	33	33	1	67	22	25	47	4	2	6	47
Jan.'75	8	15	0	23	6	11	17	0	3	3	35
May'75	18	18	0	36	12	10	22	1	0	1	54
June'75	19	18	4	41	13	13	26	1	1	2	50
July'75	50	29	4	83	27	18	45	1	0	1	60
c Sept'75	19	9	1	29	15	8	23	0	1	1	65
Nov'75	12	12	1	25	10	10	20	1	3	4	50
Jan'76	4	5	0	9	4	5	9	0	0	0	44
Mar'76	8	9	0	17	7	9	16	1	3	4	44
Totals	217	194	14	425	140	132	272	10	14	24	51.4

TABLE 2.4a The numbers of Clethrionomys caught at individual trapping sessions at Castle Eden.

Date	Captures				Individuals			Dead			% of male individuals
	♂	♀	Escape	Total	♂	♀	Total	♂	♀	Total	
a Aug'74	7	7	0	14	5	5	10			0	50
b Sept'74	28	9	0	37	18	6	24			0	75
Oct'74	43	33	5	81	29	20	49			0	59
Jan'75	42	31	0	73	23	17	40	3	2	5	58
May'75	21	12	0	33	11	8	19			0	58
June'75	14	8	0	22	7	4	11			0	64
July'75	9	13	0	22	8	9	17			0	47
c Sept'75	10	6	1	17	9	5	14			0	64
Nov'75	12	15	0	27	9	10	19			0	47
Jan'76	19	13	1	33	15	10	25			0	60
Mar'76	19	8	2	29	13	6	19			0	68
Totals	224	155	9	388	147	100	247	3	2	5	59.1

TABLE 2.4b The numbers of Apodemus caught at individual trapping sessions at Castle Eden.

a - only 50 traps on half the grid
b - 4 days catching.
c - only two days catching.

Date	Captures				Individuals			Dead			% of male individuals
	♂	♀	Escape	Total	♂	♀	Total	♂	♀	Total	
a July'74	22	11	1	34	15	8	23	0	0	0	65
Sept'74	22	19	1	42	19	16	35	5	1	6	54
Nov'74	15	12	0	27	12	9	21	2	1	3	57
March'75	8	6	0	14	6	5	11	2	2	4	54
May'75	21	9	1	31	16	8	24	3	0	3	67
June'75	17	11	0	28	15	11	26	1	1	2	58
July'75	23	9	0	32	18	9	27	1	1	2	67
Sept'75	11	18	1	30	8	14	22	1	2	3	36
Oct'75	16	13	0	29	15	13	28	5	9	14	54
b Nov'75	25	17	0	42	21	14	35	1	2	3	60
Feb'76	7	6	0	16	7	6	13	3	1	4	54
May'76	10	5	0	15	9	5	14	1	0	1	64
Totals	197	163	4	337	161	118	279	25	20	45	57.7

TABLE 2.5a The numbers of Clethrionomys caught at individual trapping sessions at Houghall.

Date	Captures				Individuals			Dead			% of male individuals
	♂	♀	Escape	Total	♂	♀	Total	♂	♀	Total	
a July'74	0	2	0	2	0	1	1				0
Sept'74	38	22	2	62	33	19	52	2	0	2	63
Nov'74	32	18	2	52	26	13	39				67
March'75	24	5	0	29	18	5	23				78
May'75	4	3	0	7	3	2	5				60
June'75	0	2	0	2	0	2	2				0
July'75	0	0	0	0	0	0	0				-
Sept'75	14	2	1	17	12	2	14				86
Oct'75	30	12	4	46	25	10	35				71
b Nov'75	15	9	7	31	13	8	21				62
Feb'76	7	1	0	8	6	1	7				86
May'76	6	1	0	7	4	1	5				80
Totals	170	77	16	263	140	64	204	2	0	2	68.6

TABLE 2.5b The numbers of Apodemus caught at individual trapping sessions at Houghall

a - only transects 1 and 2 trapped
b - two traps at each point (N = 240), 3 days catching.

It is possible that the high number of deaths at Houghall could have been reduced by visiting the traps in the afternoon as well as the morning. This was tried in September 1975 when 240 traps were set. A total of 8 Clethrionomys or 19% of the total catch were captured in 3 afternoon trap rounds but the total mortality for the trapping session was not significantly reduced.

Although Crawley (1965; 1970) found that most deaths occurred during the winter months there was no marked seasonal difference during the present study. While there is a suggestion of slightly higher mortality during the winter, the numbers are too low to allow a more detailed analysis. Deaths during the winter may be attributed to the cold while deaths during the summer are more likely to be due to dehydration than starvation as there was always plenty of food present in the traps.

Trap mortality affected both marked and unmarked animals though to slightly different extents. At Castle Eden 40% of the catch and 78% of the dead were unmarked while at Houghall 51% of the catch and 60% of the dead were unmarked. If anything these figures suggest that unmarked animals are subject to greater mortality but the difference is not significant. This agrees with the findings of other workers (Fullager and Jewell 1965; Crawley 1965) that there is no evidence for a difference in the sensitivity of marked and unmarked individuals to confinement.

Apodemus suffered very low trap mortality, all the deaths being confined to one particular trapping session at each site. This agrees with the findings of Ashby (1967), Crawley (1965) and others, that Clethrionomys react much less favourably to confinement than Apodemus. This may be attributed partly to the greater average time spent in the traps by the former species.

3. Trap-revealed sex-ratio.

The trap revealed sex-ratio of individuals captured over the whole study period was, for Clethrionomys, 1.06 males to every female at Castle Eden and 1.36:1 at Houghall. The excess of male Apodemus was somewhat greater, the ratios being 1.47:1 at Castle Eden and 2.19:1 at Houghall. Details of the sex-ratio at each trapping session are included in Tables 2.4 and 2.5 and presented graphically in Figure 2.3.

The overall sex-ratio of Clethrionomys at Houghall shows a significant excess of males ($\chi^2=6.62$, $p<0.01$) although when each trapping session is considered separately at no time does the sex-ratio differ significantly from unity. At Castle Eden there appears to be a seasonal pattern of variation in the sex-ratio with an excess of males in late summer and an excess of females during the winter; indeed if the sex-ratios are compared between winter (October-March) and summer (April-September) the difference is significant ($\chi^2=7.76$, $0.01>p>0.005$). Any overall pattern in sex-ratios at Houghall is less clear but there is some suggestion of a greater excess of males during the summer months.

The results reported here are in general agreement with those found by other workers. Ashby (1967) reported a ratio generally close to unity but with periods when there was a marked excess of males and suggested that the observed variation was not random in nature. Other authors report an excess of males (Newson 1963, Crawley 1965, 1969, Tanton 1965) but with no apparent pattern to the variation in ratio, which altered substantially from season to season.

Apodemus males outnumbered females significantly at both study sites (Houghall $\chi^2=20$, $p<0.001$; Castle Eden $\chi^2=8.9$, $p<0.01$) though the sex-ratio at Castle Eden was never significantly different from unity when each trapping session is considered separately. At Houghall

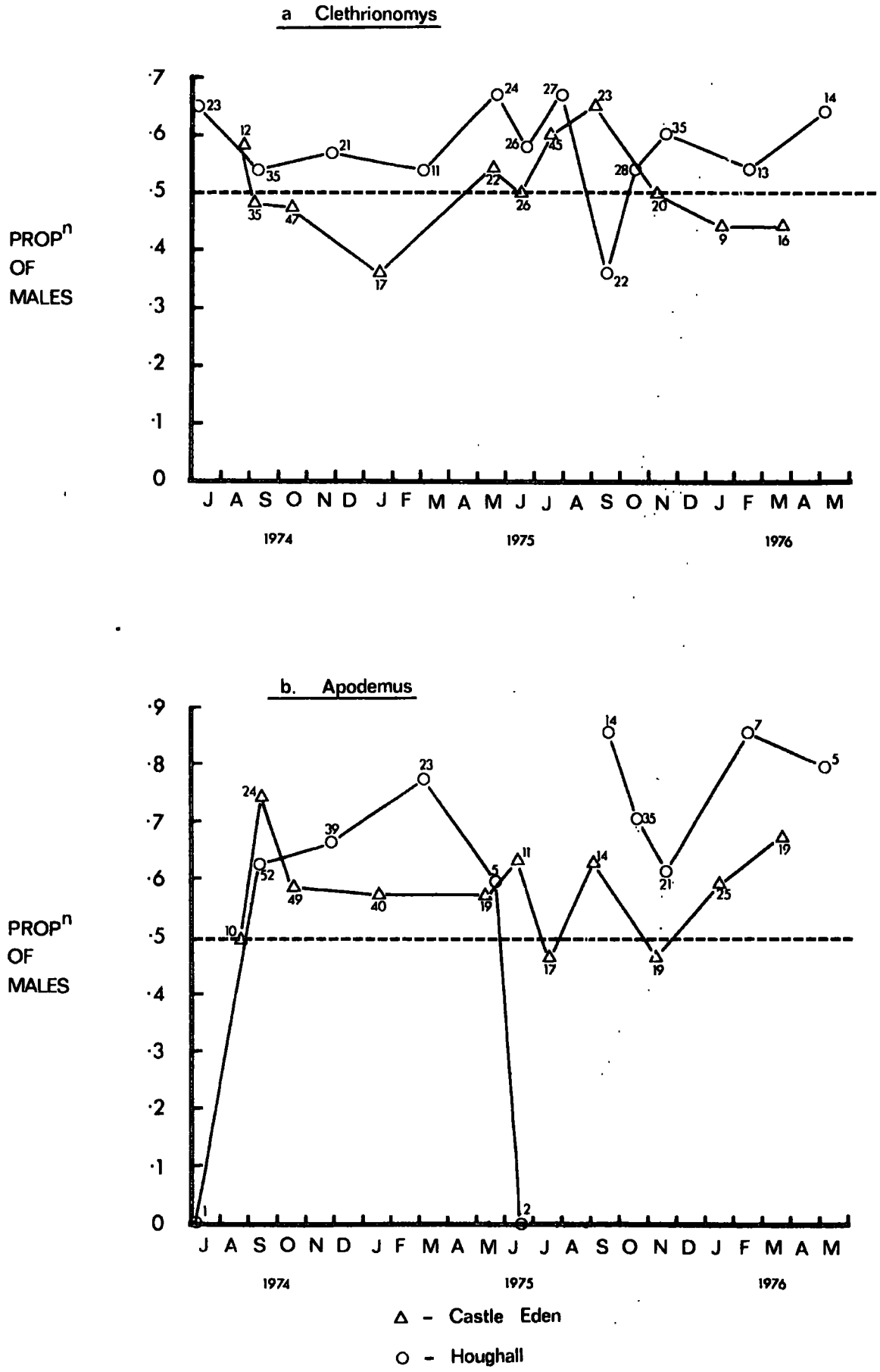


FIGURE 2.3 Trap-revealed sex-ratio of Clethrionomys and Apodemus. Figures indicate sample sizes (individuals captured).

the small numbers of individuals caught during the summer meant that although the calculated sex-ratios always showed a great excess of females, these differences have no significance when considered separately. In March, September and October 1975, when reasonably large numbers of animals were caught there was a significant excess of males ($p<0.02$).

Previous investigators have reported a general preponderance of males, although the sex-ratio may drop to equality in spring (Elton, Ford, Baker and Gardner 1931; Miller 1958; Crawley 1965, 1970; Ashby 1967). In this study the number of males exceeded the number of females at almost every trapping session although it reached equality or favoured females during August 1974, July 1975 and November 1975 at Castle Eden when sample sizes were 10, 17 and 22 respectively. Data combined from both sites indicates that during May - August the sex-ratio was generally close to unity (38 : 32) though not significantly different from the rest of the year ($\chi^2 = 3.18$, $0.10 > p > 0.05$).

4. Estimation of population size.

The estimation of population size is an important prerequisite of any ecological study and many methods have been devised. The simplest method, direct enumeration, whether on a grid or a transect requires intensive trapping so that a very high proportion of the animals present in the trapping area are captured. If this is possible the technique requires no assumptions or statistical analysis. It has been used with effect where the only information required is an index of population density (Krebs, Keller and Tamarin 1969).

Indirect methods of estimating numbers and other parameters by trapping are all based on the mark-recapture method first suggested

by Peterson in 1889. All these methods rely on the dilution and subsequent recapture of a marked sample of the population and require a number of the following assumptions (Smith,,Gardner, Gentry, Kaufman and O'Farrell 1975).

i) The animals do not lose their marks

ii) The captures are correctly recorded and identified

iii) Marking does not affect the probability of survival

iv) The population is defined as either open or closed so that either -

a) There is no loss or gain of members during sampling

or b) There is recruitment and immigration but death and emigration affect marked and unmarked animals equally. For most methods mortality rates are assumed to be constant with age although a recent model has modified this so that mortality rates may be age-related (Manly and Parr 1968).

or c) Knowledge is available from other sources which permits an allowance to be made for migration, birth and death prior to the analysis of the data.

v) The population is randomly sampled so that either -

a) Every animal has the same probability of capture

or b) If there exist strata within the population which have different probabilities of capture then the marked animals are proportionally distributed within these strata.

The first three assumptions are common to all capture-recapture methods and can be met by careful catching and marking procedures although it is impossible to test directly whether marking affects the probability of survival. Part (c) of the fourth assumption is rarely applicable to studies of wild populations so a choice must usually be made between either iv(a) or iv(b). Models are available to fit either of these assumptions.

If the study period is short there is little time for any change in the population size and a simple capture-recapture model based on assumption iv(a) may be used. If a longer study period is used then the losses and gains of the population must be considered and a more complex model making assumption iv(b) must be used.

The short discrete trapping periods of this study were spread over a period of about 20 months so it is possible to consider either the results of a single trapping session lasting only a few days, or the results of the whole study. In the former case the time between release and recapture was short so that gains and losses may be ignored whilst in the latter case a sequential method must be used which makes use of the continuity of the study to provide information about gains and losses in the population.

Assumption v, which is common to all capture-recapture methods is impossible to verify either experimentally or by statistical means (Hanson 1967, Roff 1973a, b) unless the entire population can be captured in some way. This assumption, which is a major weakness of capture-recapture methods, is certainly violated, to some extent, in all studies where the animals involved form an organised social structure or show individual variation in behaviour. D.Brown (pers. comm.) found that even with the freshwater crayfish (Austropotomobius pallipes) some individuals were caught much more easily than others. In an attempt to overcome these difficulties population size was estimated in a number of different ways at the two sites.

a) Calendar of captures (Petruzewicz and Andrzejewski 1962)

The calendar of captures is a semi-graphical direct method of determining numbers. The data are laid out with one line for each animal caught and a column for each trapping session. The sessions at which a particular animal is captured are marked and the animal is assumed to be present if a blank trapping session is followed by

a mark. An example is given in Appendix 1 as the complete tables are too large to include in full. This technique is similar to enumeration but uses the continuity of the study to include individuals not caught but known to be present.

One drawback of the method is that if an animal is not seen for a numer of trapping periods and is then recaptured a decision must be made as to whether the animal was always present in the area or left and then returned. The number of animals assumed to be present but not seen was generally low during this study and animals were very rarely absent from the catch for more than 3 trapping sessions so all animals known to be alive were assumed to be present in the trapping area.

The number derived from a calendar of captures is often referred to as the 'number known to be alive' and sets a minimum limit on the size of the population.

b) <u>The Petersen estimator or Lincoln index</u>

The Petersen estimator may be calculated from the results of a single marking period followed by a single recapture period. The population size is assumed to be constant between marking and recapturing and assumptions i, ii, ii, iv(a) and v(a) apply. The estimation of population size, N, is given by

$$N = \frac{n_1 n_2}{m} \qquad \text{S.E. of } N = \sqrt{\frac{N\,(N-n_1)\,(N-n_2)}{n_1 n_2 (N-1)}}$$

where N = estimate of the parameter N, the population size.

n_1 = the number of marked animals released from the first sample

n_2 = the total number of animals in the second sample

m = the number of marked animals in the second sample

In this equation N overestimates N by $^1/m$ so the modification

$$N = \frac{n_1(n_2+1)}{(m+1)}$$

has been suggested by Bailey (1952) for small populations. As the total number of animals captured never exceeded 52 this modified formula was applied throughout.

The Peterson estimator was applied to individual trapping sessions at Houghall Woods where a single marking session was followed by a single opportunity for recapture.

c). The regression method or Hayne's trap-out.

This method devised by Hayne (1949) was originally applied to removal methods of population estimation. It is, however equally applicable to capture-recapture studies as marked animals may be considered to have been removed from the population. If animals are caught, marked and released on successive days it follows that when no new animals are caught the total population at risk on the study area must have been captured. The ~~number~~ proportion of new animals should decrease linearly if all the animals are equally susceptible to capture and if no new animals enter the population. As the trapping session does not normally continue until all the animals captured are marked the total number present is found from the regression of the number of unmarked animals caught on the cumulative total previously marked. For this reason the catching period must be a minimum of three days. A correlation coefficient approaching 1 would indicate that the population was behaving in a random fashion and that the assumption of equal catchability was being fulfilled. Except on four occasions when an estimate was not calculated, correlation coefficients were over 0.90 suggesting that the population was behaving in an approximately random fashion.

The estimate of population size is the value of 'cumulative number marked' when 'number of new animals' is zero. The standard error of this estimate can be calculated from the formula given by Seber (1973).

The calculation was performed on a programmable calculator.

This method was applied to the trapping results at Castle Eden where the three day trapping period provided sufficient points for the regression line.

d) The 'constant proportion seen' method.

The small samples captured at several trapping sessions at both sites increased the standard errors of the methods already described to the point at which the estimates were valueless. By making an extra assumption it is possible to combine the data over the whole study period and derive a new estimator.

If it is assumed that the probability of capture of an animal present in the catchment area is constant throughout the study then, if the trapping effort is the same during each individual session, the sequence of samples taken is analogous to taking a number of samples from a population simultaneously, as the proportion of recaptures will be constant. The mean proportion of the total population captured can then be estimated.

At Houghall the results shown in Table 2.6a were obtained during this study. By assuming that a constant proportion of the population was seen at any one trapping session and dividing by the appropriate factor (.713 for Clethrionomys, .575 for Apodemus) an estimate of the total population may be derived. The proportion of animals, particularly Apodemus, recaptured during this study was rather lower than that reported by Ashby (1967) for trapping between 1954 and 1965 and possible reasons for this will be suggested in the Discussion.

It is possible to perform a partial check on the assumption of equal catchability by examining the proportion of animals released on day 1 that were captured on day 2; this should be constant. A test of equality of proportions gives $\chi^2=9.17$ with 10 degrees of free-

Species	Day 1			Day 2			
	Captured	Dead	Escaped	Captured	Previously marked	Dead	Escaped
Clethrionomys	167	35	8	113	44	10	0
Apodemus	120	0	8	138	41	2	6

	Clethrionomys	Apodemus
Released on day 1	129	112
Estimate of 'total population' (Petersen method)	331±32	377±41
Proportion of total population seen	$\frac{167+(113-44)}{331} = 0.713$	$\frac{120+(138-41)}{377} = 0.575$

TABLE 2.6a Estimation of the proportion of the total population seen at Houghall

	Day 1	Day 2		Day 3	
	Captured	Unmarked	C.T.P.M*	Unmarked	C.T.P.M.*
Clethrionomys	130	72	120	48	187
Apodemus	120	76	114	33	195

* = Cumulative total previously marked

	Clethrionomys	Apodemus
Regression estimate of 'total population'	301 ± 13 (r=0.999)	279 ± 23 (r =0.993)
Proportion of total population seen	$\frac{187 + 48}{301} = 0.758$	$\frac{195 + 33}{279} = 0.817$

TABLE 2.6b Estimation of the proportion of the total population seen at Castle Eden.

dom for Clethrionomys and χ^2=5.36 with 7 degrees of freedom for Apodemus showing that the observed variation in the proportion of recaptures is not greater than would be expected by chance ($p>0.3$ for both species).

The same reasoning may be applied to the trapping results at Castle Eden (Table 2.6b) except that here the regression method may be used to calculate the 'total population'. The assumption of equal catchability may be tested as before by examining the proportion of recaptures at any particular trapping session. This is most simply done by considering the proportion $\frac{\text{individuals}}{\text{captures}}$ for each period. For Clethrionomys a test of equality of proportions indicated heterogeneity (χ^2=25.4, d.f=11, $p<0.01$) but when the small samples of January and March 1976 were omitted the proportion of recaptures was homogenous (χ^2=13.7, d.f.=9, $p>0.20$). For Apodemus the test indicated homogeneity in the proportion of recaptures (χ^2=11.9, d.f.=11, $p>0.30$).

e) Jolly's method (Jolly 1965)

This method differs from preceding ones as the population is assumed to be open, thus requiring assumptions i, ii, iii, iv(b) and v. It is not necessary to assume that recruitment or survival are constant throughout the period of sampling. The model is termed 'stochastic' as changes are by chance rather than exactly determined thus leading to a more realistic model as it allows for the variability inherent in biological processes. For example a death rate of 50% means that the probability of an individual dying is 0.5 but it is not necessarily true that 50% of the population dies.

As with other methods the model relies on the proportion of marked animals in a sample being the same as the proportion in the population. The total numbers of marked animals in the population at a particular time is the number of marked animals captured at that time together

with those marked animals alive but not captured. This latter quantity is determined by considering the capture of marked animals at later dates.

The mathematical derivation of the model is extremely complicated but the formulae arrived at can be seen to be intuitively logical and can be explained in fairly simple terms (Parr, Gaskell and George 1968).

The notation is that of Jolly (1965), estimates of parameters being indicated with a circumflex e.g. $\hat{N}_i$.

Let

N_i = The population size at the time of the ith sample

M_i = The number of marked animals in the population at time i.

m_i = The number of marked animals in the ith sample

s_i = The number of animals released for the ith sample, so $(n_i - s_i)$ is the (loss on capture).

R_i = The number of animals in S_i that are subsequently recaptured.

Z_i = The number of animals marked before the ith sample which are not caught in the ith sample but are caught subsequently. This is the number 'known to be alive' at time i.

α_i = The proportion of marked animals in the population at time i, this is $\frac{M_i}{N_i}$.

ϕ_i = The probability of an animal released at i surviving till time i + 1.

B_i = The number of animals joining the population after i and surviving till i+1. This is the 'recruitment rate'.

On the ith trapping occasion S_i animals are released of which R_i are subsequently recaptured. Present but not caught are $(M_i - m_i)$ of which Z_i are eventually recaptured. As the chances of recapture are the same for both groups R_i and Z_i the proportions recaptured may be

equated.

$$\frac{Z_i}{M_i - m_i} = \frac{R_i}{S_i}$$

M_i can be estimated

$$\hat{M}_i = m_i + \frac{Z_i S_i}{R_i}$$

As we are assuming that -

$$\alpha_i = \frac{M_i}{n_i} \quad \text{and} \quad \hat{N}_i = \frac{M_i}{\alpha_i}$$

then,

$$\hat{N}_i = n_i + \frac{n_i Z_i S_i}{m_i R_i}$$

The standard error of this estimate is given by

$$\sqrt{\hat{N}_i (\hat{N}_i - n_i) \left\{ \frac{M_i - m_i + S_i}{M_i} \left(\frac{1}{R_i} - \frac{1}{S_i} \right) + \frac{1 - \alpha_i}{m_i} \right\}}$$

The estimate of survival is given by

$$\phi_i + \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + S_i}$$

and of the number joining the population after i and surviving to time i + 1

$$\hat{B}_i = \hat{N}_{i+1} - \phi_i (\hat{N}_i - n_i + S_i)$$

The model does not give an estimate of N_i or B_i for the first occasion of sampling or estimates of $_i$ and B for the last two sampling occasions.

The data for the complete study period at Houghall and Castle Eden were set out as detailed by Jolly (1965). A computer was used to perform the calculation according to a programme given by Davies (1971). The layout of the data and the results obtained are shown in Appendix 2.

Jolly's method may also be applied to a triple-catch trapping regime such as that employed at Castle Eden Dene, when a population estimate can be obtained only for the second day. In this special case the estimate is given by

$$\hat{N}_2 = n_2 + \frac{n_2 S_2 Z_2}{m_2 r_2}$$

with its associated standard error

$$\sqrt{\hat{N}_2(N_2 - n_2)\left\{\frac{\hat{M}_2 - m_2 + S_2}{M_i}\left(\frac{1}{R_2} - \frac{1}{S_2}\right) + \frac{1 - \alpha_2}{m_2}\right\}}$$

This formula was applied to individual trapping sessions at Castle Eden Dene.

5. Results of the population estimates

The results of the application of the methods described are shown in Table 2.7 for Clethrionomys and Apodemus in Castle Eden Dene and Table 2.8 for Clethrionomys and Apodemus in Houghall Woods. The results are discussed in the following sections.

a) Calendar of Captures

There is in general little difference between the number captured and the number known to be alive for both species at both trap sites, the biggest discrepancy occurring for Clethrionomys at Houghall in October 1975 when the trapping and marking routine was upset by the presence of a film unit.

The small number of animals known to be alive but not captured suggests that the trapping schemes employed are sampling a high proportion of the marked animals present in the trapping area at both sites.

b). The Petersen Estimator

The calculation of the Petersen estimate for both Clethrionomys and Apodemus give results which are generally considerably higher than

DATE	CLETHRIONOMYS							APODEMUS						
	No. of Individuals	Calendar of Captures	Regression method	Jolly triple catch	Jolly sequential	Constant proportion seen	'Best Estimate'	No. of Individuals	Calendar of Captures	Regression method	Jolly triple catch	Jolly sequential	Constant proportion seen	'Best Estimate'
Aug.'74*	12					15		10					12	
Sept.[1]	35	35	37±3	39±9	35±3	44	39	24	25	24±6	27±17	45±23	29	27
Oct.	47	50	55±4	49±14	76±19	59	55	49	50	56±8	53±14	92±35	60	60
Jan.'75	17	21	18±3	72±85	39±11	21	21	40	42	40±4	35±5	45±9	49	45
May	22	23	28±4	25±11	26±6	27	26	19	20	20±3	21±5	61±38	23	21
June	26	28	N.C.	37±20	35±7	33	35	11	14	11±2	N.C.	43±28	13	14
July	45	45	49±1	33±6	45±7	56	45	17	19	N.C.	49±54	37±20	21	21
Sept.	23	23	N.C.	N.C.	35±9	43	39	14	15	N.C.	N.C.	45±26	26	26
Nov.	20	21	N.C.	56±78	27±8	25	26	19	22	20±4	180	41±19	23	23
Jan.'76	9	14	10±1	N.C.	76±71	11	14	25	25	30±6	56	25±5	30	30
March	16		N.C.	N.C.		20	20	19		16±10	N.C.	-	23	23

* Result for half grid only, 1 - Total for 4 days, see Appendix 3, N.C.-not calculable.

TABLE 2.7 Population Estimates in Castle Eden Dene.

	CLETHRIONOMYS						APODEMUS					
DATE	No. of Individuals.	Calendar of Captures.	Petersen Estimate	Constant Proportion Seen	Jolly's Method	'Best Estimate'	No. of Individuals	Calendar of Captures	Petersen Estimate	Constant Proportion Seen	Jolly's Method	'Best Estimate'
July' 74[1]	23	-	-	32	-	32*	1	-	-	-	N.C.	1*
Sept' 74	35	36	66±18	50	157±81	58	52	52	98±22	90	N.C.	94
Nov.' 74	21	25	28±6	30	69±26	29	39	42	61±10	68	70±26	64
March' 75	11	18	14±4	16	35±12	18	23	24	32±7	40	41±23	36
May' 75	24	25	34±7	34	55±17	34	5	5	4	9	5±2	5
June' 75	26	28	70±34	36	60±20	36	2	2	2	3	N.C.	2
July' 75	27	28	45±12	38	40±10	38	0	1	0	0	N.C.	1
Sept' 75	22	26	28±5	31	126±60	30	12	14	24±10	24	N.C.	24
Oct' 75	28	39	36±21	40	196±99	40	35	36	52±13	61	60±26	58
Nov' 75[1]	35	37	80±39	50	52±15	50	21	23	N.C.	36	59±30	36
Feb' 76	13	17	36±35	18	97±69	18	7	9	10±5	12	N.C.	7
May' 76	14	-	27±15	20	N.C.	23	5	-	5±1	9	N.C.	7

*result for 2 transects only. 1 total for 3 days, see Appendix 3. N.C. - not calculable.

TABLE 2.8 Population Estimates in Houghall Woods.

calendar of captures method. As expected, standard errors are high because of the relatively small numbers of animals involved.

Although the estimates are high they may not be unrealistic. Ashby (1967) considered that a half transect had a mean catchment area of about 0.45 hectares for Clethrionomys and about 0.49ha. for Apodemus giving a total catchment area for the three transects of 2.70 and 2.94 hectares respectively The maximum population estimates during the present study were 80 Clethrionomys, giving a density of 30 per hectare and 98 Apodemus giving a density of 33 per hectare. Both these densities are within the range reported by other workers (French, Stoddart, and Bobek 1975).

c) The regression method.

Population estimates were only calculated by this method for trapping sessions in which the correlation coefficient was greater than 0.90. This figure provided a convenient division as correlation coefficients tended to be either greater than 0.90 or less than 0.50. The correlation coefficient gives an indication of the applicability of the assumption of equal catchability, high coefficients indicating that the population is fulfilling this assumption. A low correlation coefficient indicates that the proportion of unmarked animals is not decreasing in a linear manner and hence that the population is violating one or more of the assumptions made. In this case no capture-recapture method will give a satisfactory solution.

d) The 'constant proportion seen' method

The main advantage of this method is that an estimate of population size may be made for every trapping session, however low the number of animals caught. The method may be regarded as exchanging errors

due to the random variation inherent in small numbers of recaptures for the error in assuming that catchability does not change throughout the study period. Because of the finite number of traps used there is an inherent bias in the method so that high populations may be underestimated because of competition for traps. It seems likely however that the error introduced by this bias is small compared with the errors inherent in the assumptions made. Ashby (1967) reported that the results obtained when two traps were used at each trapping position indicated that competition for traps was of little importance at Houghall.

e) Jolly's method

This method has been applied both over the whole study period at Castle Eden and Houghall and as a triple-catch method at Castle Eden.

i) Sequential estimates

If it is assumed that the population meets assumption v, the accuracy of this method is, in common with other models, determined by the proportion of recaptures in a sample, a high proportion of recaptures leading to small standard errors and vice versa. Manly (1971) suggested two theoretical reasons why this method could give inaccurate results. Firstly, in computing the estimators Jolly (1965) assumed that samples were large and ignored mathematical terms which were insignificant on the basis of that assumption. With small samples such terms might be significant. Secondly, some of the terms in the formulae are themselves estimates and hence subject to sampling variation. The same data are used to estimate both population size and its variance so these will be correlated. Because of this, population underestimates appear more accurate and overestimates less accurate than they really are. By far the greatest cause of error in the present study is, how-

ever, that due to random variation in the small samples used. This, together with the low proportion of recaptures, leads to large standard errors of the estimates.

Because of the greater trapping effort at Castle Eden, with the resultant higher number of recaptures, the estimates for Clethrionomys have much lower standard errors than those obtained at Houghall. The only exception to this is in January 1976 when the small sample size and unusually large number of animals present but not captured gave rise to an estimate with a very large standard error.

The lower numbers of Apodemus recaptured at both sites resulted in high standard errors for the population estimates for this species and a number of estimates which are clearly too high.

ii) As a triple-catch method

The Jolly estimator is designed to take account of changes in population size from one sampling occasion to the next and, if used as a triple-catch method, is therefore sensitive to random fluctuations in the number of animals trapped on consecutive days. By employing a capture-recapture method which assumes that population size is constant this source of error can be removed. Jolly's model therefore requires unneccessary assumptions when used as a triple-catch method.

As with the sequential estimates the small number of recaptures resulted in estimates which often have very large standard errors.

f.) Conclusions.

The major problem with studies of the size reported here is the small size of many of the samples. This will continue to be a problem with small mammal population studies undertaken with limited resources and is not easily solved by statistical manipulation of the results (Roff 1973a, b). Capture-recapture methods must all rely on the use of large samples and a high proportion of recaptures

to diminish the effects of random variation and thus reduce the standard error.

Of the methods applied to individual trapping sessions neither the Petersen estimator, the regression method nor the Jolly triple-catch gave realistic estimates at every trapping session. The 'constant proportion seen' method allows the calculation of an estimate however small the sample size and is insensitive to variation in the number of recaptures in an individual trapping session. Because the number of animals captured is always increased by a fixed proportion the estimates obtained are never very much greater than the minimum number known to be alive. The main weakness of the method lies in the assumption that the probability of catching an animal is constant from season to season despite well-documented changes in range, size and activity (Brown 1966; Randolph 1977). The effect of these changes can, however, be minimised by using a close trap spacing such as those employed during this study.

If the number of individuals surviving from one trapping session to the next is fairly high the Jolly sequential estimator gives realistic results, as shown by Clethrionomys at Castle Eden. However inadequate numbers of recaptures lead to estimates with such large confidence limits as to be valueless.

Despite the limitations of all the methods applied here, there is often good agreement between them and by considering them all it is possible to suggest a best estimate of population size at any particular time. A similar technique was used by Keith and Windberg (1978) for estimating the numbers of snowshoe hares in Alaska. A subjective assessment of the reliability of this estimate can then be obtained by observing the measure of agreement between the different methods of estimation. For this to be successful it is important to perform several calculations which use the trapping data in as many

different ways as possible. The calendar of captures method gives a minimum figure for the population size so any estimates below this must be rejected, as are any very high estimates. The mean of the remaining estimates may then be taken as an estimate of population size. The results of this subjective assessment are included in Tables 2.7 and 2.8.

6. Estimation of absolute density

The estimate of the density (D) of rodents present in the trapping area (A) is given by

$$D = \frac{\hat{N}}{A}$$

The problem therefore is to estimate the catchment area (A) of the line or grid of traps. This will consist of the actual area within the trapping line or grid together with a border zone from which animals are attracted towards the traps. In the case of a transect of two parallel lines of traps, each line may be considered as an edge of a grid.

Methods for estimating the width of the border zone fall into two categories

1) Data from the current or previous studies are used to estimate the home range of the species being trapped. The width of the border zone is then considered to be the average home range radius (Stickel 1954; Pelikan 1967; Smith et al 1975).

2) The distribution of captures from outer to inner trapping points is examined. The edge effect produces an increase in the probability of capture at the outer traps compared with the inner ones (Hansson 1969; Smith, Gentry and Golley 1969, 1970). This method cannot be used on a trapping

transect, where there are no inner traps.

The application of these two methods to the trapping results is described below.

a) The home range method

By using the estimates of home range size given by Crawley (1965, 1969 and see p.12) and assuming that the home range is circular, an average home range radius may be calculated of 23m. for Clethrionomys and 26m. for Apodemus. If the width of the border zone of the trapping grid at Castle Eden is equal to the home range radius this gives a catchment area of 1.85 hectares for Clethrionomys and 2.02 hectares for Apodemus. At Houghall, Ashby (1967) found that by assuming the catchment area of his transects to extend 23m. from the lines of traps he obtained good agreement between densities found on Crawley's (1965, 1970) grid and the density found by using a half-transect in Castle Eden Dene. By assuming the figures of 23 and 26m. given above, the total catchment area of the three transects in Houghall Woods is 2.79ha. for Clethrionomys and 3.24 hectares for Apodemus.

During the present study a comparison was made between densities estimated by the two trapping methods by setting up a transect running across the grid in Castle Eden Dene during September 1975. The total number of different individuals was 9 Clethrionomys (including 1 escape) and 12 Apodemus (including 1 escape). By using the figure derived in Table 2.6 that 71.3% of Clethrionomys and 57.5% of Apodemus were seen and by assuming that the catchment area of a transect was 0.93 ha. and 1.08 ha. for the two species respectively, the densities calculated are 13 per hectare for Clethrionomys and 18 per hectare for Apodemus. Trapping on the entire grid a few days previously yielded best estimates of 33 Clethrionomys and 17 Apodemus although the figure for Apodemus is unreliable as the results of the population estimates suggest that at that time the population was not fulfilling the assumption of

equal catchability. These figures yield density estimates of 17 per hectare for Clethrionomys and 8 per hectare for Apodemus. There is therefore reasonable agreement between the densities of Clethrionomys calculated from the two trapping methods whilst the poor agreement between the estimates for Apodemus may be attributed to the violation of the assumption of equal catchability by that species at that time.

b) The distribution of captures method (Castle Eden only).

Assuming that the distribution of rodents on and around the grid is random, that animals have a circular home range and that the area of influence of each trap is circular then, because the outermost traps have a larger catchment area, as the grid is approached the probability of a given trap capturing a rodent will be maximal at the outer row and decrease to a constant probability some distance inside the grid (Smith, Gentry and Golley 1969-70). According to this hypothesis the boundary areas inside and outside the grid should be equal in width and equal to the home range of the species under consideration. As the width of the boundary inside can be determined by the distance required to reach constant probability of capture it is possible to estimate the catchment area of the grid.

Data were combined for the whole study period to determine the mean number of catches per trap in each trap belt for each species. The results of this analysis are presented graphically in Figure 2.4. For Clethrionomys the mean number of captures, which is the same as the probability of capture, decreased significantly ($t = 2.32$ $p<0.03$) from belt A to belt B and then remained approximately constant as other belts were passed. The boundary strip inside, and hence outside, the grid can therefore be estimated, according to the theory, as 10m., giving a total catchment area for the grid of 1.20ha.

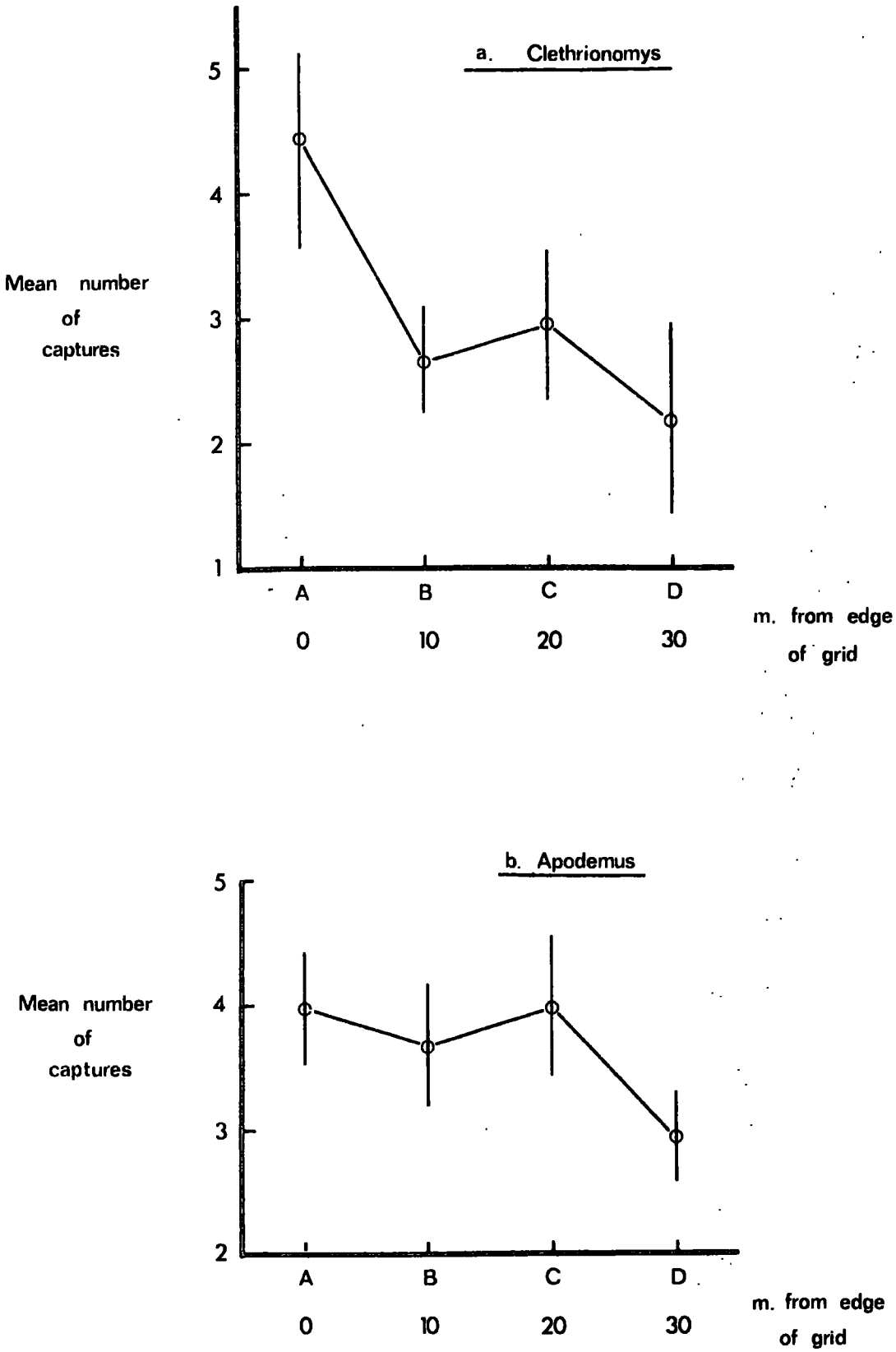


FIGURE 2.4 Estimation of the catchment area by the distribution of captures method. Vertical bars are ± 1 s.e.

The figure estimated for the width of the boundary strip by this method is less than half the radius of the home range as determined by Crawley (1965, 1969). The significant difference between the numbers caught in the first and second trap belts suggests that individuals whose home ranges are largely outside the grid are failing to penetrate beyond the first row of traps. If this is the case then the method is not strictly applicable as it relies on the fact that the probability of capturing an animal entering the grid declines linearly, rather than all intruders being stopped by the first row of traps encountered. It would appear that the trap spacing used will have a considerable effect on the results of this method. A close trap spacing will capture inward-moving individuals at the edge of the grid and suggest a boundary strip equal in width to the spacing between adjacent traps whilst a wider spacing will allow animals to penetrate further into the grid before encountering a trap and thus suggest a wider boundary strip.

If the 10m. boundary strip is applied to the density estimates at Castle Eden in September 1975 the density of Clethrionomys calculated on the grid is 28 per hectare and on the transect across the grid (with a catchment area of 0.39ha.) 31 per hectare, showing that there is still good agreement between the estimates although these are much increased.

The results for Apodemus are less clear. There is no linear decline in the mean number of individuals caught in each trap belt so it is impossible to define the point at which the influence of animals living on the edges of the grid has ceased. A possible reason for the failure of the method in this instance is that the grid was not large enough to contain a central area of equal probability of capture.

The results of both the methods described are shown in Table 2.9. For Clethrionomys the use of the 10m. boundary strip gives density

	Clethrionomys		Apodemus
	Assuming boundary strip of		Assuming boundary strip of
	10m	23m	26m
Aug' 74	13	8	6
Sept' 74	33	20	13
Oct' 74	46	29	28
Jan' 75	17	11	21
May' 75	22	14	10
June' 75	29	18	7
July' 75	37	24	10
Sept' 75	27	17	8
Nov' 75	22	14	11
Jan' 76	12	7	14
Mar' 76	17	10	11

TABLE 2.9a Estimates of population density at Castle Eden. Individuals/hectare

	Clethrionomys		Apodemus
	Assuming boundary strip of		Assuming boundary strip of
	10m	23m	26m
July' 74	27	11	0
Sept' 74	50	21	29
Nov' 74	25	10	20
Mar' 75	15	6	11
May' 75	29	12	2
June' 75	31	13	1
July' 75	35	15	0
Sept' 75	26	11	7
Oct' 75	34	14	18
Nov' 75	43	18	11
Feb' 76	15	6	3
May' 76	20	8	2

TABLE 2.9b Estimates of population density at Houghall. Individuals/hectare.

estimates over twice as large as with a 23m. strip so it is difficult to reconcile the two methods. The distribution of captures method, whilst showing a significantly higher number of captures at the edge of the grid than at the centre is apparently sensitive to the trap spacing and because of the close trap spacing employed may not be applicable in the present instance. The figure of 23m. for the radius of the home range is however agreed on by a number of authors including Southern (1964), Crawley (1965, 1969), and Ashby (1967)and may therefore yield a more realistic estimate of the actual trapping area.

7. Changes in population size in the two study areas.

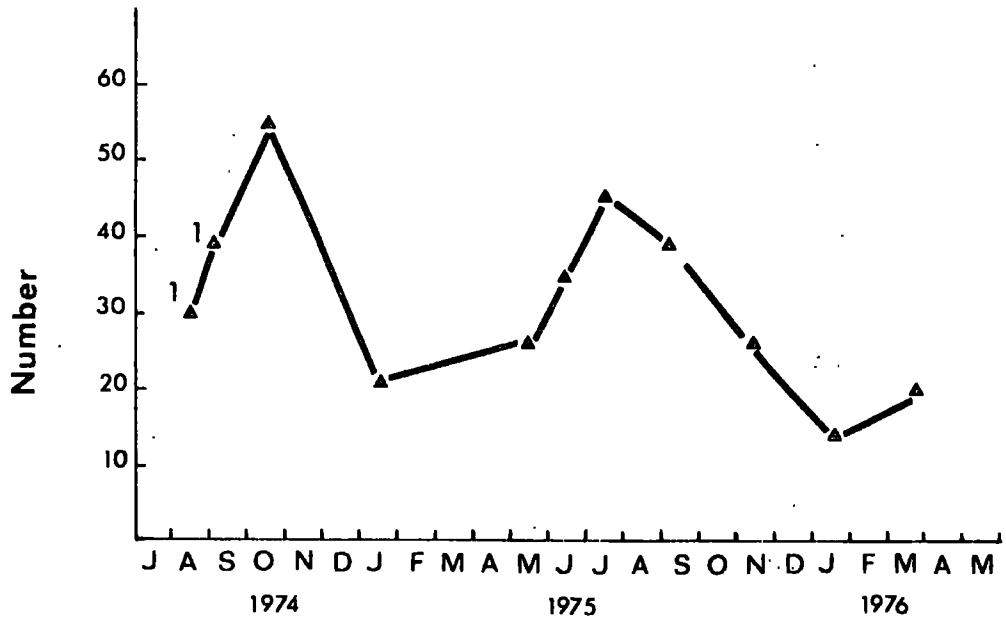
a) Clethrionomys

The best estimate of population size is presented graphically in Figure 2.5a for Castle Eden Dene and Figure 2.5b for Houghall Woods.

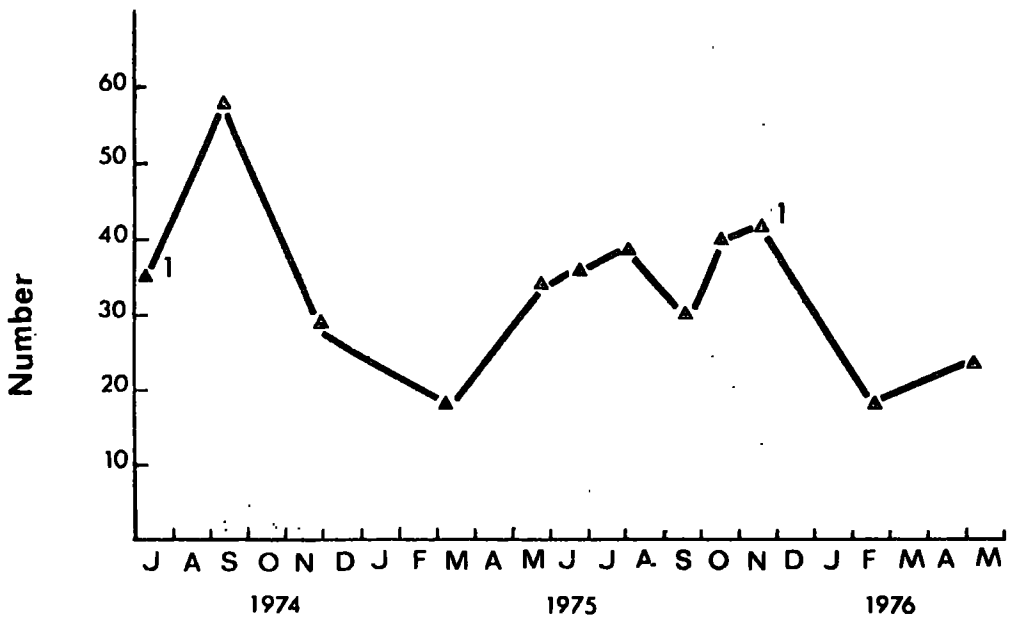
At both sites minimum numbers occurred during the first three months of the year with slightly higher numbers being captured in May although this was too early for the first litters to have appeared (see Discussion). In 3 cases out of 4 highest numbers were observed during the autumn, but at Castle Eden in 1975 the population reached a maximum in June and then declined, with poor recruitment of young animals observed in the September, and to a lesser extent the November, trappings. This decline may be at least partially a consequence of the early die back of the dogs mercury in the trapping area in that year. Although there was no such decline from an early maximum in Houghall Woods in 1975, the maximum population observed was rather lower than that of the previous year. There was a fall in numbers trapped in September followed by substantial recruitment in October and November giving a maximum during the latter month. A similar decline, attributable to poor recruitment and increased mort-

FIG 2.5 BEST ESTIMATE OF POPULATION SIZE

A. CLETHRIONOMYS CASTLE EDEN DENE



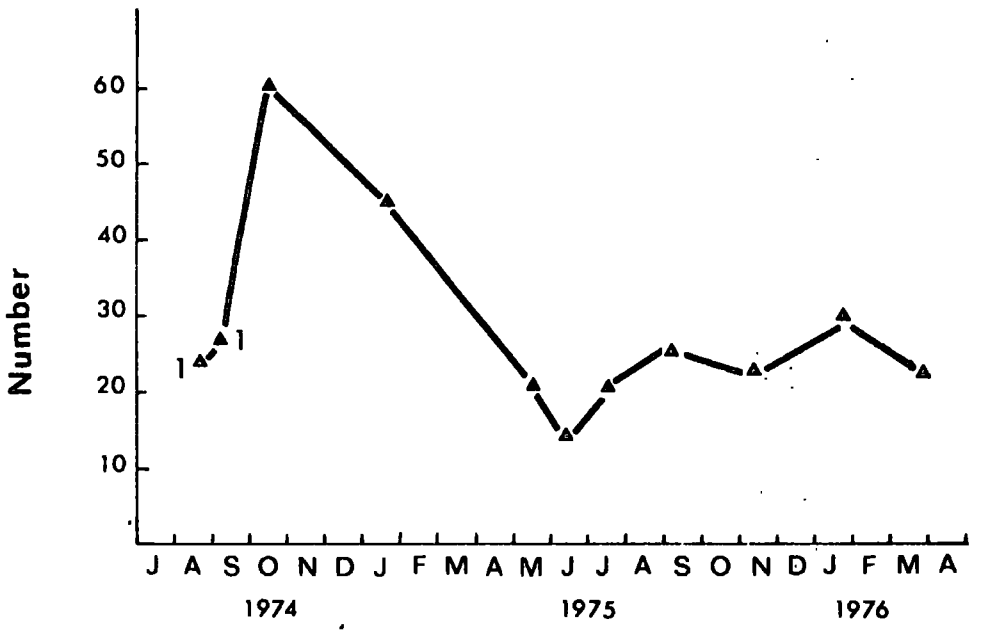
B. CLETHRIONOMYS HOUGHALL WOODS



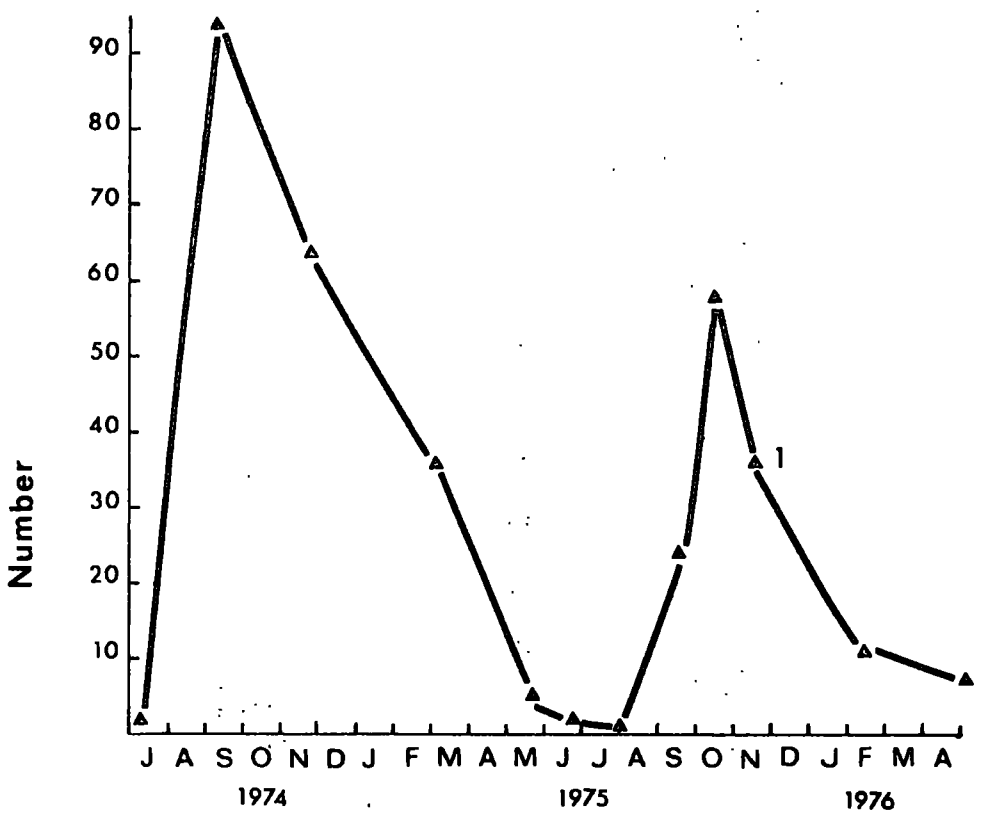
1 - Adjusted value, see Appendix 3.

FIG 2.6 'BEST ESTIMATE' OF POPULATION SIZE

A. APODEMUS CASTLE EDEN DENE



B. APODEMUS HOUGHALL WOODS



1 - Adjusted value, see Appendix 3.

ality, has been recorded by Flowerdew (pers. comm.) trapping in a fenland habitat.

b) Apodemus.

Best estimates of population size are presented graphically in Figure 2.6a for Castle Eden Dene and Figure 2.6b for Houghall Woods. Numbers generally showed the expected pattern of a maximum in autumn, a decline in spring to low numbers during the summer and a sharp increase during the autumn (Watts 1966, 1969).

At Houghall the trap revealed population size declined almost to zero during both summers of the study, a phenomenon also reported by other workers (Newson 1960; Tanton 1965; Crawley 1965, 1969; Smyth 1968) - see Discussion p. 104.

At Castle Eden the annual fluctuations in numbers, unlike those reported by Crawley (1965, 1969), were less extreme with only a four-fold difference between the maximum and minimum populations observed. Numbers showed a typical winter and spring decline, but a substantial number of individuals were present throughout the summer. In 1975 the autumn increase was small resulting in a population peak approximately half the size of that the previous autumn. The breeding performance of Apodemus was also poor in Houghall Woods during that summer and autumn.

At both sites 1974 was a more successful year than 1975 for both species. The difference between years was greater for Apodemus than Clethrionomys and was more apparent in Castle Eden than Houghall Woods. The relatively lower breeding success of both species in 1975 suggests that some external factor common to both populations was responsible, one possibility being the unusually dry summer of 1975. In support

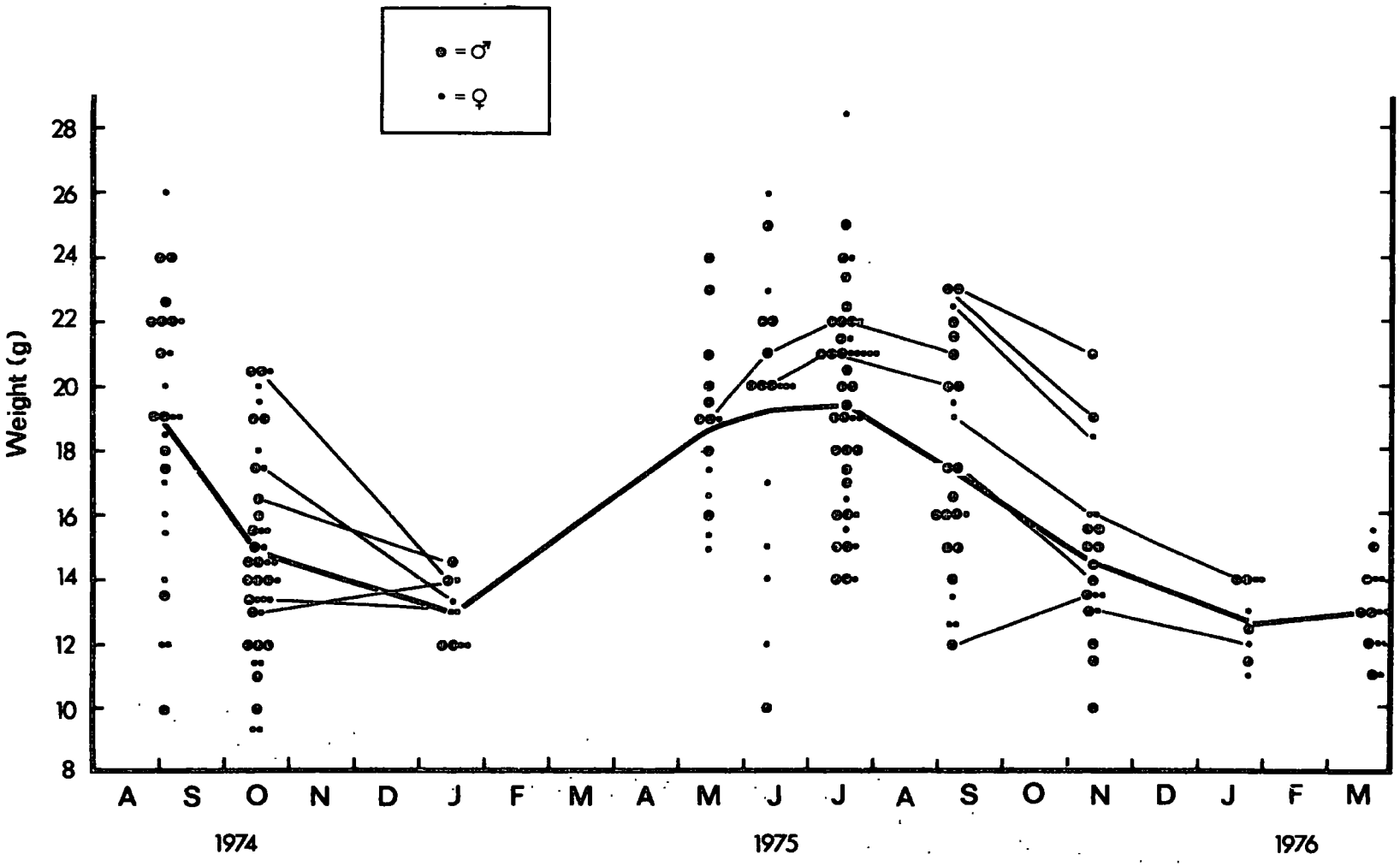


FIGURE 2.7 Weight distribution of Clethrionomys in Castle Eden Dene.
Each dot represents the weight of one individual. Thick line joins weight means (sexes combined). Thin lines show individual weight changes.

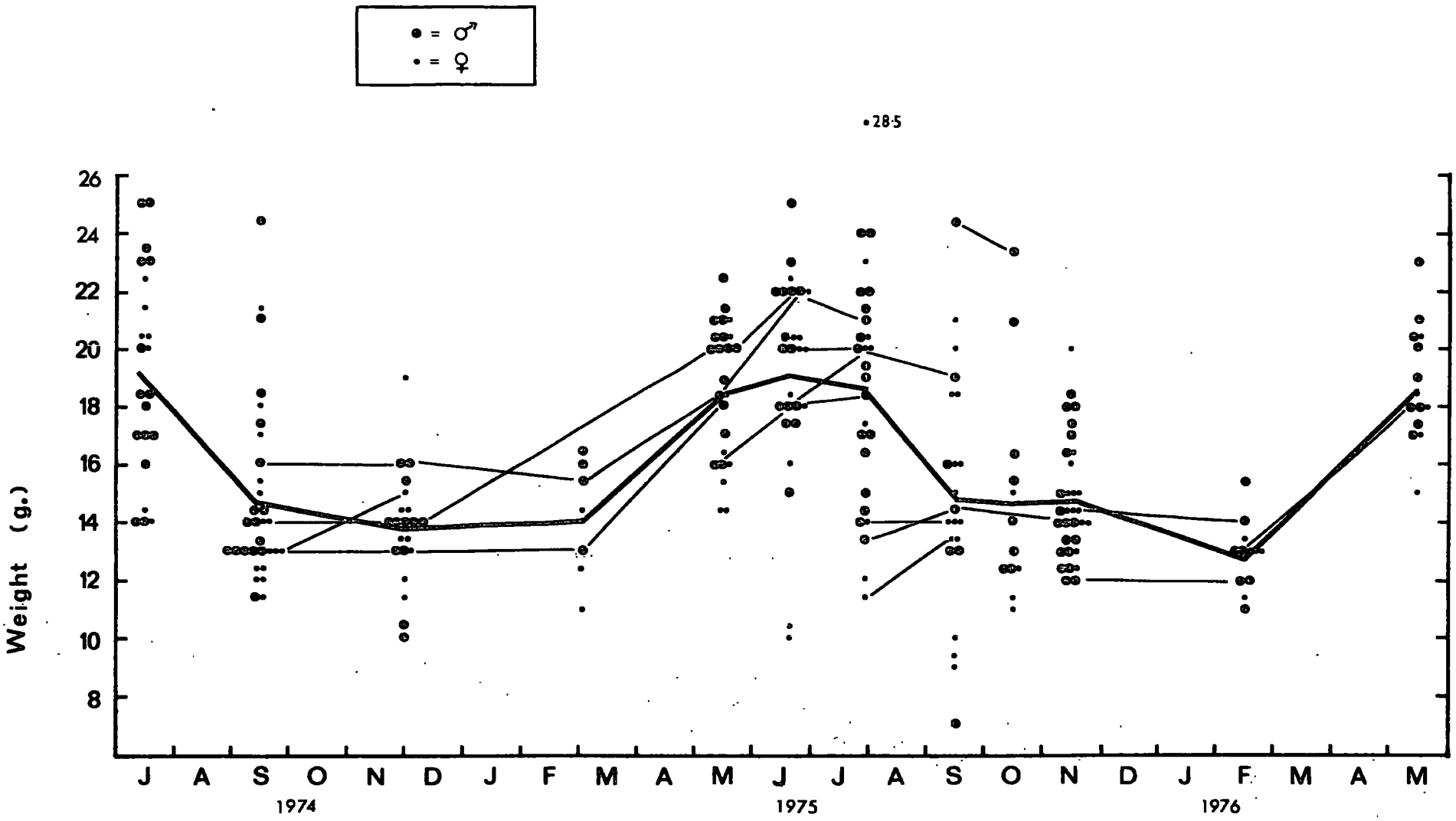


FIGURE 2.8 Weight distribution of Clethrionomys in Houghall Woods.
Each dot represents the weight of one individual. Thick line joins weight means (sexes combined). Thin lines show individual weight changes.

of this suggestion is the finding of Ashby (pers. comm.) that the proportion of water in stomach contents was markedly below normal in Clethrionomys in 1975, but normal in Apodemus which tends to eat drier food.

8. Age structure. Weights and lengths.

a) Clethrionomys.

i) Weight.

Although it is known that the pattern of growth of Clethrionomys is highly variable (Ashby 1967), weight is easily measured and provides useful information about both the general age structure of the population and the growth of individuals.

The weight distributions for males and females combined are shown in Figures 2.7 and 2.8 for Castle Eden Dene and Houghall Woods respectively. Both populations showed a weight distribution similar to that recorded by other workers (Ashby 1967; Flowerdew 1977). Mean weight was at a minimum during the winter (December-February), when there was little variation between members of the population. In April and May these overwintered individuals, the majority of which were subadults, increased in weight. There was considerable variation in the amount of weight gained but no evidence for any differential growth between the sexes. The pattern of winter and spring growth is illustrated in Figure 2.9 where the mean weight of all males which were subadults during the autumn has been plotted. This pattern of growth may be contrasted with that of Apodemus (see Discussion p. 92).

The population maintained a high mean weight during May, June and July, the continuing growth of older animals balancing the recruitment of juveniles during June and July. It was during these months that the heaviest individuals were found. During June it was possible to

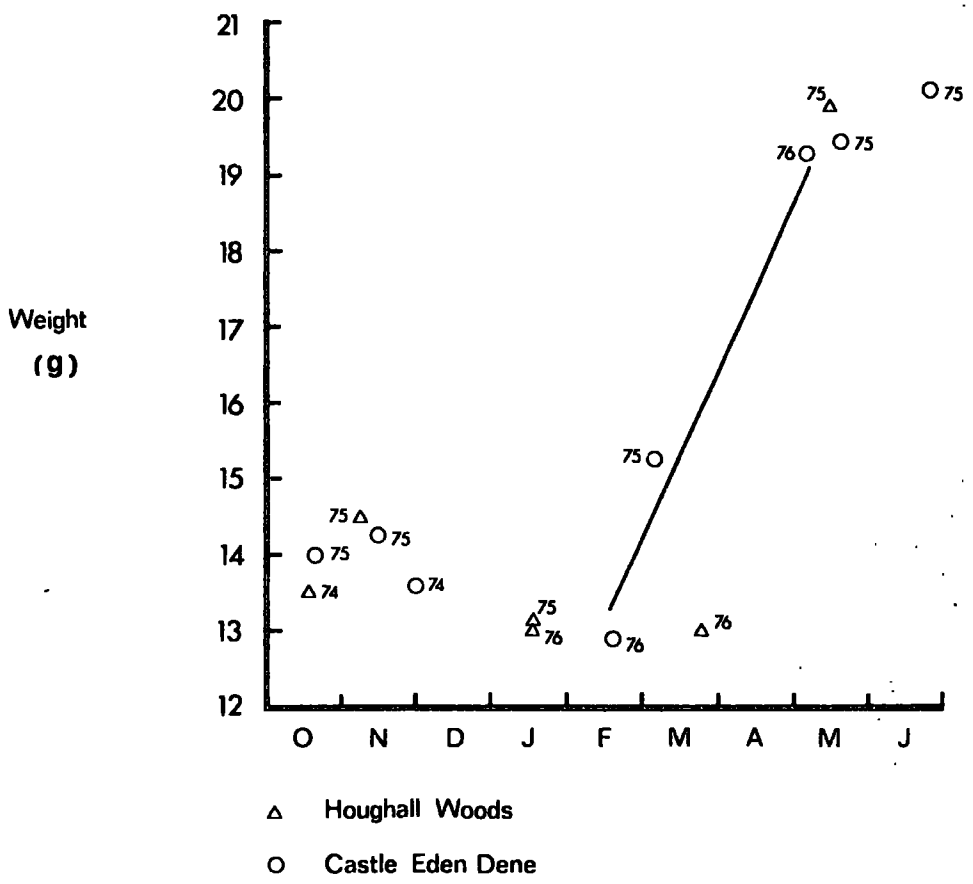


FIGURE 2.9 Winter and spring growth (weight increase) of Clethrionomys. Points show mean male weight at each trapping session. Late summer recruits only. Figures show year of observation. Line fitted by eye.

distinguish juveniles from adults by their weight being less than 14g. By July this was no longer possible as there was some overlap between the largest young, which grow rapidly at this time of year (Ashby 1967; Vincent 1974 for Arvicola terrestis) and the smallest adults. At this time the growth of juveniles is highly variable and provides a poor indicator of age (Ashby 1967).

After July the continuing disappearance of the previous season's large adults and the increasing proportion of young of the year, which never grew as heavy as overwintered adults, led to a decrease in both the mean and maximum weight of individuals captured. During the summer the variance of the weight distribution was high reflecting the diverse age structure and variable growth rate at that time.

The growth of autumn recruits appeared to be much slower than that of recruits earlier in the season. Over the winter none of the autumn recruits gained weight and many older individuals lost weight (see Figures 2.7 and 2.8) so that the mean individual weight declined slightly to a minimum in February or March. At this time the majority of animals weighed between 11 and 14g , though the lightest ones may have been in poor condition (Ashby pers.comm.).

ii) Length.

As noted by Jewell and Fullager (1966) the measurement of length is likely to be influenced by both the technique and experience of the researcher. The lengths recorded for Clethrionomys during the present study provide an example of this.

At Houghall the measurements in May and November of each year were taken by K.R.Ashby as part of a long term study (Ashby 1967 and pers.comm) while all others were taken by myself. The resulting length distribution (Figure 2.10) shows clear peaks above the general trend

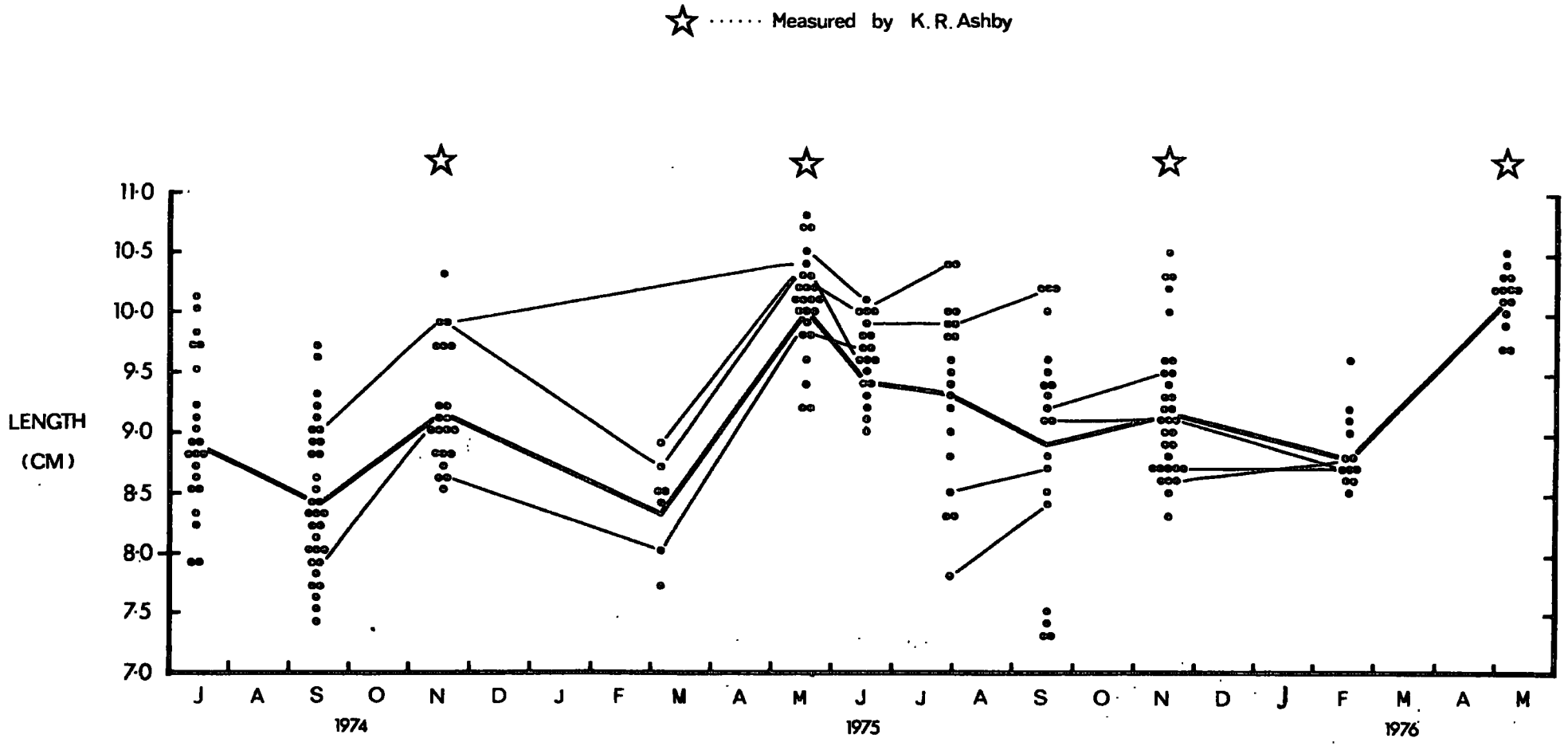


FIGURE 2.10 Length distribution of Clethrionomys in Houghall Woods. Each dot represents the length of one individual; thick line joins means.

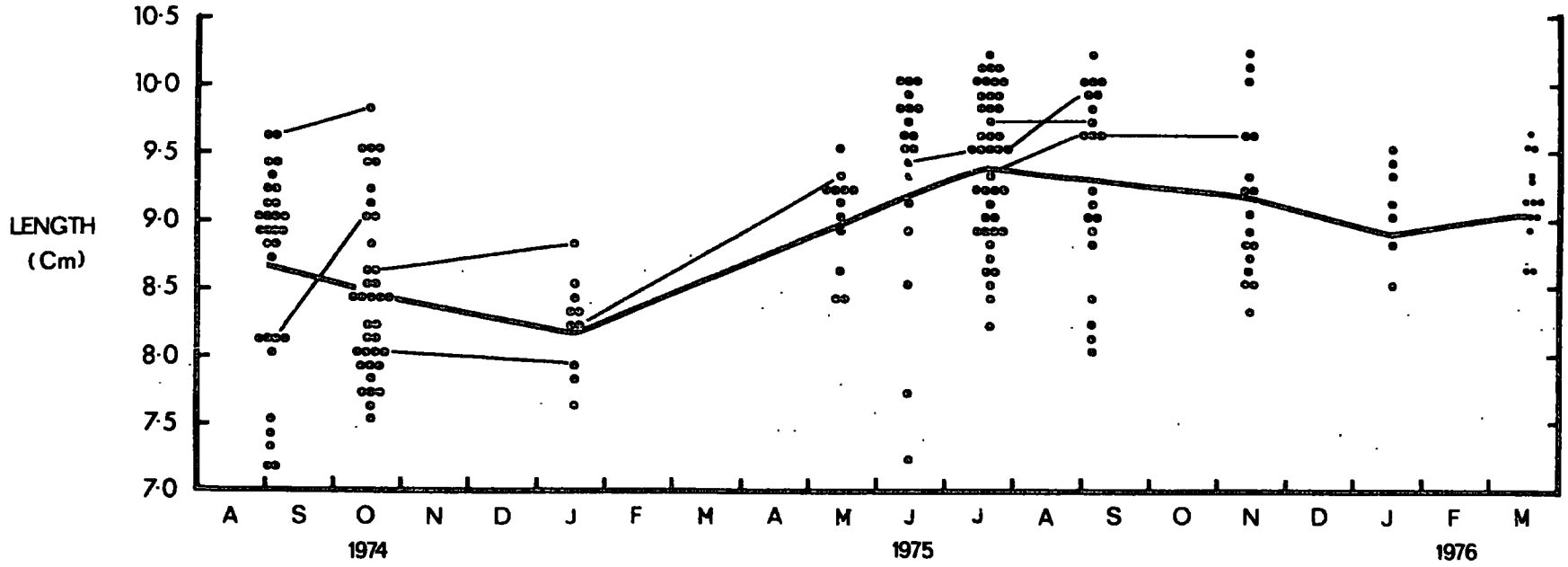


FIGURE 2.11 Length distribution of Clethrionomys in Castle Eden Dene. Each dot represents the length of one individual; thick line joins means.

at all times when Ashby was responsible for the measurements and thus presents rather a confused picture.

At Castle Eden all measurements (Figure 2.11) were taken by myself, resulting in much smoother changes in the mean between trapping sessions. There appears however to be a considerable difference between the lengths of the animals during the two winters; indeed a t-test shows both the September and January means for the two years to be significantly different at the 1% level. Such large differences have not been reported by other workers. It seems unlikely that a mean difference of more than 10mm. could be the result of demographic changes, particularly as the mean weights for the two winters were very similar. The apparent increase in length can therefore be attributed to a change in the measurement technique, presumably as the result of increasing experience. The same effect can be observed in the results from Houghall Woods but is masked by the variation resulting from the different techniques of Ashby and myself.

It must be concluded that, although length may provide a better indication of age and growth than weight, its sensitivity to the technique of the researcher makes it unsuitable for projects involving more than one person or for short term studies where the researcher starts with no previous experience of the technique.

b) Apodemus

i) Weight

Although the weight distributions of Apodemus (Figures 2.12 and 2.13) were generally similar to those of Clethrionomys there was one important difference. It appears, that, as reported by Ashby (1967), Apodemus continues to grow during the winter as the mean weight in late winter was higher than the mean weight the previous autumn. The

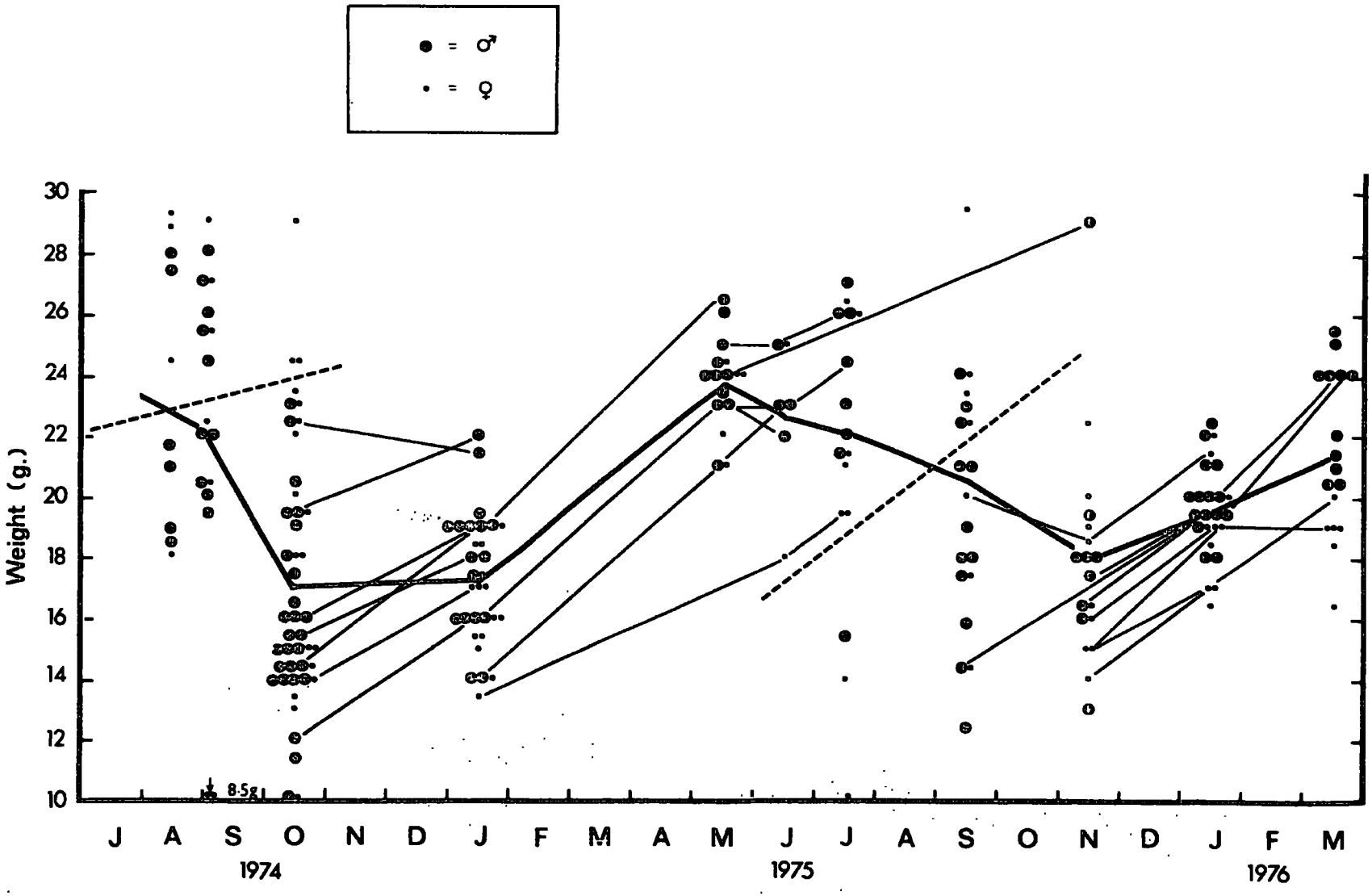


FIGURE 2.12 Weight distribution of Apodemus in Castle Eden Dene.
Each dot represents the weight of one individual. Thick line joins weight means (sexes combined). Thin lines show individual weight changes. Dotted line shows estimated division of year classes.

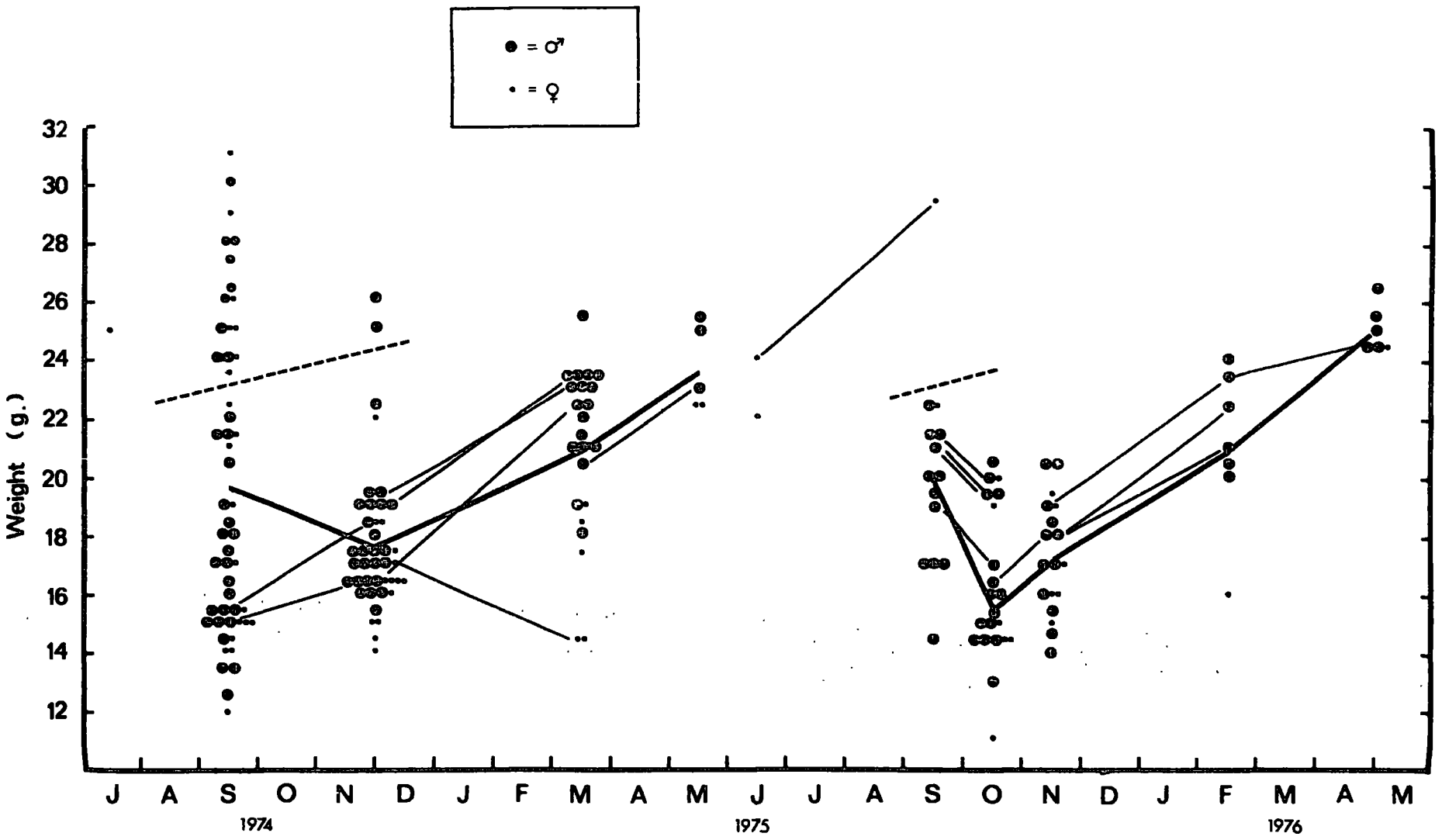


FIGURE 2.13 Weight distribution of Apodemus in Houghall Woods.
Each dot represents the weight of one individual. Thick line joins weight means (sexes combined).
Thin lines show individual weight changes. Dotted line shows estimated division of year classes.

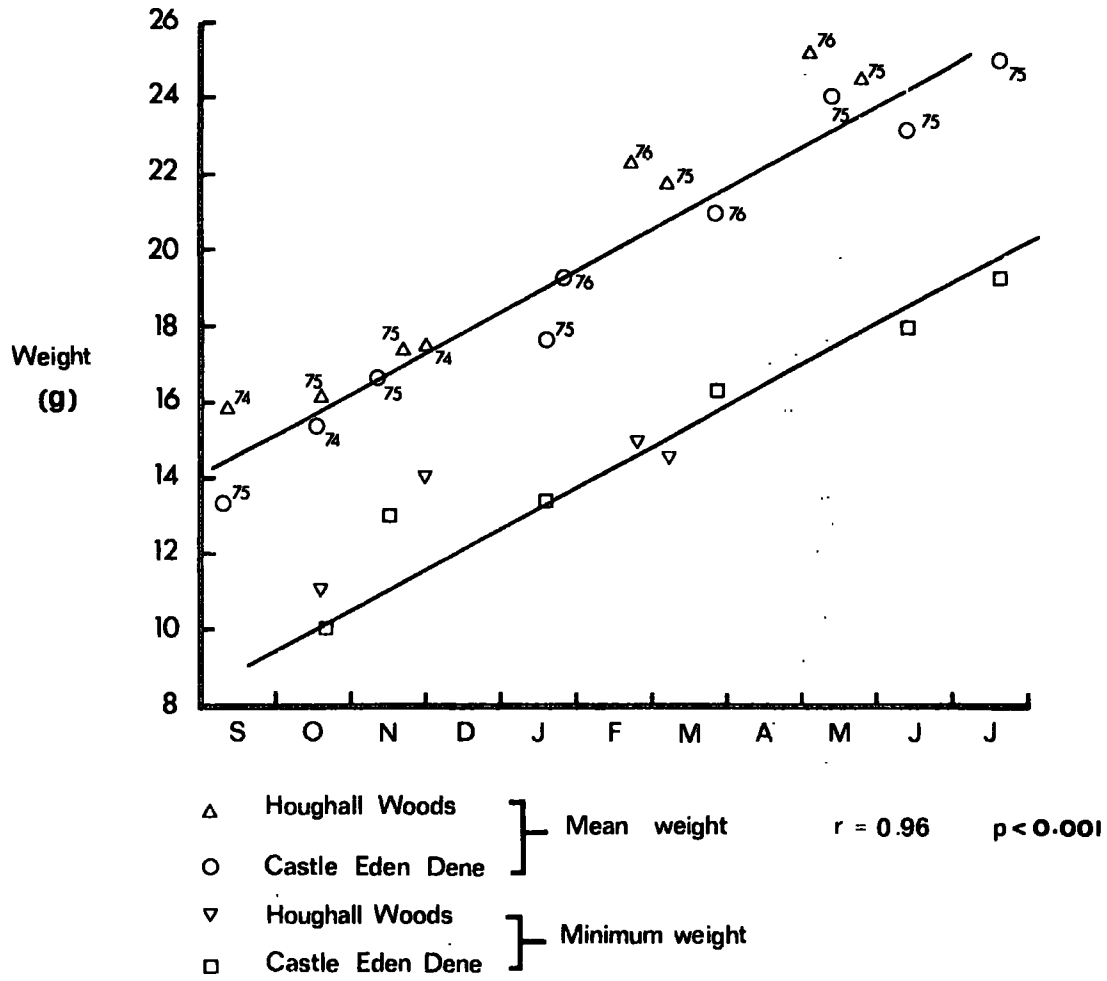


FIGURE 2.14 Winter and spring growth (weight increase) of Apodemus. Upper line shows mean male weight, lower line shows minimum male weight. Late summer recruits only. Figures show year of observation.
Growth rate = 1.125g./30 days

rate of weight increase appears to be linear from September till June. By plotting the mean individual weight, excluding any overwintered adults, against time for the two seasons (Figure 2.14) it was possible to estimate the growth rate over this season as approximately 1.3g per month.

The maximum mean weight occurred early in the summer, after which it declined as large,old animals died and juveniles were recruited. At Houghall few animals were caught during the summer but the difference in mean weight between May and September 1975, about 3.5g., was very similar to that at Castle Eden over the same period.

The first juveniles were captured in July at Castle Eden, when they could be distinguished by this low body weight. At this time the smallest adult weighed 19.5g , which is large for the minimum adult weight (Ashby 1967). Later recruits were of a diversity of body weights suggesting a wider range of ages. In September 1975 all adults known to have overwintered at Castle Eden Dene weighed 24g or more but there was no clear distinction between these and the largest young of the year. By November only one overwintered animal, a very large male survived. If all the remaining animals alive in November are assumed to be young of the year then a line suggesting the most likely division between year classes may be drawn on Figure 2.12.

If the criterion of a weight greater than 24g in September is used to divide year classes in Houghall Woods it is apparent that the large influx of September 1974 contained both overwintered adults and young of the year. There was a diverse weight distribution at this time and the use of probability paper showed a disjunction between 22 and 24 g supporting the contention that individuals above and below this weight belonged to different year classes. By November the majority of the older, heavier individuals had disappeared and there

was further recruitment of lighter animals leading to a drop in mean weight.

In the autumn of 1975 the situation was rather different. The influx was not nearly so large and appeared to consist only of animals born that summer, the only old adult being one that was present in the woods in June. The mean weight was similar to that in September 1974 but its variance was lower indicating that the age structure was much more restricted. The September influx was supplemented in October by the recruitment of more light, young individuals resulting in a sharp drop in mean weight.

9. Breeding

a) Classification of breeding status.

Adult animals were classified into breeding or non-breeding condition by the presence or absence of scrotal testes in the male and by the appearance of the vagina, pregnancy or lactation in the female. During the months of June to September any individual not in breeding condition which was not a juvenile could be assumed to be a subadult which had not yet bred. Juveniles could be distinguished both by their low weight and by their pelage which remains greyer and fluffier for up to 20 days after leaving the nest (Ashby 1967).

b) Clethrionomys.

The proportions of adults in breeding condition at each trapping session are shown in Table 2.10. Overwintered adults came into breeding condition between March and May and survivors remained in breeding condition throughout the summer. At both study sites many of the unmarked animals captured in July were in breeding condition. While a few of the largest, weighing up to 21g. for males and 19g. for

	Castle Eden Dene							Houghall Woods						
	♂		♀		Subadult			♂		♀		Subadult		
	B	NB	B	NB[1]	♂	♀	Juv.	B	NB	B	NB[1]	♂	♀	Juvenile
July'74	-	-	-	-	-	-	-	12	0	6	0	2	1	2
Aug'74	7	0	5	0	0	0	0	-	-	-	-	-	-	-
Sept'74	11	0	8	6	3	2	6	6	0	3	-	8	9	4
Oct'74	3	4	3	7	13	8	9	-	-	-	-	-	-	-
Nov'74	-	-	-	-	-	-	-	3	1	4	0	11	6	0
Jan'75	0	0	0	2	5	7	0	-	-	-	-	-	-	-
Mar'75	-	-	-	-	-	-	-	0	2	0	0	2	5	0
May'75	11	0	11	0	2	0	0	17	0	8	0	0	0	0
June'75	11	0	8	0	-	0	5	15	0	9	0	0	0	2
July'75	20	0	13	0	4	2	6	13	0	9	0	2	0	3
Sept'75	10	0	4	-	7	4	3	3	0	6	0	3	5	4
Oct'75	-	-	-	-	-	-	-	3	0	0	0	4	5	0
Nov'75	0	2	0	2	8	6	0	4	3	2	0	12	13	0
Jan'76	0	0	0	0	4	5	0	-	-	-	-	-	-	-
Feb'76	-	-	-	-	-	-	-	0	0	0	0	7	5	0
Mar'76	1	0	0	0	7	6	0	-	-	-	-	-	-	-
May'76	-	-	-	-	-	-	-	8	0	4	0	0	0	0

1 - individuals whose weight and trapping record shows that they have previously been in breeding condition.
Subadults are young non-breeding individuals which have lost the juvenile pelage.

B = individuals in breeding condition.

NB = individuals not in breeding condition.

TABLE 2.10. Breeding condition of Clethrionomys at the two study areas.

	Castle Eden Dene							Houghall Woods						
	♂		♀		Subadult			♂		♀		Subadult		
	B	NB	B	NB[1]	♂	♀	Juv.	B	NB	B	NB[1]	♂	♀	Juvenile
July'74	-	-	-	-	-	-	-	0	0	1	0	0	0	0
Aug'74	6	0	4	0	0	0	0	-	-	-	-	-	-	-
Sept'74	14	0	5	0	0	0	4	23	0	22	0	10	6	0
Oct'74	6	0	11	0	21	7	5	-	-	-	-	-	-	-
Nov'74	-	-	-	-	-	-	-	2	1	2	0	22	12	0
Jan'75	2	0	0	0	15	12	4	-	-	-	-	-	-	-
Mar'75	-	-	-	-	-	-	-	14	0	1	0	4	5	0
May'75	11	0	6	0	0	0	0	3	0	0	0	0	0	0
June'75	7	0	4	0	0	0	0	0	0	2	0	0	0	0
July'75	6	0	8	0	2	0	1	-	-	-	-	-	-	-
Sept'75	8	0	8	0	6	3	0	8	0	2	0	5	0	0
Oct'75	-	-	-	-	-	-	-	4	3	2	2	16	7	0
Nov'75	1	0	1	1	8	9	0	0	1	0	0	12	8	0
Jan'76	5	0	0	0	10	10	0	-	-	-	-	-	-	-
Feb'76	-	-	-	-	-	-	-	3	0	0	0	2	1	0
Mar'76	9	2	1	0	0	5	0	-	-	-	-	-	-	-
May'76	-	-	-	-	-	-	-	5	0	1	0	0	0	0

1 - individuals whose weight and trapping record shows they have previously been in breeding condition.
Subadults are young non-breeding individuals which have lost the juvenile pelage.

B = individuals in breeding condition.

NB = individuals in non-breeding condition.

TABLE 2.11 Breeding condition of Apodemus at the two study areas.

females, could have been overwintered adults many must have been individuals from the first litters which had matured rapidly. Perforate females were captured with body weights as low as 14g. indicating that they were coming into breeding condition within two or three weeks of being weaned. From July onwards there was a decline in the proportion of recruits in breeding condition (Table 2.10) as an increasing proportion showed delayed maturation in order to overwinter as subadults. None of the October recruits was in breeding condition (data from Castle Eden 1974 and Houghall 1975) although a few of the older resident males still had scrotal or partially scrotal testes.

c. Apodemus.

The proportions of adults in breeding condition are shown in Table 2.11.

Males came into breeding condition during February and March. By March 60% of males had scrotal testes (N = 30, data from both sites combined) and 33% partially scrotal testes but only 2 out of 11 females were in breeding condition. One of these had a perforated vagina and the other had recently mated, as evidenced by the presence of a vaginal plug. Although sample sizes were small the results support the findings of Elton (1942) that females come into breeding condition a little later than males.

At Castle Eden in 1975 the first juveniles appeared in the traps in July, when only 2 were trapped despite the presence of 6 pregnant females during May. The obviously pregnant condition of these females at that time suggests that, as the young can leave the nest 20-25 days after birth (Ashby 1967), the first juveniles should have appeared in June. A similar failure to catch many juveniles during early summer has been recorded by other workers and has been interpreted as being the result of either poor survival (Watts 1969; Flowerdew 1971, 1977)

or trap avoidance (Tanton 1965; Gliwicz 1970; see Discussion p.95).

There is good evidence for believing that breeding continued late into the winter at both sites in 1974-5. In October 7 pregnant females were captured at Castle Eden and 3 females were in breeding condition in Houghall Woods. The unexpectedly large January cohort at Castle Eden contained four juveniles so, as the juvenile coat is retained for about 50-65 days from birth (Ashby 1967), these must have been born in November.

There was no evidence for such late breeding in 1975-6 as no individual was in breeding condition and the weights of the recruits during late autumn suggest that they were two or three months old.

10. Survival.

a) Calculation of survival rates.

Although Jolly's method of calculating population size gives an estimate of survival (see p. 29) this suffers from the same inaccuracies as those already discussed for the estimation of numbers. All survival estimates have therefore been calculated from the actual survival of marked animals using the calendar of captures. In order that comparisons might be made both between seasons and sites these estimates have been standardised to give mean survival per month of 30 days. Standardisation was accomplished by assuming that the number surviving followed a logarithmic decline. That this is a reasonable assumption is shown by Ashby's (1967) estimates of numbers known to be alive at intervals after marking, which show an approximately logarithmic decline. Deviations from this assumption may occur however, particularly during the breeding season.

Because survival is measured as the actual survival of marked animals and only a proportion of the population was sampled on each occasion this may be considered to be minimum rate of survival.

Tamarin and Krebs (1969), who used a similar technique, considered that because of this, rates should not be analysed using conventional statistical tests and that any difference in survival rates greater than 0.10 over 2 weeks (equivalent to 0.14 over one month) should be considered biologically significant. A similar convention has been applied here; differences in survival of greater than 0.14 are considered to be biologically significant and statistical tests have only been used to emphasise large differences in survival rates.

Mean monthly survival rates for both species at both study sites are given in Tables 2.12 and 2.13 and presented graphically in Figures 2.15 and 2.16. Standard errors for the uncorrected estimates were calculated from the binomial formula. Data for males and females have been combined throughout to provide adequate sample sizes, as Crawley (1965, 1970) found no consistent or significant differences between the survival rate of the two sexes.

b) Clethrionomys.

If the rate of disappearance of marked Clethrionomys from the trapping area is assumed to follow a logarithmic decline, the weighted mean monthly probability of survival over the study period as a whole was 0.717 at Houghall and 0.698 at Castle Eden indicating mean residence times of 2.1 and 1.9 months respectively. There is therefore reasonable agreement between survival rates calculated for the two sites.

The pattern of variation in survival rates was similar to that reported by other workers (Crawley 1965, 1970; Flowerdew 1977). The difference between survival during the period January-June and the period July-October was significant at the 1% level at both sites. Changes in survival rates during either of these periods were not significant. The year may therefore be divided into a period of relatively high survival during the winter and early spring, when individuals were not in breeding condition, and a period of relatively

Month of trapping sessions	Interval since previous trapping (months)	Nett survival (± s.e.) since previous trapping	Estimated monthly survival
Aug'74	-	-	-
Sept'74	1.00	.500±.14	.500
Oct'74	1.33	.594±.08	.676
Jan'75	2.97	.295±.06	.662
May'75	3.87	.666±.10	.899
June'75	0.93	.809±.08	.796
July'75	1.07	.640±.09	.658
Sept'75	1.61	.390±.07	.557
Nov'75	1.20	.366±.10	.433
Jan'76	2.27	.400±.11	.710
Mar'76	2.03	.500±.13	.711

TABLE 2.12a Estimated survival of marked Clethrionomys between trapping sessions at Castle Eden.

Month of trapping session	Interval since previous trapping (months)	Nett survival (± s.e.) since previous trapping	Estimated monthly survival
Aug'74	-	-	-
Sept'74	1.00	.500±.158	.500
Oct'74	1.33	.381±.097	.484
Jan'75	2.97	.423±.070	.748
May'75	3.87	.405±.076	.791
June'75	0.93	.714±.101	.697
July'75	1.07	.666±.126	.682
Sept'75	1.61	.277±.102	.451
Nov'75	1.20	.292±.117	.358
Jan'76	2.27	.600±.104	.889
Mar'76	2.03	.478±.100	.692

TABLE 2.12b Estimated survival of marked Apodemus between trapping sessions at Castle Eden.

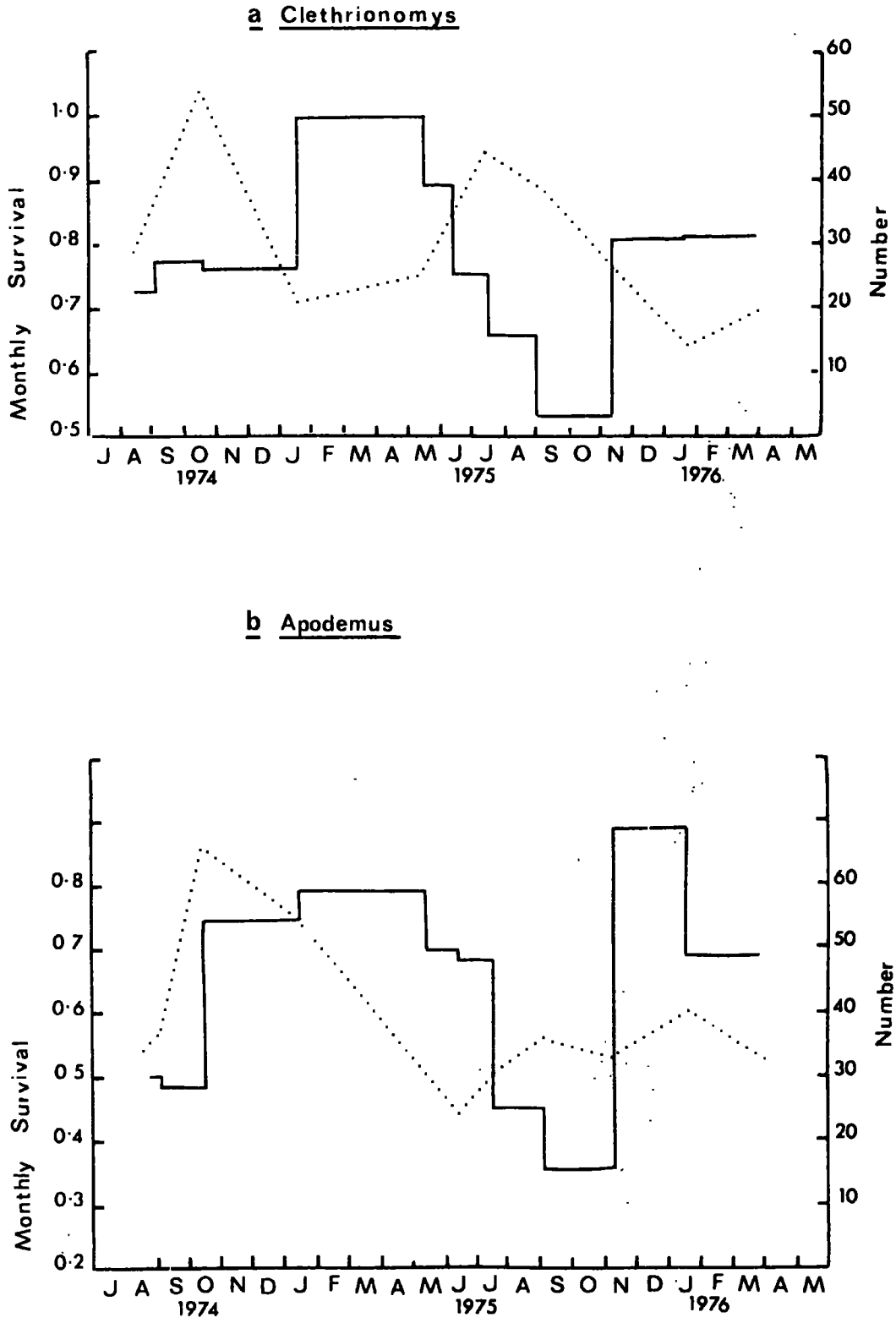


FIGURE 2.15 Survival of marked Clethrionomys and Apodemus in Castle Eden Dene.
Solid line shows mean monthly survival of all cohorts estimated from calendar of cantures, dotted line shows best estimate of population size.

Month of trapping session	Interval since previous trapping (months)	Nett survival (± s.e.) since previous trapping	Estimated monthly survival
July'74	-	-	-
Sept'74	2.26	.429±.103	.688
Nov'74	2.57	.393±.081	.695
Mar'75	3.13	.579±.099	.839
May'75	2.57	.857±.082	.942
June'75	1.13	.529±.100	.570
July'75	1.13	.545±.094	.585
Sept'75	1.60	.500±.094	.649
Oct'75	0.90	.620±.095	.587
Nov'75	1.10	.700±.058	.710
Feb'76	3.00	.294±.075	.582
May'76	2.50	.400±.120	.693

TABLE 2.13a Estimated survival of marked Clethrionomys between trapping sessions at Houghall.

Month of trapping session	Intervals since previous trapping (months)	Nett survival (± s.e.) since previous trapping	Estimated monthly survival
July'74	-	-	-
Sept'74	-	-	-
Nov'74	2.57	.224±.060	.558
Mar'75	3.13	.389±.075	.740
May'75	2.57	.130±.069	.452
June'75	1.13	.200±.180	.241
July'75	1.13	-	-
Sept'75	1.60	-	-
Oct'75	0.90	.643±.130	.612
Nov'75	1.10	.276±.074	.309
Feb'76	3.00	.318±.097	.683
May'76	2.50	.375±.160	.675

TABLE 2.13b Estimated survival of marked Apodemus between trapping sessions at Houghall

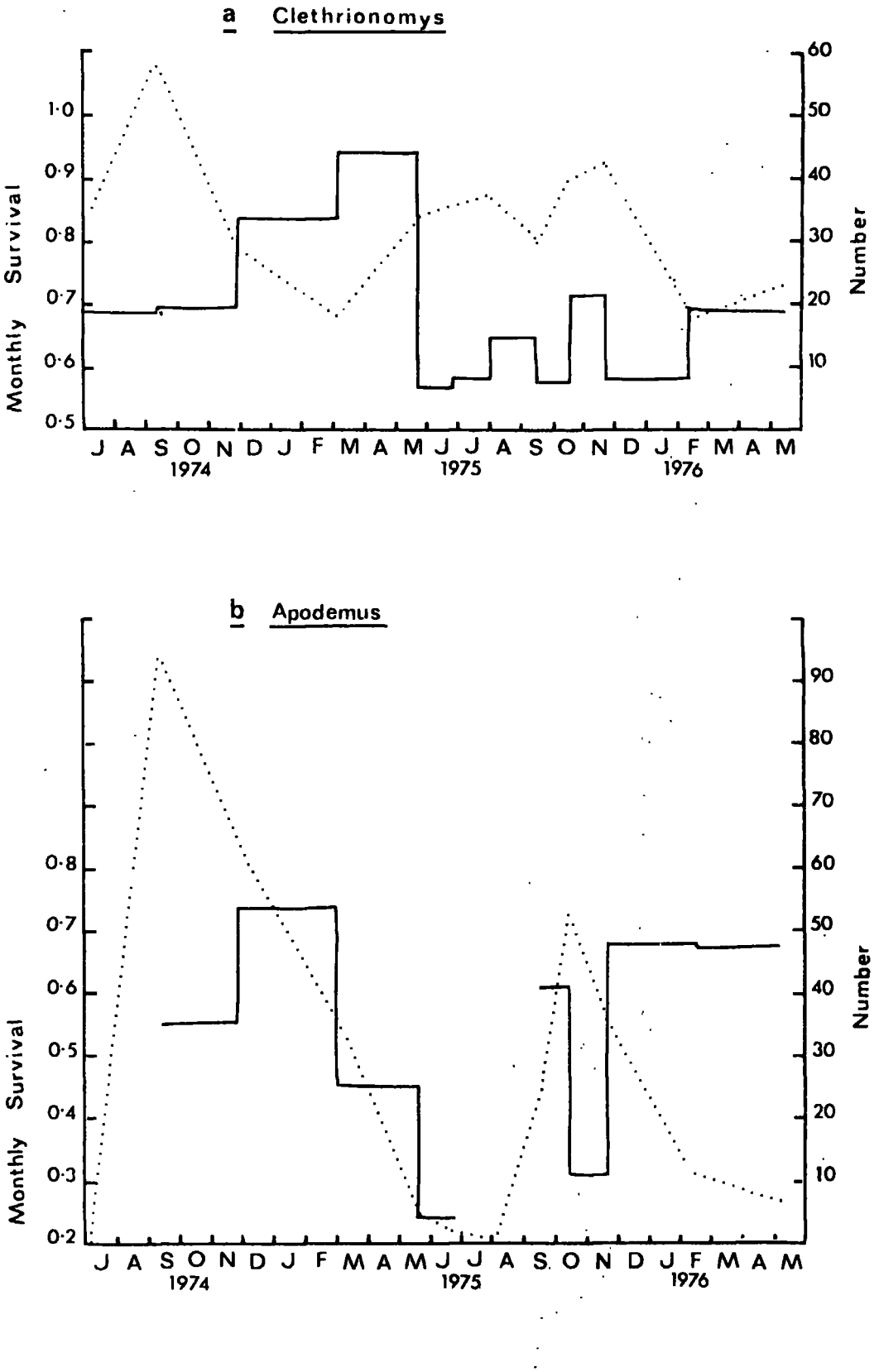


FIGURE 2.16 Survival of marked Clethrionomys and Apodemus in Houghall Woods.
Solid line shows mean monthly survival of all cohorts estimated from calendar of captures, dotted line shows best estimate of population size.

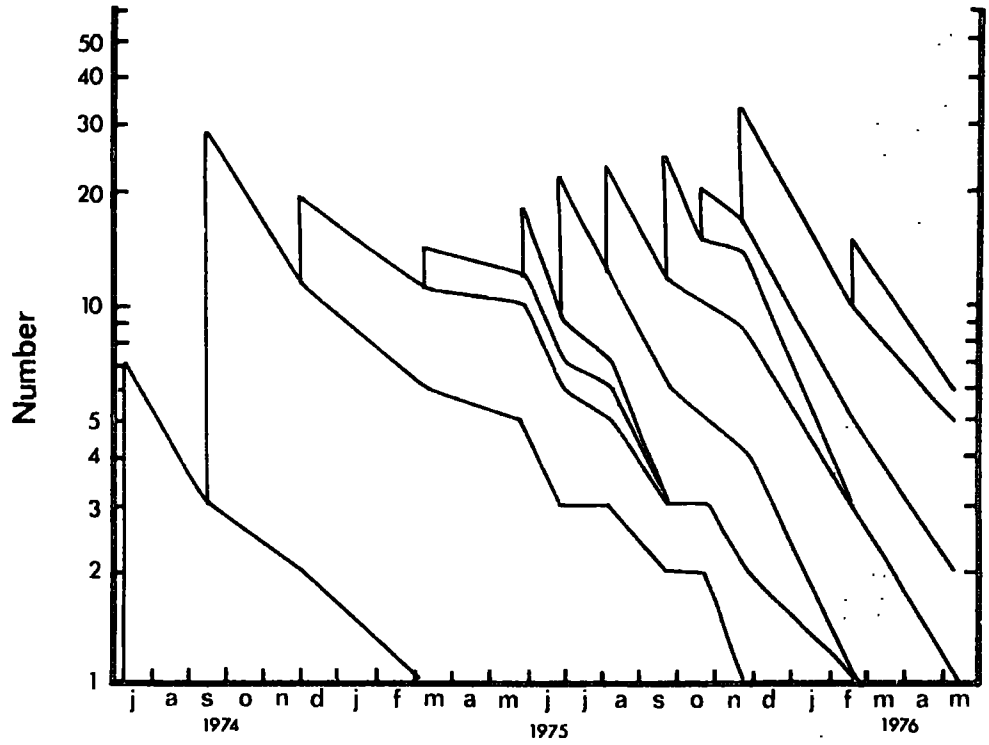
low survival whilst breeding was in progress. Though juveniles certainly contribute increasingly to the reduction in mean survival of the population during the breeding season, at both sites survival declined during May and June before any juveniles were captured (see Discussion).

The estimates of survival calculated from the recapture of marked individuals give no indication of any differences in survival between different age groups. In general, sample sizes were not large enough to calculate survival for different age groups separately, but the survival of the individuals marked at each trapping session is shown in Figure 2.17.

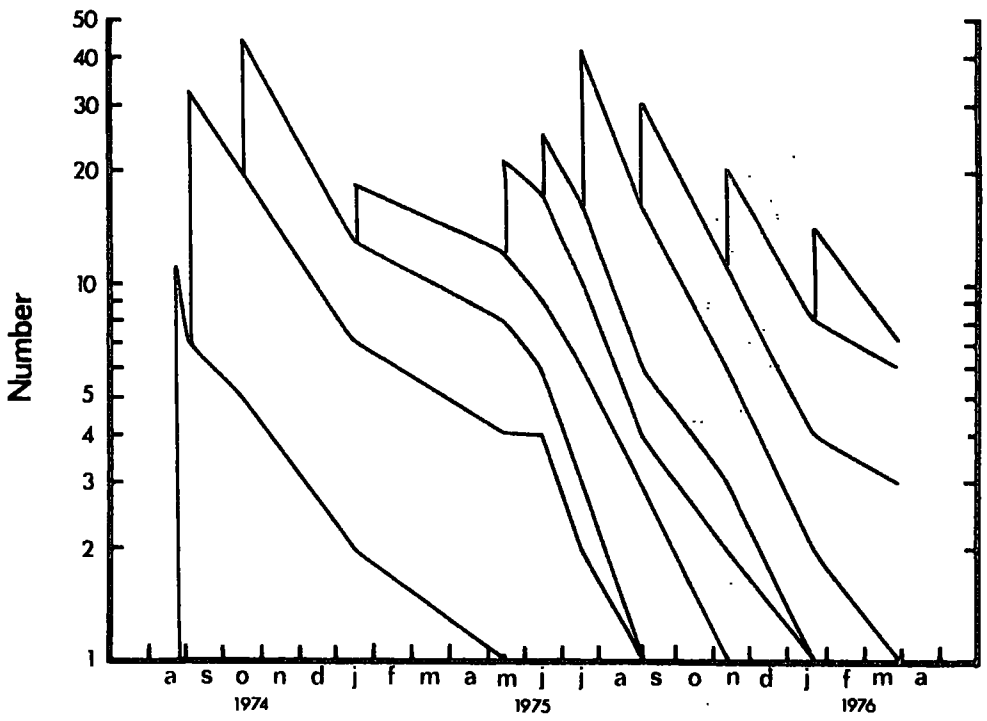
c.) Apodemus.

The weighted mean monthly probability of survival of marked individuals of this species was 0.677 at Castle Eden and 0.581 at Houghall, indiciating mean residence times of 1.8 and 1.3 months respectively.

In Houghall Woods the very large number of recruits in September 1974 showed initially poor survival of both old and young marked individuals, but survival improved over the winter months. Coincident with the start of the breeding season in March it declined to a very low level as the overwintered population disappeared from the woods (see Discussion p.111). At this time survival was significantly lower ($p<0.01$) here than in Castle Eden Dene. Survival at Houghall in September 1975 was similar to that in 1974, but there was a rapid decline during October and November due to the poor survival of the October cohort which constituted the majority of the population. During the winter months (November-February) survival at Houghall was similar during the two years though the actual number of animals present in spring was much lower during 1976 resulting in a large standard error for the survival estimate over this period. The pattern of survival at Houghall was thus one of moderate and variable survival

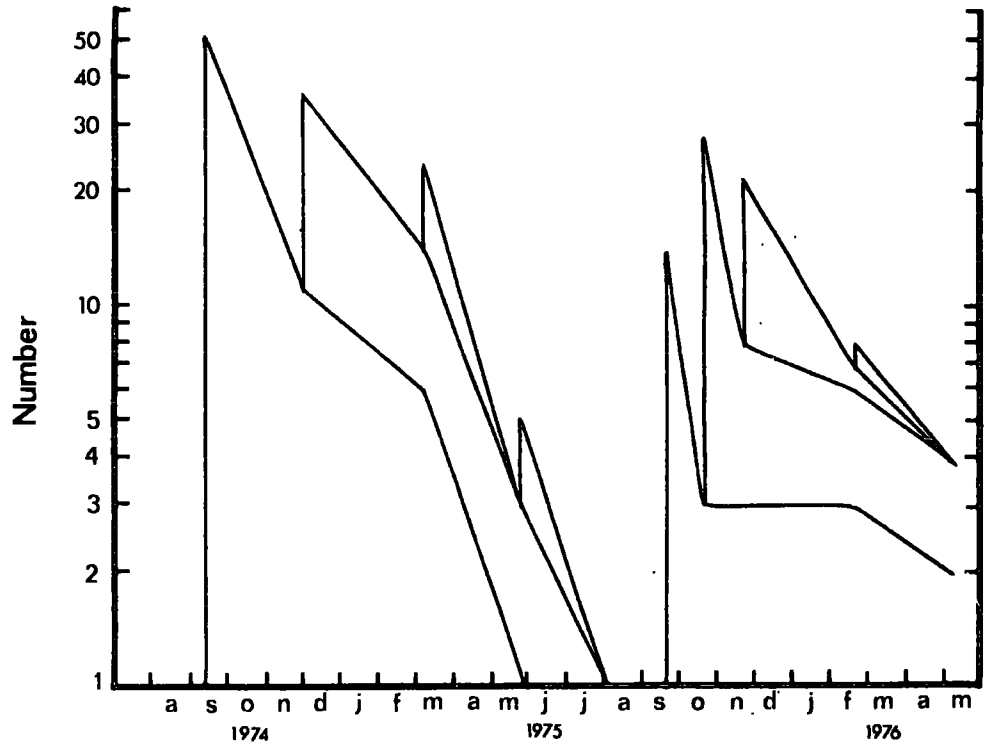


A. HOUGHALL WOODS

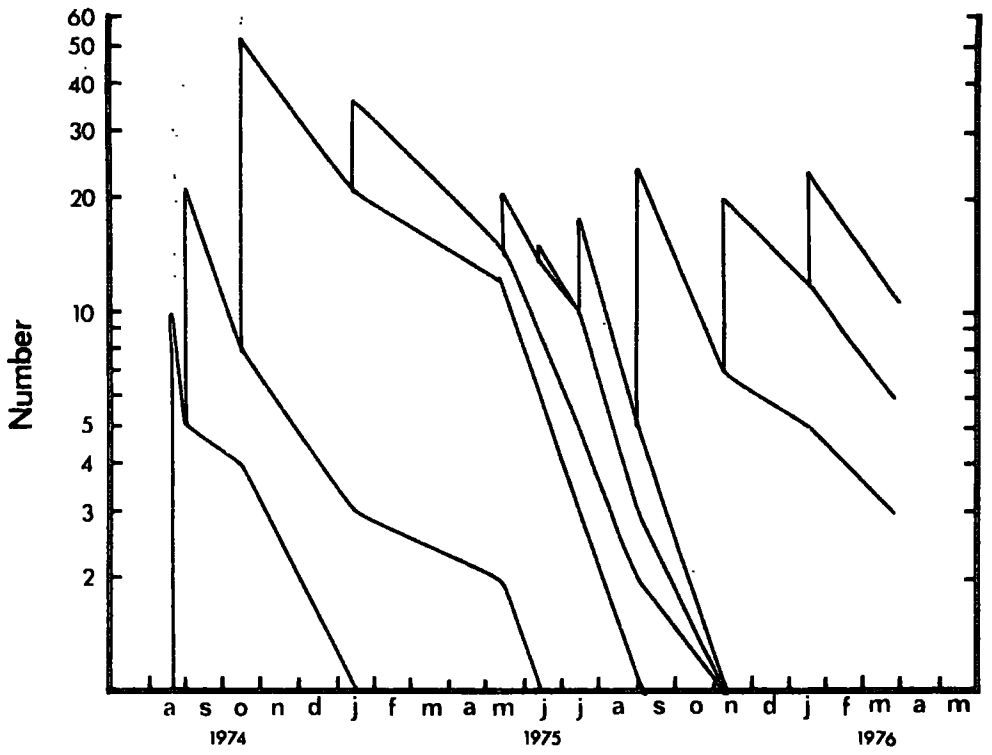


B. CASTLE EDEN DENE

FIGURE 2.17. Survival of Clethrionomys marked at each trapping session in Castle Eden Dene and Houghall Woods.



A. HOUGHALL WOODS



B CASTLE EDEN DENE

FIGURE 2.18 Survival of Apodemus marked at each trapping session in Castle Eden Dene and Houghall Woods.

during the autumn increase in numbers, high survival over the winter and rapidly decreasing survival at the start of the breeding season.

In Castle Eden Dene, where a number of individuals were present throughout the summer and the autumn increase was not so large, the data were more complete. During both years survival was high during the winter and fell slightly at the start of the breeding season. Data from 1974 and 1975 show that during the period of juvenile recruitment, which lasted from July till October or November survival was rather low. Once juvenile recruitment had ceased, survival improved rapidly and remained high until the start of the following breeding season.

As with Clethrionomys sample sizes were not generally large enough to separate the survival of different age groups but the survival of all the individuals marked at each trapping session is shown in Figure 2.18.

11. Recruitment.

a) Estimation of recruitment.

The total number of unmarked but trappable animals present at the time of each trapping session may be estimated by multiplying the actual number of unmarked captures by the reciprocal of the figure derived on p.28 for the proportion of the population sampled. On the figures showing recruitment (Figures 2.19 and 2.20) the actual recruitment is shown as a solid vertical line and the estimated total number of previously unmarked individuals by a dot above it. The recruitment in September 1974 at Castle Eden has been adjusted to account for the previous trapping being carried out on only half the grid; the estimated number of recruits shown assumes that older animals were present on both halves of the grid in equal proportions.

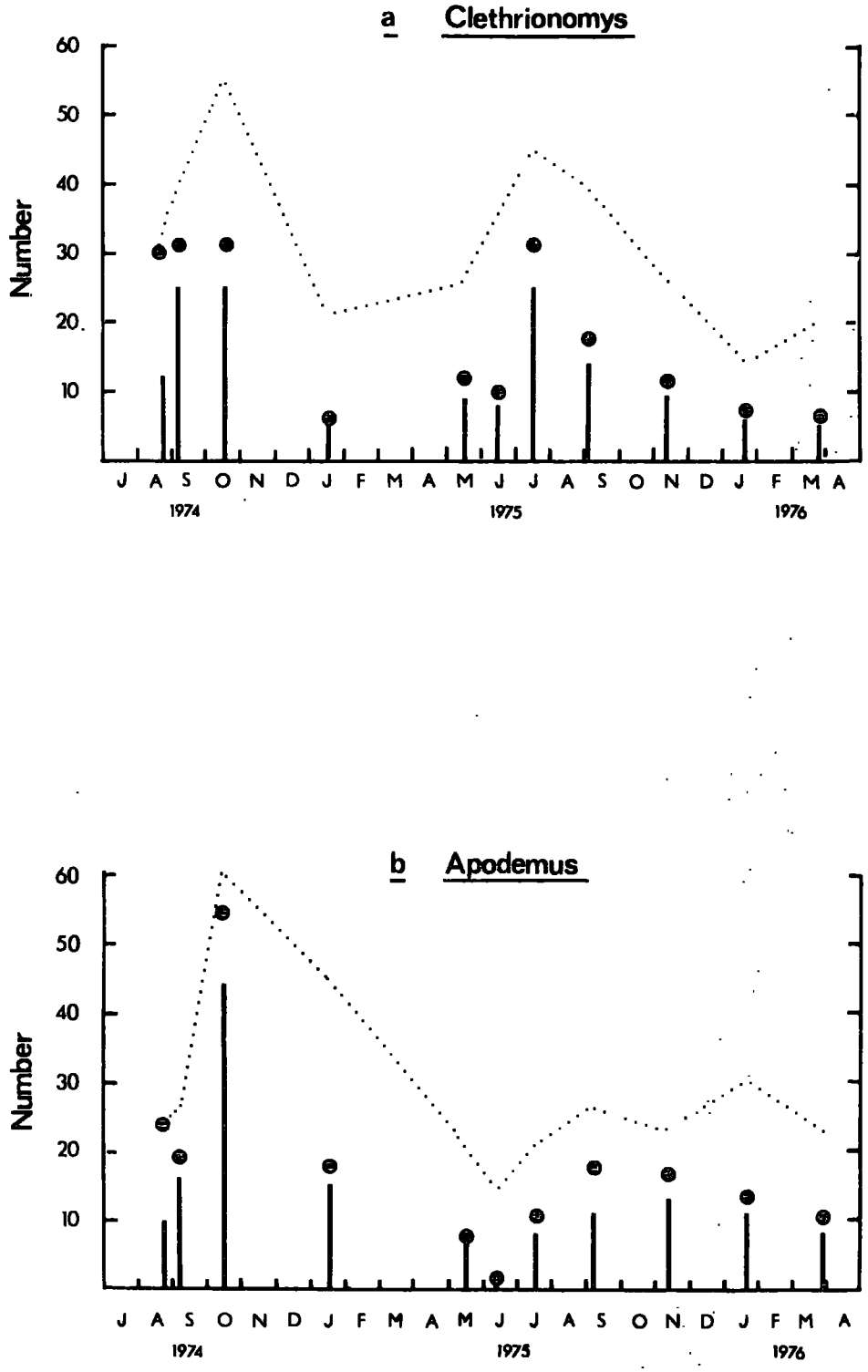


FIGURE 2.19 Recruitment of Clethrionomys and Apodemus at each trapping session in Castle Eden Dene. Solid vertical shows actual recruitment, dot shows recruitment estimated from the 'constant proportion seen' method. Dotted line shows best estimate of population size.

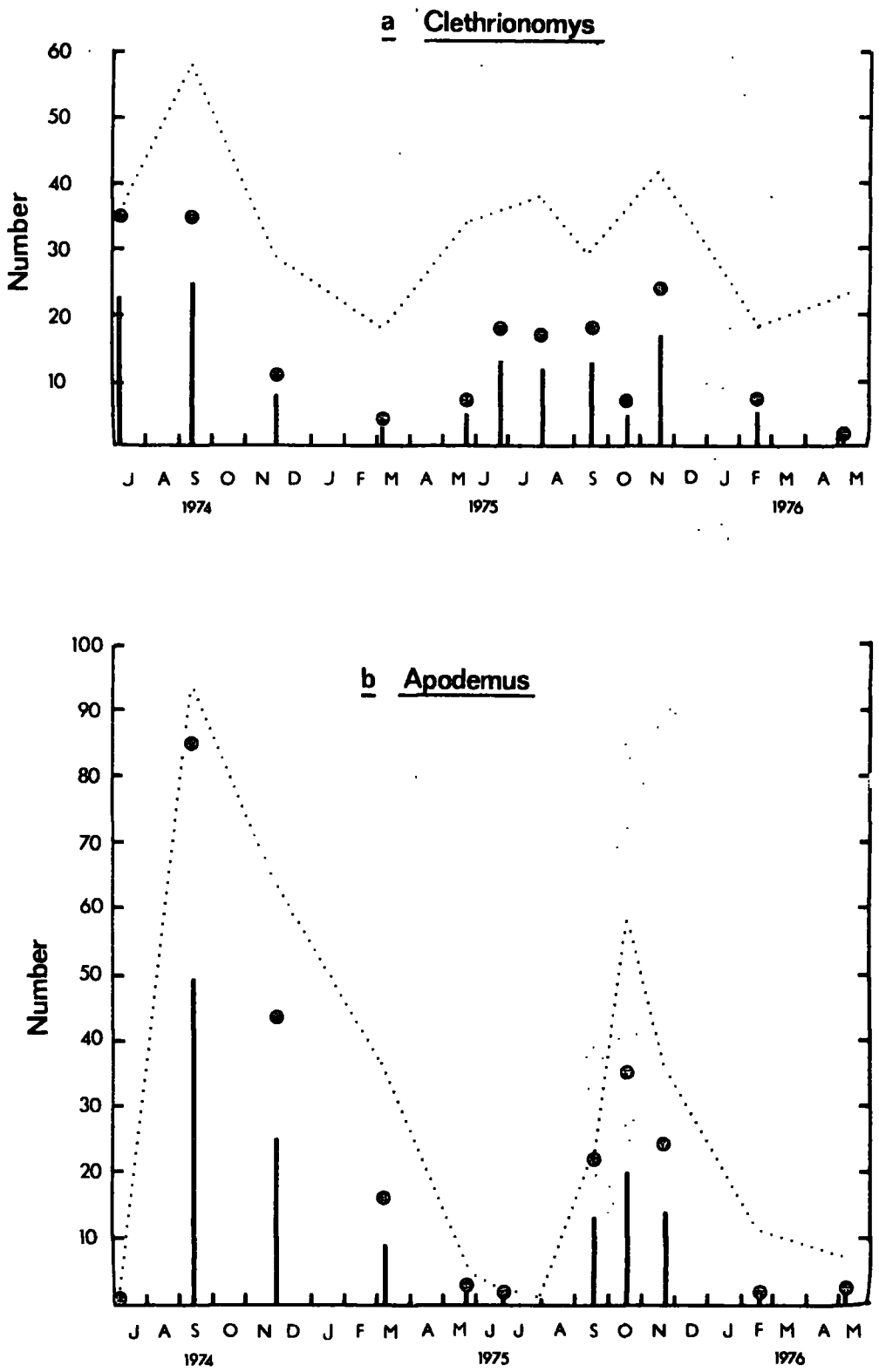


FIGURE 2.20 Recruitment of Clethrionomys and Apodemus at each trapping session in Houghall Woods. Solid vertical shows actual recruitment, dot shows recruitment estimated from the 'constant proportion seen' method. Dotted line shows best estimate of population size.

Whether the number of unmarked juveniles and subadults captured at any one trapping session during the breeding season can be accounted for by reproduction on the trapping area since the previous trapping, may be examined by calculating a ratio of young recruits at one trapping session to adult females at the previous trapping session. This is in effect the number of recruits that each female would have to produce to account for the calculated recruitment. The mean litter size of both Clethrionomys and Apodemus is about 4 per month (Brambell and Rowlands 1936; Baker 1930) so ratios much in excess of this figure, assuming there was one litter every three or four weeks, would suggest that immigration had taken place. The ratio of recruits to females for trapping sessions during the breeding season is shown in Tables 2.14a and b for Clethrionomys and Tables 2.15a and b for Apodemus.

b) Clethrionomys.

The estimated and actual numbers of recruits at the two study areas are presented graphically in Figures 2.19a and 1.20a.

Both populations showed the expected general pattern of high recruitment during the breeding season and low recruitment during the non-breeding season but there are differences in detail both between populations and between years. These will be referred to in more detail in the discussion. At both sites the amount of recruitment during the autumn could be accounted for by reproduction in the trapping area. The high ratio of recruits to females in September 1974 at both sites can be attributed to the fact that this was the first trapping session to cover the full study area.

c) Apodemus.

The actual and estimated number of recruits at the two study areas are presented graphically in Figures 2.19b and 2.20b.

Date	No. of non-adult recruits[1]	No. of breeding ♀♀ at previous trapping[2]	ratio recruits:females
Sept'74	11	5	2.2
Oct'74	25	8	3.1
July'75	12	8	1.5
Sept'75	14	13	1.0
Nov'75	9	4	2.2

TABLE 2.14a Ratio of Clethrionomys recruits to females during the breeding season at Castle Eden.

Date	No. of non-adult recruits[1]	No. of breeding ♀♀ at previous trapping[2]	ratio recruits:females
Sept'74	21	6	3.5
Nov'74	8	3	2.7
July'75	5	9	0.55
Sept'75	12	9	1.3
Oct'75	5	6	0.6
Nov'75	17	6(in Sept.)	2.8

TABLE 2.14b Ratio of Clethrionomys recruits to females during the breeding season at Houghall.

1. - the actual number of juvenile or subadult individuals captured.

2. - calculated from the calendar of captures.

Date	No. of non-adult recruits[1]	No. of breeding ♀♀ at previous trapping[2]	ratio recruits:females
Sept'74	4	4	1.0
Oct'74	33	5	6.6
July'75	2	4	0.5
Sept'75	9	8	1.1
Nov'75	13	8	1.6

TABLE 2.15a Ratio of Apodemus recruits to females during the breeding season at Castle Eden.

Date	No. of non-adult recruits[1]	No. of breeding ♀♀ at previous trapping[2]	ratio recruits:females
Sept'74	16	1	16
Nov'74	25	22	1.1
Sept'75	5	0	high
Oct'75	20	2	10
Nov'75	14	2	7

TABLE 2.15b Ratio of Apodemus recruits to females during the breeding season at Houghall.

1. - the actual number of juvenile or subadult individuals captured.

2. - calculated from the calendar of captures.

At Houghall Woods the number of recruits in September of both years was too large to be accounted for by reproduction on the trapping area and an alternative explanation must be sought (see Discussion p104). The age structure of the October and November recruits suggests that they too were not the result of reproduction on the trapping area but were of the same age as the September recruits.

At Castle Eden the estimated number of recruits in October 1974 was likewise too large to have been derived from breeding during August and September and may be partly the result of immigration (see Discussion p. 104). The same explanation is not required for the autumn of 1975 when recruitment was much lower and the population size did not rise to a typical autumn peak. Recruitment was on a similar scale in January of both years. Whilst the presence of juveniles in January 1975 confirmed that winter breeding had taken place (see p. 64) no young individuals were captured in January 1976. It must be concluded that the recruits in the latter year were animals born the previous autumn and, as there was little discrepancy between the estimated and known number of animals present in November, the majority must have been either immigrants or individuals which had not entered the trappable population by November.

D. Vegetation and Distribution.

1. General.

The relationship between the density of ground vegetation and the distribution of *Clethrionomys* and *Apodemus* has been well documented (Evans 1942; Brown 1954; Morris 1955; Delany 1957; Newson 1960; Crawley 1965; Ashby 1967). *Clethrionomys* has been shown to have a strong preference for areas of thick ground cover and a positive correlation between the number of voles captured at a particular trap site

and the density of vegetation around that site has been reported (Crawley 1965; Ashby and Crawley 1969). Little preference appears to be shown for any particular type of vegetation as long as it provides adequate cover (Crawley 1965).

By contrast Apodemus has been reported as either being distributed randomly with respect to cover (Newson 1960; Ashby 1967; Southern and Lowe 1968) or showing a preference for open areas (Delany 1961; Crawley 1965) with some evidence that elevated positions on small scale irregularities of topography are favoured (Ashby 1967).

Seasonal changes in the density of ground vegetation are likely to influence the distribution of the two species to some degree and are therefore an important factor in any ecological study. The relationship between the density of cover and the number of captures at a particular trap location was investigated by subjectively assigning the density of ground cover around a particular trap location to a place on a scale ranked from 1 - 8 such that

1 = very poor cover, much of the area bare.

2 = poor cover, large bare areas with discrete clumps of vegetation.

3 = some bare areas, numerous discrete clumps of vegetation.

4 = no bare areas but rather thin cover.

5 = a few areas of good cover, the remainder poor cover but not bare.

6 = good cover over the majority of the area.

7 = good cover over the whole area.

8 = very good cover, usually thick bramble, covering the entire area.

If each trap, regardless of its position, has the same chance of capturing a rodent, the distribution of captures would form a Poisson (random) distribution. If some trap positions were more attractive to rodents the distribution of captures would tend towards a negative binomial (aggregated) distribution. An index to the pattern of dispersion of captures may be calculated by examining the ratio of the

variance to the mean. This should equal 1 if the distribution is random, be less than 1 if the distribution is regular, and be more than 1 if the distribution is aggregated. There are many ways of calculating such an index but the one suggested by Morisita (1962) has been widely used and has the advantage of being relatively independent of the type of distribution, the size of the mean and the number of samples (Southwood 1966).

The index, I_g, is calculated from -

$$I_g = \frac{N \sum x^2 - \sum x}{(\sum x)^2 - \sum x}$$

where

N = the number of trapping points

Σx = the sum of all captures

x = the number of individuals in each sample.

The significance from any departure from a random distribution may be calculated from the F-ratio.

$$F_o = \frac{I_g (\Sigma x - 1) + N - \Sigma x}{N - 1}$$

with N-1 and ∞ degrees of freedom.

While this index is relatively independent of sample size the large number of traps with zero catches at individual trapping periods together with small sample sizes at some times of the year would have led to inaccuracies. It was essential therefore to combine data from a number of trapping sessions. The way in which this was done is explained in the following sections.

2. Castle Eden Dene.

The importance of dog's mercury as a seasonal source of cover is shown by the fact that at 44 trap positions it provided at least 75%

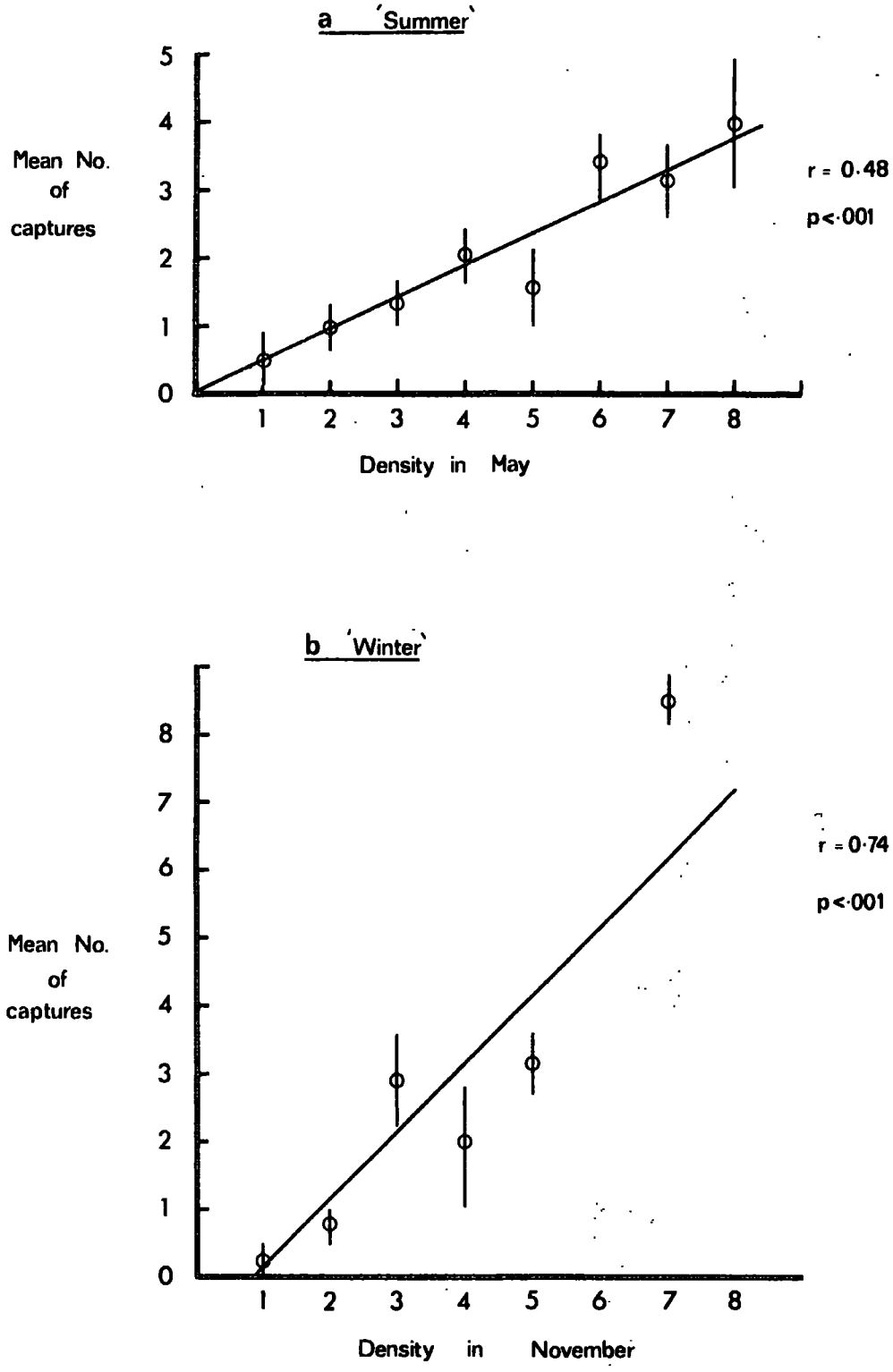


FIGURE 2.21 Relationship between mean number of captures of Clethrionomys and vegetation density during 'summer' and 'winter at Castle Eden. Vegetation densities during May and November were typical of those during the following months.

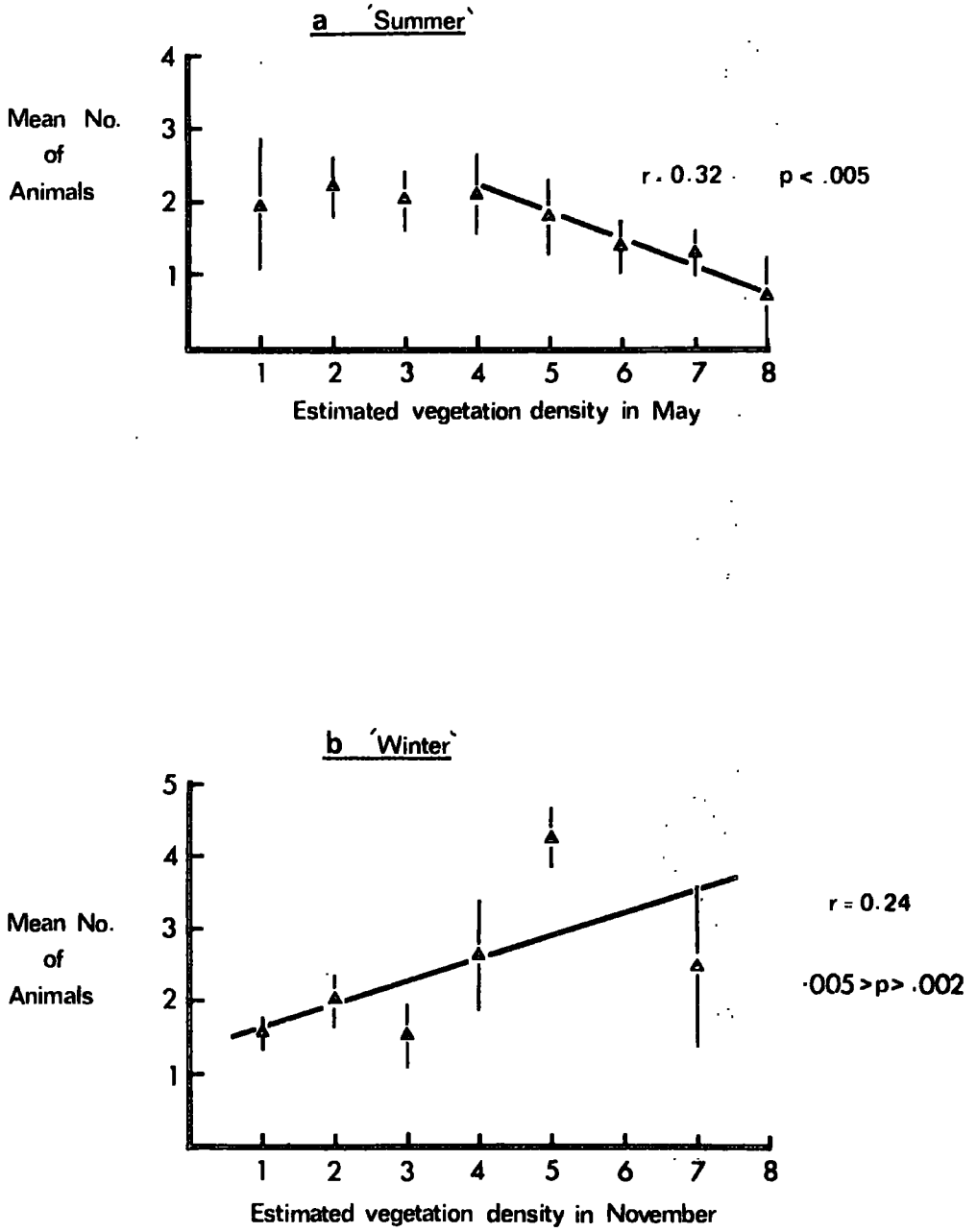


FIGURE 2.22 Relationship between mean number of captures of Apodemus and vegetation density during 'summer' and 'winter' at Castle Eden.
Vegetation densities during May and November were typical of those during the following months.

of the available cover during its growing season. Once the dog's mercury had withered away many of these areas were poorly covered.

The availability of cover was documented by dividing the year into two periods and assessing the amount of cover present at each site for each period. One period ran from 1st November - 30th April, when little dog's mercury was visible. This will be referred to as 'winter'. The other period ran from 1st May - 31st October when the dog's mercury provided cover and will be referred to as 'summer'. Cover was assessed for a 10m. square centred on each trap position during November and May with the results shown in Table 2.16.

Density Class	'Winter' Frequency(%)	'Summer' Frequency(%)
1	48	2
2	31	14
3	10	21
4	3	16
5	6	7
6	0	11
7	2	20
8	0	9

Table 2.16 The frequency of vegetation cover density classes in Castle Eden Dene.

For each period the number of animals caught at each trap position and the cover index of that position were used to calculate the mean number of individuals captured in each density of vegetation. The results of this analysis are shown in Figure 2.21 for Clethrionomys and Figure 2.22 for Apodemus.

There is a good correlation between distribution and vegetation for Clethrionomys during both periods which is highly significant ($p < 0.001$). The gradient of the 'winter' regression is significantly

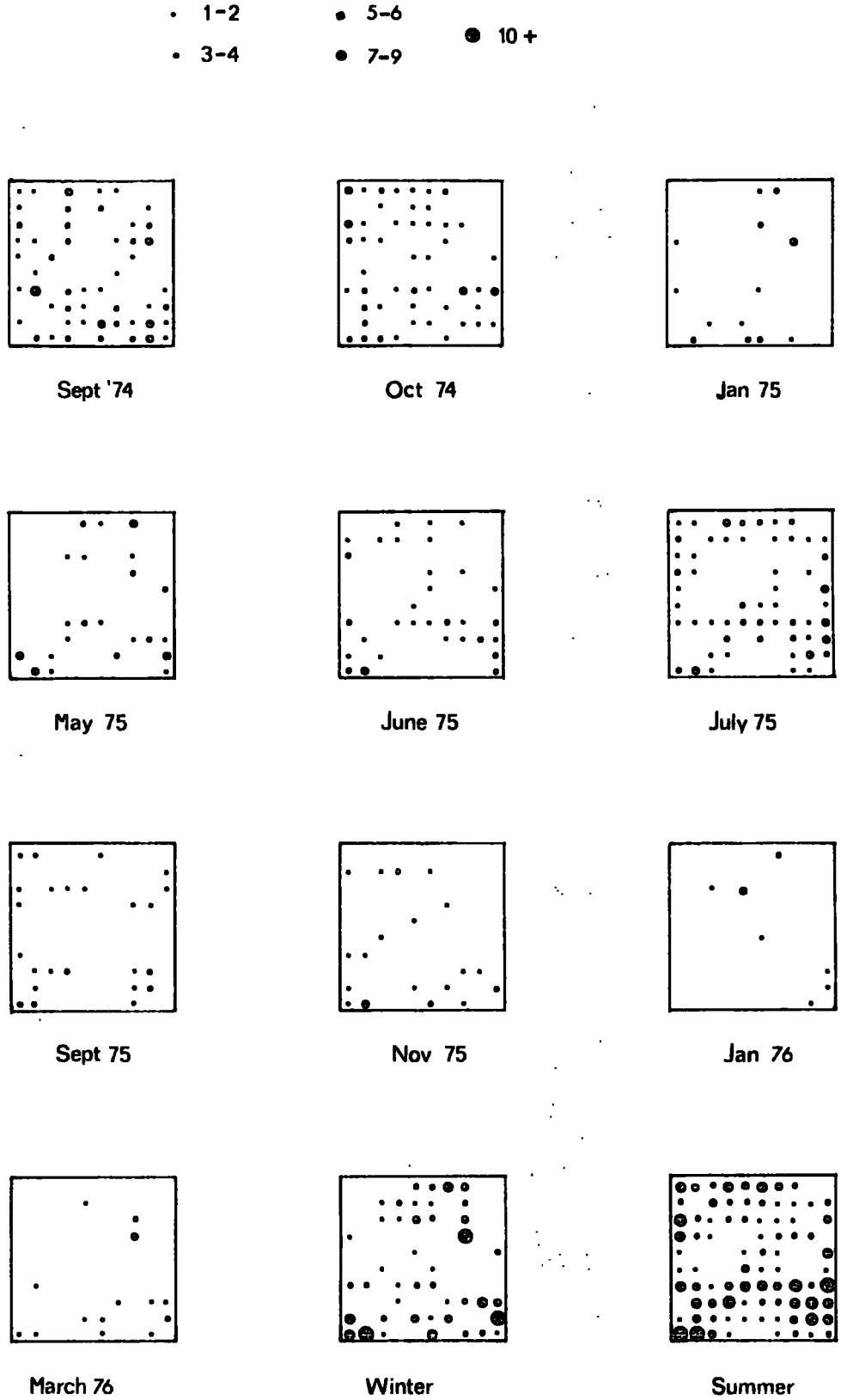


FIGURE 2.23 Number of captures of Clethrionomys at each trapping point in Castle Eden Dene.
The total number of captures is given for the 'winter' and 'summer' periods as defined in the text.

greater than that of the 'summer' one suggesting that during the winter the voles are aggregated in the few areas of good cover whilst during the summer the greater amount of cover permits them to disperse more widely.

A map of the distribution of captures of Clethrionomys both for each trapping session and for 'summer' and 'winter' is shown in Figure 2.23.

A frequency distribution of the number of captures in each trap during each period (Table 2.17) was used to calculate Morisita's index.

Total no. of captures in trap	'Winter' frequency(%)	'Summer' frequency(%)
0	57	19
1	17	27
2	12	19
3	6	15
4	3	3
5	2	9
6	0	4
7	0	1
8	2	2
9	1	0
10	0	1

Figure 2.17 Frequency distribution of captures of Clethrionomys in Castle Eden Dene.

For 'Winter' $I_g = 2.88$ $F = 2.99$ $p < 0.001$

For 'Summer' $I_g = 1.99$ $F = 1.99$ $p < 0.001$

Thus Clethrionomys shows a significantly aggregated distribution throughout the year but Morisita's index is much larger for the 'winter' period in line with the more aggregated distribution at that time. A similar pattern of aggregation in winter and dispersal in summer has

been reported by West (1977) in C.rutilis on the Alaskan taiga. Such seasonal changes are discussed on page 102.

During the 'summer' Apodemus appears to be distributed at random with respect to vegetation classes 1 to 3 and then shows a negative correlation with cover density for vegetation classes 4 to 8 ($p = 0.01$) suggesting that this species favours the more open areas of the trapping grid. During the winter there is no significant correlation with vegetation density and Apodemus may be said to be distributed at random with respect to cover.

The frequency distribution of the number of captures at each point (Table 2.18) was used to calculate Morisita's index

Total no. of captures in trap	'Winter' frequency(%)	'Summer' frequency(%)
0	19	27
1	34	21
2	15	26
3	11	12
4	10	5
5	8	7
6	3	1
7	0	1

Table 2.18 Frequency distribution of captures of Apodemus in Castle Eden Dene.

For 'Winter' $I_g = 1.23$ $F = 1.45$ $0.02>p>0.01$

For 'Summer' $I_g = 1.24$ $F = 1.43$ $0.02>p>0.01$

A χ^2 test shows that the winter and summer frequency distributions are not significantly different ($\chi^2 = 11.2$, $p \cdot 0.005$).

Thus Apodemus showed a similar distribution in summer and winter which did not differ significantly from a Poisson distribution at the 1% level.

These results agree well with the results of the vegetation analysis and show that the distribution of this species was not influenced to any great extent by the amount or distribution of the available cover. During the 'summer' however the mice were less liable to capture in the areas of thick cover much frequented by Clethrionomys. This may have been either because of competition with Clethrionomys for the limited number of traps, because areas of thick vegetation are unattractive to Apodemus or because the two species tend to avoid contact (c.f. Greenwood 1978).

3. Houghall Woods

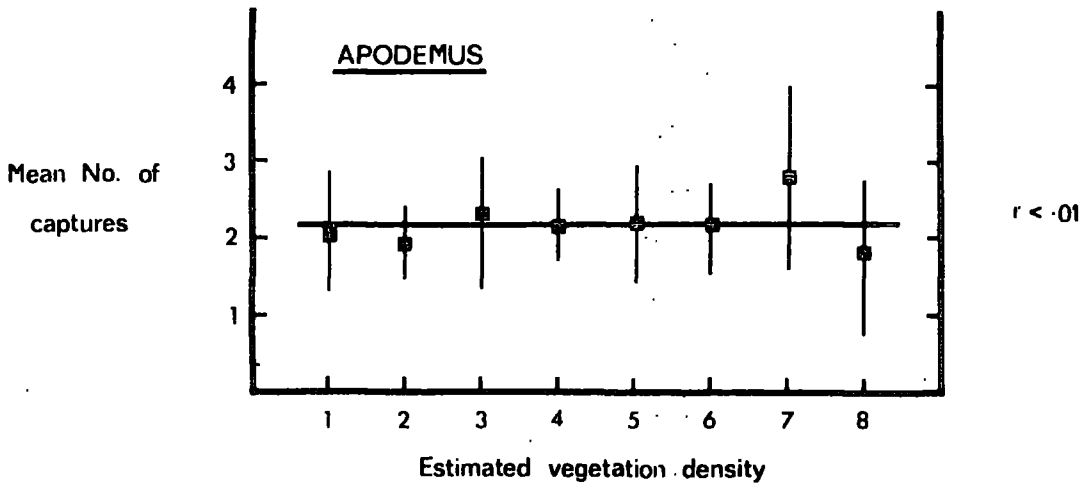
Because seasonal changes in the amount of cover were slight the relationship between numbers caught and the density of cover is based on vegetation survey results for September rather than dividing the year into 'summer' and 'winter'. September was chosen as at this time the density of vegetation lies midway between a 'summer' maximum and a 'winter' minimum.

The frequency distribution of vegetation density classes is shown in Table 2.19.

Vegetation Density Class	Frequency (%)
1	10.8
2	22.5
3	21.7
4	14.2
5	8.3
6	11.7
7	8.3
8	2.5

Table 2.19 Frequency distribution of vegetation density classes in Houghall Woods.

The number of captures at each trap over the whole study period



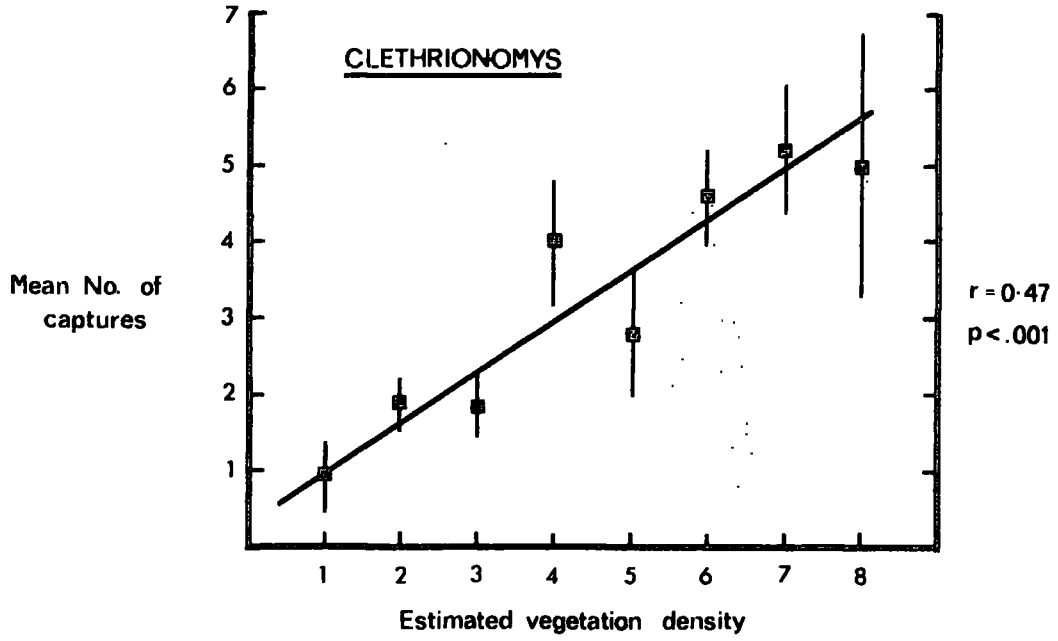


FIGURE 2.24 Relationship between mean number of captures of Apodemus and Clethrionomys and vegetation density at Houghall.

together with the vegetation density around each trap were used to calculate the mean number of captures in each density class. The results of this analysis are shown in Figures 2.42a and b for Clethrionomys and Apodemus.

For Clethrionomys there is, as expected, a significant relationship between the two variables ($p<0.01$). The slope of regression of 0.67 is midway between the values of 0.48 and 1.0 calculated for 'summer' and 'winter' in Castle Eden Dene.

In order to support the assertion that seasonal vegetational changes at this site had a lesser effect on the distribution of voles, frequency distributions for the number of captures per traps were calculated for 'summer' and 'winter as defined previously. These frequency distributions (Table 2.20) were used to calculate Morisita's index.

Total no. of captures in trap	'Winter' frequency (%)	'Summer' frequency(%)
0	72	37
1	20	20
2	18	18
3	4	16
4	2	15
5	3	4
6	1	7
7	0	2

Table 2.20 Frequency distribution of captures of Clethrionomys in Houghall Woods.

For 'Winter' $I_g = 2.24$ $F_o = 2.00$ $p<0.001$

For 'Summer' $I_g = 1.48$ $F_o = 1.95$ $p<0.001$

For both seasons the distribution does not differ significantly from a negative binomial series (U-test, Southwood 1966). Although Morisita's index is higher during the 'winter', indicating a more

aggregated distribution, the difference between 'summer' and 'winter' is less than at Castle Eden Dene suggesting that at Houghall there was a less marked aggregation of animals during the 'winter'.

The distribution of captures of Apodemus (Figure 2.24)showed no correlation with the amount of cover available in September, the number captured in each density class remaining constant. This random distribution of Apodemus is reflected in the frequency distribution of captures (Table 2.21).

Total no. of captures in trap	'Winter' frequency(%)	'Summer' frequency(%)
0	43.3	31.7
1	30	34.2
2	13.3	22.5
3	10	8.3
4	2.5	2.5
5	0.8	0.8

Table 2.21 Frequency distribution of captures of Apodemus in Houghall Woods.

For 'Winter' I_g = 1.46 F = 1.12 p>0.10

For 'Summer' I_g = 0.85 F = 0.78 p>0.10

Morisita's indices for 'winter' and 'summer' do not differ significantly from a Poisson distribution. Apodemus appears, therefore, to be randomly distributed over the trapping area with no preference for any density of cover.

E. Discussion,

1. General.

In capture-mark-recapture studies the extent to which the assumptions made on page 23 are violated will depend on trap layout and spacing (Smith et al 1975), the amount of prebaiting and length of the trapping period (Tanaka 1970), the behaviour of the species under consideration and other factors. The present study has used two very different trap layouts, a transect at Houghall and a grid at Castle Eden. If the population dynamics of a rodent species are to be compared between the two areas then the influence of the trapping method used must be considered.

There is little published work comparing grid and line trapping methods. Like Ashby (1967), Petticrew and Sadleir (1970) working on Peromyscus reported good agreement between grid and transect trapping methods in the same area. For a given population density they found that males and females were captured on the transect in proportions similar to those caught on the grid. It should be noted however that in their study the transect was formed by removing most of the traps from the grid. The resulting line was then trapped for two days immediately after two days trapping on the grid, with the consequence that the rodents may not have had time to become accustomed to the new arrangement of traps. Their grid and line samples were therefore not strictly independent.

The differences in sex-ratio between the two sites during the present study, with a greater excess of males of both species at Houghall, may be at least partially attributable to the different trapping techniques employed. At Castle Eden traps were spaced only 10m. apart whilst Ashby (1967) concluded that the catchment area of a transect extended a mean distance of 23 metres from

the line of traps. If the rodents are distributed at random over the trapping area then the average distance moved before encountering a trap will be greater at Houghall than Castle Eden, thus favouring the capture of males moving over their larger home ranges (Crawley 1965, 1969; Randolph 1977). It should be noted however that this effect will be partly balanced by the closer trap spacing at Houghall.

Differential movement between the sexes may also account for some of the seasonal variation in sex ratio if the larger home ranges of males, particularly during the breeding season, make them more liable to capture. Randolph (1977) in a faecal-tracking study of Apodemus, reported that the home range size of males apparently altered from month to month with maxima in April-May and August. The home range size of females by contrast, changed very little. These fluctuations in range size could appear in the trapping results as fluctuations in sex ratio if the trapping method is sensitive to the home range size of the species being studied. Ashby (1967) did not record sudden or short term variations in the sex-ratio of either species, perhaps because he did not trap often enough to detect them (Ashby pers. comm.), but reported that males usually outnumbered females, particularly in Apodemus. He tentatively attributed this to differential survival both before and after leaving the nest on the basis that in both species there were sustained periods when the sex ratio was approximately 1:1. In one year the sex ratio of Apodemus favoured females during the late summer and through to the following spring, a situation he attribued to reduced competition between young males and females as the result of favourable breeding conditions due to low population density. Although Ashby's (1967) explanations could account for changes in

sex ratio from year to year they do not account for changes from month to month. The social organisation of small mammal communities, which plays a large part in determining the relative trappability of males and females (Crowcroft and Jeffers 1961 for Mus) may result in variations in the trap revealed sex-ratio not accurately reflecting any real variation in the sex-ratio of the population (Southern 1964).

A conclusion from many live trapping studies (but not Ashby 1967) has been that the number of individuals recruited as juveniles is much lower than might be expected from the calculated birth rate. This has usually been interpreted as being the result of high mortality between birth and weaning but a number of recent studies have suggested that other factors may be involved. Andrzejewski and Rajska (1972, for Clethrionomys glareolus) and Boonstra and Krebs (1978, for Microtus townsendii) have shown that if an area is trapped during the breeding season with a combination of live and pitfall traps, a large number of juveniles are captured in the pitfalls but never appear in the live traps. Both authors attributed the failure to live-trap many juveniles to their low position in the social hierarchy and Boonstra and Krebs (1978) suggested that inexperience caused many juveniles to be caught in pitfalls as adults rarely entered them. Gliwicz (1970) reported that the trappability of Clethrionomys was related to age so that young animals, though present were under-represented in live-traps. She suggested that the most easily captured individuals were those at the top of the social hierarchy. A similar increase in trappability with age was reported by Gurnell (1978a) who studied the trap responses of a laboratory colony of Apodemus. Some evidence that it is the presence of adults which causes trap avoidance by juveniles was provided by Watts (1970) who reported that on an area from which adults were removed the mean

weight at recruitment of juvenile Clethrionomys rutilis was reduced.

The weights of the young of both species trapped during the present study indicate that in the majority of cases these individuals had been independent for some weeks before capture as, although growth is rapid at this stage, very few were captured at weights of less than 10g. (see weight distributions, Figures 2.8 to 2.12) and most weighed at least 12g. The weights of many of the Clethrionomys captured between September and November together with the growth data on recaptured individuals suggest that many of these unmarked animals were independent at the previous trapping session when, however, few were caught. It must be noted that the variable growth rate of this species makes the estimation of age difficult, but Ashby (1967) reported that in a laboratory culture the relationship between age and weight was linear up to the age of about 8 weeks. In Apodemus the relationship between age and weight is less variable and data from Ashby (1967) suggest that the majority of Apodemus were not recruited until they were at least 8 weeks old. At Houghall the estimation of age at recruitment was complicated by the migratory nature of this population.

For both species the weights of the recruits followed a similar pattern. The first few juveniles appeared in June or July, when their weights suggested that they were members of the earliest litters born in April. In July or August the weights of the majority of recruits suggested that they too were members of early litters and very few members of later litters were captured. A similar absence of small individuals at this time has been recorded by Kikkawa (1964) and Crawley (1965, 1970) and implies that the trappability of this age group was low. After July there was a decline in both species in the minimum weight at recruitment, reflecting perhaps the declining

growth rate of young animals. It may be concluded, in agreement with Gliwicz (1970), Andrzejewski and Rajska (1972) and Boonstra and Krebs (1978) that the trap avoidance by these recently weaned animals will lead to a considerable underestimate of their number and suggest that the estimates of birth rate or survival of young before weaning, are lower than their true values

The proportion of the trappable population sampled at Houghall during the present study appears to have declined somewhat since the study of Ashby (1967) as he reported that the mean proportion sampled between 1955 and 1963 was 76% for Clethrionomys and 81% for Apodemus. Some of the decline in the catchability of both species may be due to a real change in behaviour over the years as Ashby (pers.comm.), using a standard trapping technique, has found trappability to have been lower between 1967-77 than between 1953-1967. Reasons for such a decline in trappability are not apparent but may be the result of altered patterns of foraging activity due to changes in the vegetation of the woods. The very great reduction in the trappability of Apodemus during the present study can also be accounted for by the capture during the two autumns of the study of a large number of subadults which appeared in the traps only once. A case in point is September 1974 when the population estimates suggest that only 55% of the population was captured. Movement within the woods has been suggested on page 109 as the reason for the single appearance of many of these young individuals and the capture in the following trapping session of many unmarked animals of the same age. Most of this movement appeared to take place during September whereas Ashby's (1967) early autumn trapping sessions were usually undertaken during October, by which time many of the apparently transient individuals had dispersed.

2. Clethrionomys.

The population dynamics of Clethrionomys may show considerable

variation from year to year (Ashby 1967, Southern 1970) but numbers are typically high in late summer, decline during the winter to reach a minimum in April or May and increase until September or October (Crawley 1965, 1970; Ashby 1967; Southern 1970; Flowerdew 1977). In general the population dynamics presented here support this view, though the changes in numbers at Castle Eden during the summer of 1975 are unusually small.

At both sites the recapture data confirm the view that few individuals survive to breed in more than one summer. At Castle Eden about 85% of the overwintered breeding population was first captured the previous September or later and the same is true at Houghall. There was good agreement between the mean survival of marked animals at the two sites. The figure of 2 months for mean residence time in the trapping area agrees well with those reported by Crawley (1965, 1970) and Ashby (1967) and confirms that very few individuals survived for more than a year.

The size and growth data are in good agreement with those of other workers (Crawley 1965, 1970; Ashby 1967; Iverson and Turner 1974; Fuller 1977). Individuals which came into breeding condition in the year of their birth generally lost weight during late autumn so that during the winter they were indistinguishable from subadults on the basis of weight alone. Winter weights of all individuals at both sites fell within the range 11-15g. Whilst voles weighing as little as 11g. may have been in poor condition (Ashby pers.comm.), such a low mean weight and its associated low variance might be advantageous to the species during the winter. Iverson and Turner (1974) have put forward the hypothesis that a low winter weight may be an adaptation to reduce food requirements and hence foraging time during cold weather, a view supported by the findings of Petterborg (1978)

who demonstrated that for Microtus montanus in the laboratory, winter weight loss is a response to decreased photoperiod even when unlimited food is available. There is some evidence to suggest however that food supplies may limit overwinter survival (Flowerdew 1971, 1973; Flowerdew and Gardner 1978).

The start of spring growth and the onset of sexual maturity have been shown to be brought forward by artificially improving the food supply (Watts 1970; Flowerdew 1973) and may also be influenced by temperature (Fuller 1976; Clarke 1977). In Clethrionomys spring growth consisted of an increase in both weight and length. A similar conclusion was reached by Ashby (1967) although Vincent (1974) reported that in Arvicola a spring increase in weight was not accompanied by any increase in length. The spring weights recorded during the present study (Figure 2.9) indicate that at both sites growth may have resumed earlier in 1975 than 1976 suggesting that, as winter temperatures in the two years were similar, food may have been more plentiful during the former winter. This would agree with the conclusion from the recapture data that survival was better during the former winter. The rate of spring growth in Clethrionomys was rather greater than that of Apodemus (page 59), with an approximate weight gain between February and June of just over 2g per month. By May the variance of the mean weight was considerably greater than during the winter. This is in contrast to the length distribution in which the variance during the spring was similar to that during the winter. This apparent paradox is due to those older individuals which lost weight during the winter being able to regain it rapidly during the spring and thus being considerably heavier by May than individuals which overwintered as subadults (Bergstedt 1965). After June there appeared to be a cessation of further growth as, although

it was no longer possible to calculate a mean weight for all overwintered adults, the maximum male weight in July was the same as that in June and individual records show that on average there was no further increase in weight. A similar conclusion was reached for Clethrionomys by Ashby (1967) and contrasts with the situation in Apodemus where growth appears to continue for much longer (see page 59).

Seasonal variation in the growth rate of young Clethrionomys, with juveniles showing rapid growth and maturation at the beginning of the breeding season and delayed growth and maturation towards the end, has been remarked on by a number of authors (Bergstedt 1965; Ashby 1967; Hyvärinen and Heikura 1971; Vincent 1974 for Arvicola) and is well illustrated by the weights of the recruits during the present study. The mean weight of the July 1975 recruits, for both sites combined, was 16.9 $\pm$ 0.56g (s.e.) but by September this had declined to 14.7 $\pm$ 0.47g (s.e.). The difference is significant at the 0.02% level. This decline in growth rate was accompanied by a similar decline in the proportion of recruits in breeding condition. In July 52% ($^{15}/_{29}$) were sexually mature but by September the figure was only 27% ($^{12}/_{48}$) (data for both sites combined). The factors that determine whether an individual will exhibit the early summer type of rapid growth or late summer delayed maturation are presumably the same as those that determine whether or not an individual will come into breeding condition. As well as photoperiod (Petterborg 1978) these will include plane of nutrition, temperature, social influences and genotype (Bujalska 1971; Petruşewicz, Bujalska, Andrzejewski and Gliwicz 1971; Clarke 1977). Negus and Pinter (1965) have shown that in the laboratory, female Microtus montanus which exhibit delayed maturation have larger litters than females which mature rapidly and breed in the year of their birth. Selection may

therefore be acting to delay reproduction in individuals born late in the summer. In Clethrionomys the switch from rapid to delayed maturation appeared to take place during July or August as a proportion of the young captured at this time showed delayed maturation while the rest did not.

The rate of survival of marked Clethrionomys has been very similar at both study sites, though generally slightly higher at Houghall, and resembles that reported by other investigators (Newson 1963; Bergstedt 1965; Crawley 1965, 1970; Watts 1966; Flowerdew 1970; Merritt and Merritt 1978). At both sites the spring decline in survival appeared to begin between May and June, before many juveniles had been trapped, and must therefore be accounted for by the decreased survival of overwintered adults. A decline commencing in the spring has also been reported for Clethrionomys by Newson (1963), Crawley (1965, 1970) and Merritt and Merritt (1978) but Ashby (1967) recorded high survival of adults until well into the summer. Results for other species including Microtus agrestis, M. californicus (Krebs and Myers 1974), Apodemus sylvaticus (Watts 1969; Flowerdew 1978) and Peromyscus maniculatus (Sadleir 1965; Fairbairn 1977) have shown a similar, though often more marked decline, which has been attributed at least partially, to increased movement within the population at this time. Consideration of spring recruitment rates during the present study suggests that the same may be true for Clethrionomys. At both sites the number of unmarked overwintered adults captured in May or June 1975 amounted to about a third of the population whereas in January or March only about a quarter of the catch were previously unmarked (see Figures 219 and 220). A further indication that increased movement is at least partially responsible for the

apparent decrease in survival is provided by Crawley's (1965, 1969) finding that Clethrionomys made larger movements during the spring and early summer than at any other time of year.

As well as 'activities concerned with breeding' (Crawley 1965, 1970) including, perhaps, increased aggression between adults, the increased movement during the spring may also reflect the recolonisation of previously unfavoured areas following the growth of vegetation to provide cover. Evidence for such movement was particularly strong at Castle Eden (see Figure 2.23) where of the 10 recruits in May 1975 only one was captured at a trapping position occupied during January, the remainder being captured in previously uninhabited areas of the grid.

Perhaps the greatest difference between the population dynamics of Clethrionomys at the two sites has been in recruitment. While part of the difference in the number of recruits may be attributed to the two different trap layouts employed, there are considerable differences in the seasonal rates of recruitment which must reflect differences in the ecology of this species at the two sites. At both Castle Eden and Houghall at least part of the recruitment at any trapping session consisted of adults at least several months old. Some of these may have been present at the previous trapping session but numbers are such that some must have moved into the trapping area. Once these animals had entered the marked population their survival appears to have been generally no worse than that of residents so it is apparent that these were not permanently transient individuals but ones which had shifted their home range. Similar movements were recorded by Crawley (1965, 1969) who reported that both changes in home range and wandering movements were common in Clethrionomys populations.

As well as differences between the sites in winter recruitment rates, there were differences in the rates of juvenile and subadult recruitment during the breeding season. From June till October the recruitment rate at Houghall was nearly constant and there was little change in total numbers, showing that recruitment to the trappable population did little more than replace animals that died or moved. By contrast, the rate of recruitment at Castle Eden was high during July and then declined steadily so that population density reached a peak in July and then declined to the following winter. Both types of population fluctuation have previously been reported for Clethrionomys (Flowerdew 1977), with that at Houghall being the more typical pattern. These differences in recruitment rates may be the result of vegetational differences at the two sites (see Section 2D). In Houghall Woods the relatively constant amount of cover throughout the year may have resulted in the utilisation of the entire trapping area and its division into territories by adults during the spring, with the consequent behavioural exclusion of all juveniles except those which were able to fill a space resulting from the death or disappearance of an adult. Towards the end of the summer a decrease in adult aggression (see Chapter 3) may then have allowed an improvement in juvenile recruitment and a consequent rise in numbers. Population processes at this site would thus appear to be dominated during the summer by social interactions between adults and juveniles.

At Castle Eden, the increase in numbers during July 1975 followed the spring increase in the amount of cover available. The survival of early litters may thus be improved by the availability of areas of previously unused habitat as these may serve as dispersal 'sinks' enabling juveniles to avoid, to some extent, the aggression of overwintered adults. Once these areas have been filled the population

size might be expected to remain relatively constant like that in Houghall. However the autumn die back of the dog's mercury resulted in a decrease in the area available to voles forcing individuals to concentrate in the more favourable areas. Whilst population processes at such sites undoubtedly involve social behaviour, numbers may proximately be limited by the amount of cover available.

The two types of area, those providing cover throughout the year and those providing cover only during the summer may be regarded as complementary in the population dynamics of this species. During early summer, vole populations in permanent habitats may 'export' surplus juveniles to seasonal areas or types of habitat not normally occupied by this species (Flowerdew 1969). Here they are able to mature and breed with relatively little interference by overwintered adults. During the autumn the availability of seasonal areas declines forcing individuals to seek a place to live in the permanent areas, where changes in social behaviour permit an increase in population density.

The animals involved in these seasonal movements appear to be those which have recently been weaned, as survival in live-trappable individuals appears to be fairly independent of age. Watts (1970) reported that the majority of juveniles which were later captured had dispersed long distances, though few were ever recaptured.

The two types of summer population fluctuation, that where numbers are constant during the summer and rise in autumn and that where numbers rise during the summer and decline during autumn, may be viewed as the ends of a continuum. At one end lies population dynamics in uniformly favourable habitat and at the other, population dynamics in habitat which can only be occupied during the summer. The observed changes in numbers in any study will therefore depend

to some degree on the ratio of permanent to seasonal habitat in one particular trapping area in one particular year.

The variable nature of the population dynamics of Clethrionomys (Ashby 1967; Southern 1970; Flowerdew 1977) may be ascribed in part to changes from year to year in the availability of cover. An example of this is provided by the present study when the early dieback of dog's mercury at Castle Eden during the dry summer of 1975 led to an early decline in trappable vole numbers compared with 1974.

3. Apodemus

The population dynamics of Apodemus in either woodland (Watts 1969; Flowerdew 1978) or arable land (Green 1978) show less variation from year to year than those of Clethrionomys. Numbers are typically low and constant during the summer months, rise rapidly during the autumn and then decline to the following spring.

A prominent feature of the present study has been the large increase in numbers during the autumn, except during 1975 in Castle Eden Dene. At both sites recruitment cannot easily be attributed to recent breeding within the trapping area. At Houghall the September 1974 cohort contained individuals of a diversity of weights (Figure 2.13) none of which had previously been captured. Similar increases in numbers have been reported by Miller (1958), Kikkawa (1964), Tanton (1965) Bergstedt (1965) Corke (1974) and Leigh Brown (1977) and have generally been attributed to immigration from nearby arable land, although Tanton (1965) suggested that changes in trappability might be important (see page 106). At Houghall the nearby fields (Figure 2.2) were sown with barley during both years of the present study. This was planted in March and

harvested in September so there is good agreement between the time of the autumn immigration and harvesting. The direction of movement within the wood, though not statistically significant also suggests that animals were coming from the fields. Of the 7 animals released on the first day which were recaptured on the second, 5 had moved away from the fields and two were recaptured in the same trap.

Whilst there can be little doubt that immigration was largely responsible for the upturn in numbers during the autumn of 1974 at Houghall, the importance of immigration at Castle Eden and at Houghall during 1975 is less clear as in these cases all the unmarked animals were young of the year. The autumn increase in both woodland (Watts 1969; Flowerdew 1971) and field (Green 1978) populations of Apodemus has been attributed to an increased rate of juvenile survival, possibly as a result of decreased adult aggression (Sadleir 1965; Watts 1969; Flowerdew 1977). At Castle Eden, the October 1974 recruitment, which resulted in a peak in population density, consisted of young of the year with weights ranging from 10 to 18g. The relationship between age and weight (Ashby 1967; Flowerdew 1972) suggests that the youngest of these was about 5 weeks old and that most were aged between two and three months. It may be concluded therefore that the majority of these animals would have been born during July and August and most would have been weaned by the September trapping. A similar failure to catch many juveniles during the summer followed by a period of rapid recruitment of subadults is also apparent from many other studies including those of Tanton (1965); Crawley (1965; 1970); Watts (1969); Flowerdew (1971) and Green (1978).

The failure to catch many of the October recruits at Castle Eden in August or September could be explained either by trap avoidance, similar to that suggested for Clethrionomys, or immigration during September and

October from nearby arable land. There are several factors in favour of the trap-avoidance hypothesis. The total number of recruits in October is not too large to be attributed to breeding by females in the trapping area during July and August as during that period each female could produce two litters. Similar rates of increase during the autumn have been reported for woodland sites some distance from arable land (Watts 1969) and also for arable land with no alternative habitat (Green 1978). There is some evidence from laboratory studies (Gurnell 1978a) that the trappability of Apodemus may increase with age and many of the factors discussed in relation to the low trappability of juvenile Clethrionomys may also apply to Apodemus. Tanton (1965) reported a sharp autumn increase in numbers in oak woodland with a weight distribution very similar to that recorded at Houghall Woods in 1974. He suggested that many of the older individuals caught during the autumn were also present as adults during the summer but were not catchable due to a lack of interest in the traps. All the evidence, however, points to baited traps being attractive throughout the year (Gurnell 1978a) and to grain being a highly favoured food (Cleminson unpubl.).

In the present study the data show that at Castle Eden many adults remained catchable throughout the summer and neither the calendar of captures nor the recapture proportion suggest that there was any decline in trappability. Whilst the weight data from the present study suggest that animals born during July and August may avoid the traps until October or November there is no evidence to suggest that such trap avoidance was prevalent in older animals. A similar conclusion was reached by Ashby (1967) and Watts (1969) who attributed the autumn reappearance of overwintered adults during Tanton's (1965) study to immigration from nearby fields.

There is little to suggest that during the present study immigration from the fields was important in Castle Eden Dene but this has not always been the case. Crawley (1965; 1970) reported sharp autumn rises in numbers after very low summer populations in two years. The weight distributions showed that these influxes contained only young of the year and Crawley (1970) tentatively attributed their appearance to immigration. Unlike the situation in 1974 these autumn rises were too large to be accounted for by breeding by the few animals present during the summer. Why the summer population should have been smaller and the autumn rise relatively larger during the years of Crawley's (1965, 1970) study is not certain but may be the result of changing land use. In recent years the amount of agricultural land, and hence alternative habitat for mice, around the Dene has been considerably reduced, making migratory phenomena less important in the dynamics of this species. The reverse has taken place around Houghall Woods where fields which were previously permanent pasture are now used for growing a variety of cereals (Ashby pers. comm.). This has resulted in an increased area of alternative habitat becoming available, with a consequential increase in the importance of migration.

If few animals were present in Houghall Woods during the summer then the autumn 1975 rise in numbers, though much smaller than that in 1974 and consisting only of young of the year, must also be attributed to immigration. This view is supported by the fact that some of the September recruits were young which bred in the year of their birth and so should have been trappable during the summer had they been present.

The low summer numbers at Houghall Woods suggest that during this season this habitat is less attractive to Apodemus than the

surrounding fields. That these woods are capable of supporting a breeding population during the summer is apparent from the study of Ashby (1967) who recorded substantial breeding within the woods during the 1950's when there was less surrounding arable land (Ashby pers. comm.). Very low summer numbers followed by autumn immigration have also been recorded for the Pasticks, Oxford, a small copse surrounded by arable land (Miller 1958; Kikkawa 1964), for strips of woodland surrounded by arable fields in Sweden (Bergstedt 1965), and for other areas of woodland close to arable land (Crawley 1965, 1969; Leigh Brown 1977). It would thus appear that if a favourable field or hedgerow habitat is available Apodemus will emigrate from the woods during the spring (Bergstedt 1965; Corke 1974; and see page 111), breed in the open fields (Green 1978), or hedgerows bordering fields (Huband, quoted in Ashby 1967), and return to the woods in the autumn. The preference of this species for arable land during the summer may be due either to its preference for open areas (see page 79), the existence of a more plentiful food supply in the fields or interspecific competition with Clethrionomys. The latter reason is unlikely as interspecific competition appears to be minimised by the differing habitat and food requirements of the two species (Watts 1968) and their different activity patterns (Greenwood 1974). In any case Apodemus may be dominant to Clethrionomys (Greenwood 1974, 1978). A shortage of food during the summer is also unlikely as woodland of a similar vegetational type but some distance from arable land is quite capable of supporting a breeding population and Watts (1969) has suggested that in general food is not a limiting factor in Apodemus populations during the summer. The preference of this species for open areas has already been referred to and as well as suggesting a reason for the occupation of the fields during the summer may also

explain why the trapping area at Castle Eden, though as close to arable land as Houghall Woods, supported a much denser summer population (see Section D for comparison of vegetation density at the two sites).

Whilst survival during late winter may be limited by the food supply (Watts 1969; Flowerdew 1972) there is some evidence from the present study that survival estimates were depressed by considerable movement of Apodemus , particularly during early winter. The initially poor survival of individuals marked in September 1974 at Houghall may be the result of a combination of death and dispersal. Almost all the 16 overwintered adults and 29 parous young of the year recruited in September had disappeared by November when there was no recruitment of animals in these age classes (see weight distribution, Figure 2.13). There is good reason for believing therefore that the majority of these animals died during this period. By contrast, although the survival of marked subadults appeared no better than that of adults, the recruitment of a large number of unmarked individuals in this age class during November suggests that many of the September recruits had dispersed rather than died. The autumn may perhaps be viewed as a time when large numbers of subadults, which had left the fields during September, were moving through the woods seeking a favourable place to overwinter. Similar, though smaller, periods of subadult recruitment after the end of breeding are apparent in November 1975 at Houghall and January 1975 at Castle Eden.

Because of movement within the wood during the autumn and winter, the trap-revealed survival of marked animals at this time may be a poor guide to the actual mean survival of individuals of this species. As there was no evidence for breeding during either winter of the study the decline in the estimated population size may provide a

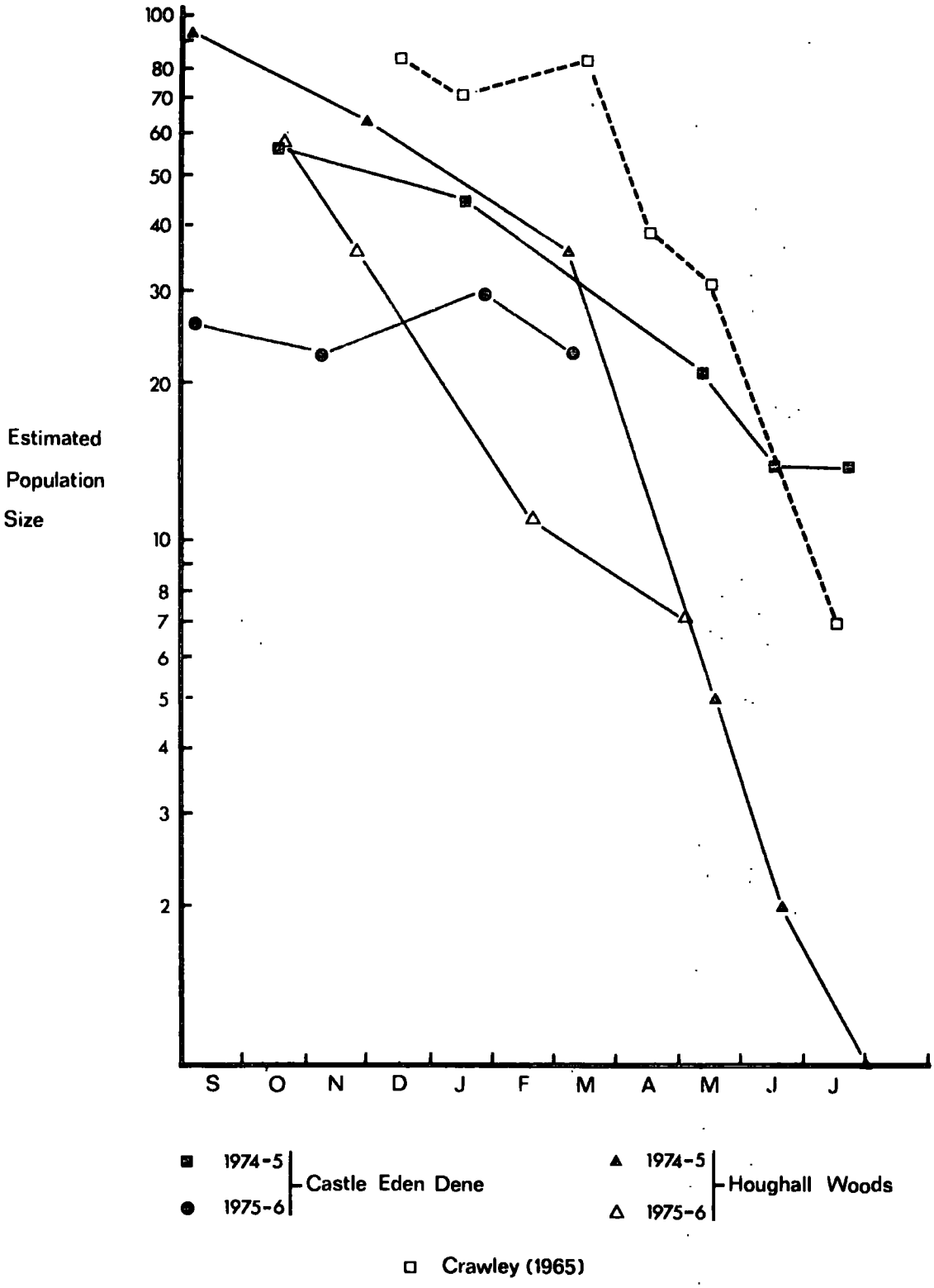


FIGURE 2.25 Winter and spring declines in Apodemus populations. The figures from Crawley(1965) are for his northern grid in Castle Eden Dene during 1963-4.

better guide to actual overwinter survival. This decline in numbers is shown in Figure 2.25. From this graph it is apparent that the pattern of decline was rather different both between sites and between winters. At Houghall in 1974-5 and to a lesser extent at Castle Eden in 1974-5 survival decreased from winter to summer. At Houghall Woods the rapid and continued spring decline, together with the known utilisation of the fields during the summer, suggest that animals were emigrating from the woods to the fields. Similar spring movements have been recorded by Bergstedt (1966) and Corke (1970, 1974). As there is no evidence to suggest that large-scale emigration was responsible for the spring decline in survival at Castle Eden, food shortages (Flowerdew 1972), increased intraspecific strife (Watts 1969; Gurnell 1972, 1978b) or predation (Southern 1969) may all have been involved.

In 1975-6 at Houghall, survival was uniformly poor from October onwards, so that by February few animals survived. Because of the low numbers it is impossible to say with any certainty whether there was a spring period of emigration but the long term trapping record would suggest that numbers would decline still further. The reasons for the poor survival over this winter are not apparent but, as the survival of Clethrionomys was also poor, may have been the result of generally unfavourable environmental conditions.

Overwinter survival at Castle Eden in 1975-6 was unlike any of the patterns previously described as numbers remained virtually stationary throughout the winter. In many respects the population dynamics of Apodemus during this summer and winter were exceptional as there was no autumn rise in numbers and the recruitment of sub-adults during November was much lower than expected. The weights

of the subadults recruited in November and January (Figure 2.12) suggest that they were the same age as the small September recruits and must have been independent in September. There is no evidence therefore for either poor breeding during the summer or breeding during the winter. Although the weather during the November trapping session was cold and damp there was no reason for supposing that the trappability of young animals was particularly low so there is every indication that recruitment was not seriously underestimated. The high number of recruits in January was sufficient to maintain population size close to that observed in the previous January and suggests that, in the Dene as a whole, numbers in the autumn were not deficient. It is possible therefore that the trapping area was particularly unattractive to Apodemus during November but that later in the winter either it became as attractive as in the previous January or the surrounding areas became less attractive.

The reasons for such changes in attractiveness are not clear but may involve the availability of food. Flowerdew (1976, 1978) reported that the majority of immigrants in an area with extra food in winter appeared to have moved only a short distance. He concluded that such winter movements allowed numbers to be adjusted to the local food supply and predicted that 'areas of continuous habitat should show more regular and stable fluctuations than others adjacent to seasonally suitable areas'. Whilst it is true that autumn movements from one habitat to another appeared during the present study to be less important at Castle Eden than Houghall, the population dynamics of Apodemus seemed equally irregular at the two sites. Much of the apparent variation between years at Castle Eden may, however, be a consequence of the relatively small area trapped there rather than a real difference between years in the population dynamics of

this species in the Dene as a whole. This hypothesis is supported by the similarity of the number present during the two springs of the study.

The great mobility of Apodemus and its apparent willingness to move in order to exploit most fully the available food supplies mean that in a heterogeneous piece of woodland such as Castle Eden Dene, numbers trapped in a particular type of habitat may be markedly influenced by the current attractiveness of that habitat. Even in what appears to be a human observer to be a homogeneous piece of woodland there may be differences between areas in the availability of food and the suitability of burrow sites. An example of this variation is apparent from Bergstedt's(1965, 1966) study which showed that there was great variation in the acorn crop of individual oak trees.

CHAPTER 3

The Aggressive Behaviour of Clethrionomys

A. Introduction

There have been many suggestions that social behaviour, particularly aggressive behaviour, may be important in regulating population density (Calhoun 1949; Wynne- Edwards 1962; Chitty 1967) either by controlling the proportion of adults breeding (Christian and Davis 1964; Krebs and Myers 1974) or by limiting the recruitment of young into the population (Sadleir 1965; Chitty and Phipps 1966; Watts 1969; Christian 1970; Flowerdew 1977).

Evidence supporting the importance of aggressive behaviour in the regulation of population density has been sought from two main sources. Experiments on enclosed or laboratory populations of small mammals have shown that social dominance plays a key role in the structure of high density populations (Crowcroft and Rowe 1957; 1958) and that some individuals gain dominance by being able to defend territories (Mackintosh 1970). Clarke (1956a) in a study of M.agrestis in 67 $m.^2$ enclosures found that fertility was reduced as densities approached 4000/ha. and that adult males could subjectively be divided into three overlapping categories which he termed dominant, sub-dominant and subordinate, each class having a clearly defined place in the social structure. In a similar experiment Van Wijngaarden (1960) reported that M.arvalis in 100 $m.^2$ enclosures reached densities of up to 72,500/ha. with only a slight drop in fertility. Although he gave little detail about the social structure it appeared that the area was divided up between 'clans' of animals with sharply defined boundaries. There was severe wounding amongst adults with dominant animals receiving wounds to the head and subordinates to the back and tail, though there appeared to be little mortality as

the result of wounds.

Although these experiments have suggested that voles will maintain a complex social system even at very high densities, their chief interest lies in the finding that densities of several individuals per square metre can be maintained provided there is sufficient shelter, and that only at these unnaturally high densities is fertility reduced. The rapid growth of confined populations has emphasised the importance of emigration in natural populations in maintaining densities below a level at which damage to the herbage becomes apparent (Krebs, Keller and Tamarin 1969), and has suggested that the poor juvenile survival observed in wild populations may be attributable largely to emigration from the place of birth, followed by death.

Field experiments and studies on social behaviour have proved difficult to perform because of the problem of observing small mammals in the wild. Social behaviour has been studied either indirectly, using methods such as automatic photography (Pearson 1960), multiple capture traps (Kolodziej, Pomianowska and Rajska 1972; Rajska-Jurgiel 1976) or levels of wounding (Christian 1971; Lidicker 1973; Rose and Gaines 1976), or more directly by removing individuals to the laboratory for behavioural studies. Krebs (1970) has used the latter method to study changes in aggression during a population cycle of two species of Microtus. He reported that males from peak density populations were the most aggressive and that for M. ochrogaster, home range size was related to the level of aggression shown by individual males, the most aggressive having the largest territories.

As well as changes in aggression related to the perennial population cycle there can also be seasonal changes in aggression. Turner and Iverson (1973) reported an annual cycle of aggression in male M. pennsylvanicus with a peak during the breeding season. At

that time of year, aggressiveness in overwintered animals, as measured in the laboratory, and subsequent survival in the field were strongly correlated. During the summer, overwintered adults were more aggressive and had larger home ranges than animals which matured in the year of their birth. These authors were, however, unable to find any consistent correlation between the level of aggression and population density. Sadleir (1965) and Healey (1967) had earlier reported that there was an increase in the level of aggression of adult Peromyscus coincident with the start of the breeding season, and that as long as adult aggression was high, juvenile recruitment was low. They claimed that during the early autumn, juvenile survival improved as adult aggression declined. Juvenile survival, as measured by recapture rate was also improved on an area from which adults were removed. Smyth (1968) however, failed to find the removal of adult Clethrionomys from an area to have any effect on the survival of the remaining voles.

Suspected changes in the level of aggressive behaviour may be assessed indirectly by examining everted small mammal skins for evidence of wounds caused by fighting, though of course such a technique cannot be combined with live-trapping. Studies of this type on house-mice in corn ricks by Southwick (1958) and Rowe, Taylor and Chudley (1964) have related levels of wounding to density and also to the rate of emigration from the population. Christian (1971) concluded from monitoring a crash in a vole population that levels of wounding in Microtus pennsylvanicus were directly related to density and that wounding was confined almost exclusively to adult males. Lidicker (1973) however, concluded that in M. californicus season, and therefore breeding condition, was more important than density in determining the level of aggression as indicated by wounding. The importance of season in determining the level of wounding in populations

of M.ochrogaster was stressed by Rose and Gaines (1976) who reported that high levels of wounding occurred both during the winter (December-February) and during early spring (March-April) and early autumn (October), the times of greatest reproductive activity, although during these latter periods wounding was confined almost exclusively to adults. They suggested that high levels of aggression during the winter tended to space out individuals; reduced aggression, as indicated by reduced amounts of wounding, during most of the summer months then allowed a higher density to be tolerated as juveniles were not attacked. This hypothesis, which suggests that aggression may not be related primarily to breeding condition, is at variance with other hypotheses of causes of variation in levels of aggression, but unlike most other species of small rodents in temperate climates, the species studied in this instance did not have a clear division between breeding and non-breeding seasons.

The results of these and other field studies (see p.200) have led to a number of different theories about the relationship between aggressive behaviour and the self-regulation of population density. Chitty (1955; 1967), who was mainly concerned with perennial vole cycles, introduced the concept of a genetic component of aggressive behaviour, suggested that the level of aggressive behaviour was positively related to population density, and hypothesised that a high level of aggression during the breeding season would reduce breeding success, leading to either a stabilisation of or a decline in population density. This hypothesis has gained some support from the studies of Krebs (1970) and Christian (1971), but enclosure experiments (Clarke 1956; Van Wijngaarden 1960; Krebs 1970) have suggested that juvenile mortality limits population density and that adult fecundity does not show any marked decline until very high densities are reached.

Sadleir's (1965) suggestion (page 116) that seasonal effects on aggression might be as important as density effects has been supported by the findings of Lidicker (1973) and Rose and Gaines (1976). Indirect evidence that both effects might be important in natural populations was provided by Watts (1969) who found an autumn upturn in the survival of juvenile Apodemus over a number of years. He attributed this to a change in the behaviour of the adults and was able to show that the timing of the increase was density dependent as high numbers during the summer delayed the onset of the increase.

A relationship between aggression, recruitment and population density has been claimed by a number of authors, (Sadleir 1965; Healey 1967; Krebs 1970; Christian 1971) although the exact role of aggressive behaviour in both annual and cyclical changes in number is still uncertain. Investigation of this presumed relationship should help in formulating a more general concept of the interaction between behaviour, ecology and population regulation in small mammal communities.

There is little published work on the aggressive behaviour of Clethrionomys. Comparative behavioural studies on laboratory populations have been performed by Johst (1967) on four species of Clethrionomys and by Ashworth (1973) on two subspecies of C.glareolus and their hybrid. Oldfield (1968) undertook a general laboratory study on the aggressive behaviour of C.glareolus and Apodemus sylvaticus and observed the interactions in small colonies consisting of between two and five animals of one species. Cody (1969) investigated the levels of aggression in a laboratory population of Clethrionomys during the spring and summer. Using a subjective 'index of aggression' he showed a significant increase in the level of aggression from April to August, when the experiment was terminated. Gipps (1977)

has studied the level of aggressive behaviour in enclosed populations of Clethrionomys, using methods similar to those employed in the present study, but was more interested in differences in the level of aggressive behaviour of adults, juveniles and castrates than in seasonal changes. The lack of knowledge about the aggressive behaviour of wild Clethrionomys and the need to know about the relationship between aggressive behaviour and population density in as many species as possible suggested that a study of this relationship in Clethrionomys would be useful.

It was decided therefore to examine the level of aggressive behaviour throughout the year using techniques similar to those of Sadleir (1965).

B. Methods

1. The Measurement of Aggressive Behaviour

Ideally one would hope to assess the level of aggressive behaviour in a population by observing interactions between members of that population in the wild. Unfortunately the observation of small mammals in the field, though possible (Kikkawa 1964; Greenwood 1975, 1978, in press; Bullock 1977) is not easy, as they are rarely seen except at artificial feeding stations. The only practical method of examining their aggressive behaviour is to bring them into the laboratory and observe interactions in a rather artificial situation. A basic, but untested assumption of this type of test is that the amount of aggressive behaviour shown in the laboratory is related to the aggressive behaviour of the animals in the field. It seems most unlikely that after capture an animals behaviour will remain unchanged, as it is in a totally unfamiliar environment where it can neither flee nor hide. The only assumption required however is

that there is a correlation between behaviour in the wild and behaviour in captivity.

Although handling animals in the field has given a strong impression to diverse experimenters that individuals are much more likely to bite during the breeding season and are usually more or less docile during the winter, changes in the level of aggressive behaviour have proved to be difficult to measure in the laboratory. In most cases workers have had to either combine data over several months to show significant changes in aggression between breeding and non-breeding seasons (Healey 1967; Turner and Iverson 1973), or resort to a complex statistical analysis of 'behavioural profiles' (Krebs 1970). Other workers have failed to demonstrate changes in aggressive behaviour in the laboratory (Tamura 1966; Flowerdew 1971) despite strong evidence from field studies for the behavioural regulation of numbers (Watts 1969, Krebs and Myers 1974).

Previous studies have used only male animals for behavioural tests as enclosure experiments have suggested intermale aggression to be the more important in the formation and maintenance of a social structure (Clarke 1956). In fact some aggression is shown by females (Rose and Gaines 1976) but its measurement is complicated by changes related to the oestrus cycle (Sadleir 1965; Hyde and Sawyer 1977). For these reasons it was decided to use only male animals for this project.

The two main methods of pairing animals for aggressive encounters which have been used by previous investigators are described below.

(i) Wild-caught animals are tested against laboratory-kept animals which form a graded series of males of known relative aggressiveness, prepared by pairing a number of males in a 'round-robin' series of encounters. From the results of these tests the males can be placed in a hierarchy of increasing aggressiveness

which must be retested periodically to monitor any changes in their aggressive state or the order of the hierarchy. The object of this method of aggression testing is to determine the position of the wild-caught subjects in relation to members of the graded series. A measurement of the relative level of aggressiveness is thus determined for each animal. Major difficulties result from the level of aggressiveness being liable to change over periods of a few weeks and from aggression not being measured on an absolute scale. Even under an unvarying regime voles and mice show a definite breeding season, indicative of an annual variation in hormonal condition (J. Godfrey, pers. comm.). A futher problem is that the behaviour of the standard animal may be influenced by that of its opponent. In laboratory rats (Barnett 1969) and mice (Parsons 1967; Brain and Nowell 1970) the amount of aggressive behaviour shown during a test was observed to be strongly related to the previous experience of the animals. If these findings apply to voles then the aggressiveness of the individuals in the graded series will change as they become more experienced.

Denenberg, Gaulin-Kremer, Gandelman and Zarrow (1973) have reported that many of these problems can be overcome by using mice with their olfactory bulbs removed, as standard opponents. These bulbectomised mice show very little aggression themselves but elicit aggression from their opponents. They show little variation in their response both between individuals and over a period of time. As bulbectomy is a complex operation and as there is no certainty that voles would show the same reaction this method was not adopted.

There are clearly considerable practical difficulties in

keeping a graded series over a long period of time. Previous investigators have generally used this method for experiments covering no more than one breeding season (Sadleir 1965; Healey 1967) but even over this relatively short period changes in behaviour may occur.

(ii) Two wild-caught animals are tested against each other (Oldfield 1968; Krebs 1970; Colvin 1973; Turner and Iverson 1973). Both the timing and number of any interactions are recorded and the frequency or latency (time till first occurrence) of these is used to give a measure of the level of aggression of the animals. Although this method avoids the problems associated with a graded series of males it has a number of different deficiencies. The behaviour of each member of any pair of animals is dependent on that of the other. As the scores given to the animals therefore lack, to some extent, statistical independence, the results of each bout must be treated as one event, so reducing the number of results by a half (Denenberg et al 1973). Although wild-caught animals will certainly have had some social experience, the laboratory testing procedure is totally unfamiliar to them. It is likely that experience will allow them to become more accustomed to the situation and perhaps modify their behaviour in consequence. For this reason the laboratory experience of an animal must be considered an important variable, and animals with different amounts of laboratory experience should not be compared.

Despite these difficulties, this second method of assessing the level of aggressive behaviour was used in the present study because the problems associated with the maintenance of a graded series seemed more serious. Matching two wild males

is the more likely to give a measurement of aggressive behaviour which can be compared with results obtained subsequently.

2. Preliminary Experiments and Observations

Initially preliminary observations and experiments were made on vole social behaviour in order to gain experience both in trapping and observation techniques. Because of the difficulty experienced in observing aggressive behaviour in recently captured voles, these were extended in order to find an experimental regime which encouraged the display of aggressive behaviour by individuals during the tests.

Voles were trapped in Houghall Woods during late 1973 and early 1974 and the males brought back to the laboratory for observation. Animals were generally housed singly in wire topped aluminium cages containing a layer of peat or sawdust with straw as bedding. Rat-cake and water were freely available and were supplemented occasionally by fresh carrot or cabbage. The animals were kept in a room in a quiet part of the building which was subject to natural lighting only and was not heated, although being in a heated building it was warmer than outdoors.

The description of Oldfield (1968) was used as a guide to enable specific behavioural elements to be identified, but the number of elements recorded was later reduced to the six described on page 130. Although the methods of lighting, recording and observation were varied during these experiments, the arena in which the encounters were staged was always a clear plastic tank with a floor area of 20 x 30cm, containing about 2cm of sawdust.

The first observations were made during the winter on voles which were not in breeding condition and had been maintained in the laboratory for at least a week. The arena was illuminated from a

distance of one metre by two 60W spotlights. The observer sat about 2m. away with the room darkened, so he was not easily seen by the voles. Observations were recorded by speaking quietly into a tape recorder. It was soon evident that the voles were easily disturbed by any noise made by the observer so a radio was used to provide background noise; this masked most of the sound made by the observer but the voles were still aware of sudden noises, perhaps because of their ultrasonic or subsonic content. Little social behaviour was observed between individuals under these conditions although pairs of animals were watched for up to one hour. The general response of two animals on being placed in the arena was to move to opposite ends of the tank, where they would remain motionless for long periods. On the occasions when social interactions were observed these were initiated when one animal left its corner and began to explore the arena. After a short period of exploration the subject would approach its opponent and the two voles would investigate each other by nose to nose contact. The investigation was terminated either when the second vole responded with a defence posture, causing the first to turn and retreat, or when the latter turned and continued to explore, though this was less common.

In view of the considerable amounts of interaction reported by both Oldfield (1968) and Ashworth (1973) the lack of aggression between individuals was surprising. Two possible reasons for this difference were considered; either the voles were not aggressive towards each other because during November to February, when these observations were made, they were not in breeding condition, or their normal social behaviour was inhibited by the testing procedure. The studies of Oldfield (1968) and Ashworth (1973) were both carried out during the breeding season, when voles might have been expected to be aggressive. In the present study voles tested during the

breeding season showed more activity than those tested during the winter (see page 142), but the amount of interaction was still less than that reported by Oldfield (1968) and Ashworth (1973) confirming that the testing conditions, in the most general sense, are an important variable in quantifying aggressive behaviour.

Two possible ways of altering the testing procedure to maximise the amount of social behaviour shown were investigated. The first was to alter the conditions of the test so the voles were subjected to as little disturbance as possible and were allowed a short time to become accustomed to the arena. The second was to keep the voles in captivity for some time before the test so they adjusted to laboratory conditions. Although retaining animals in the laboratory for more than a few days was incompatable with the aims of this study (see page127) it was felt that investigation of the habituation to laboratory conditions would indicate differences between this and other studies and quantify the importance of the time between capture and aggression testing.

For further preliminary experiments the testing conditions described on page 123 were altered by removing the two spotlights so the arena was illuminated only by natural light, and confining the subjects for 10 minutes under translucent plastic containers so they became more accustomed to the arena. The observer sat about 2m. away in a shaded corner of the room and observed the voles as quietly as possible whilst making pencilled notes about the behaviour observed. When a number of voles were tested using these conditions about a week after their first test rather more activity was observed though the voles still spent long periods in opposite corners of the arena. The tape-recorder and radio were then reintroduced and the remaining voles tested. Although the number of fights recorded was

small, the results (Table 3.1) suggest that the noise of the tape-recorder and radio made little difference to the behaviour of these animals and that the increase in activity observed after being at least two weeks in captivity could be attributed to a change in the behaviour of the animals themselves. This could be either an accommodation of the voles to captivity or an increase in individuals levels of aggression as the result of changes in their hormonal condition.

The effect on behaviour in the arena of keeping animals in captivity for an extended period was investigated further by comparing laboratory-kept and wild-caught animals. Seven male Clethrionomys were captured in February 1974 and maintained in the laboratory for approximately one month without being tested. After this time a further four were captured and all eleven animals tested two days later using natural daylight conditions and the tape-recorder. Interactions were recorded using the behavioural elements described by Oldfield (1968) rather than those defined on page 132 and the results have been analysed to present the information shown in Table 3.2. There is clearly a considerable increase in activity between individuals which have been kept in captivity for some time prior to testing, a procedure adopted by Oldfield (1968), Cody (1969) and Gipps (1977). In the cases where a laboratory-kept animal was tested against a recently captured one, all the Approaches were made by the laboratory-kept individuals whilst the recently captured animals spent much time in a corner of the arena and responded to Approaches with a Defence Posture.

Although these results suggest that maintaining voles in the laboratory for between two and three weeks before aggression testing would have resulted in more activity being recorded, such a procedure

Testing conditions	No. of observations	Mean number of Approaches in 10 mins. (± s.e.)
Freshly captured, tape recorder not used	12	0.58±0.22
After 1 week in captivity tape recorder not used	7	2.42±0.40
After 1 week in captivity tape recorder used	6	2.66±0.51
Total after 1 week in captivity	13	2.54±0.32

TABLE 3.1 Effect of time in captivity and altering the testing conditions on the level of aggressive behaviour of Clethrionomys.

Subjects	No. of observations	Mean number of Approaches in 10 mins (± s.e.)
Recently captured vs recently captured	9	1.66±1.2
Recently captured vs laboratory kept	7	9.85±2.8*
Laboratory kept vs Laboratory kept	13	8.07±1.3

* All Approaches made by laboratory-kept individuals.

TABLE 3.2 Effect of time in captivity on the aggressive behaviour of Clethrionomys

was not compatable with the aims of the present study. As demographic events were to be monitored on the areas from which voles were removed for testing, it was considered essential to upset the social system as little as possible. Removing males for long periods would have allowed immigrants to establish themselves, leading perhaps to the forced emigration or reduced survival of the ex-residents on release from captivity.

Further attempts were made to increase the amount of social behaviour shown by recently captured voles by lengthening the time for which subjects were confined under the plastic containers before the start of a test. A number of voles were captured and tested after a minimum of 24 hours in captivity. Lengthening the time under the containers to 30 minutes appeared to increase slightly the amount of social behaviour shown, although by this time (April) the animals were in breeding condition and appeared more active under all conditions. As making pencilled notes was not quick enough and the noise of the tape-recorder appeared to upset slightly the recently captured animals, a twelve-track paper-tape event-recorder operated by a push-button keyboard was constructed. This recorded at a chart speed of approximately 6cm. per minute. As so little activity was shown in many encounters, the number of behavioural elements recorded was reduced to the six described on page 132. Although the event recorder was fairly quiet the voles appeared to be sensitive to the slight click when buttons were activated. The problems of disturbance were finally eliminated by installing a closed circuit television camera and monitor in an adjacent room whilst recording activity on the event recorder. The translucent plastic containers were left in position over the voles for 30 minutes before the start of the experiment and then raised by a system of cords and pulleys controlled from outside the room. The time for which pairs of individuals were watched was

standardised at five minutes as experience showed that if neither contestant had moved within this time they were unlikely to do so for at least a further ten minutes.

Although this elaborate system was adopted in order to cause the least disturbance to the voles, the amount of activity recorded throughout the study was still less than that observed by Oldfield (1968), Ashworth (1973) or Gipps (1977). This could be attributable to the greater length of time that these workers' subjects had been in captivity.

3. The Testing Procedure

The results of the preliminary observations and experiments led finally to the adoption of the procedure described below.

On the second and third days of trapping at Castle Eden Dene and the second day in Houghall Woods all adult male voles captured were brought back to the laboratory. Previously captured animals could be identified by their toe clipped marks, previously uncaptured males were not marked or bled when captured to avoid disturbance but were marked later, before release. Voles were housed individually in wire topped mouse cages with food and water freely available. The room in which the voles were kept and tested was unheated and subject to natural lighting conditions. Voles were kept in the laboratory for a minimum of 24 hours before being tested and were released at the point of capture between three and four days later.

The amount of times that an animal fights in the laboratory must be a compromise between allowing the animal to accommodate to the testing procedure with a consequent change in behaviour, and obtaining sufficient results to make the experiment meaningful. For this project each animal was allowed to fight only twice, the minimum

number of fights which allowed an estimation of the repeatability of each animals performance. Each of these two fights was against a different opponent wherever possible and these were at least 24 hours apart.

The testing arena was the clear plastic tank described on page 123a and the bouts were watched using the closed circuit television system. Before the beginning of the bout the subjects were placed under the translucent plastic containers which were raised after 30 minutes by remote control. Behavioural acts were recorded by the observer for a period of five minutes using the push button keyboard and event recorder. The behavioural acts, which are described in the next section, were generally sufficiently infrequent for each occurrence to be recorded separately, but in cases where the same behavioural act occurred twice within a ten second period without any other act intervening, the two were assumed to be part of one behavioural sequence. This arbitrary ten second rule has been used by other investigators (Oldfield 1968, Krebs 1970). Apart from their toe-clipped numbers, voles were not marked in any way as it was always possible to follow the movements of both individuals. At the end of the test the two subjects were removed, their identities checked and they were returned to their respective cages. Brief comments were written about the behaviour of the two animals with particular reference to any apparent dominance. The paper tape was later transcribed to give a written record of the timing and frequency of the acts recorded.

4. Behavioural Acts Recorded

The aggressive behaviour of Clethrionomys in the laboratory has been described in detail by Johst (1967), who defined a series of 'behaviour complexes' such as 'attack complex' or 'defence complex',

and by Oldfield (1968) and Ashworth (1973) who followed the scheme of Grant and Mackintosh (1963) in dividing social behaviour into a number of acts and postures. Oldfield (1968) divided behaviour on the basis of presumed motivation, into introductory, aggressive, contactual, defensive, withdrawal and ambivalent categories, each category being further sub-divided to describe a total of 19 elements of behaviour. Ashworth (1973) used a similar system but recognised only 12 elements.

A number of classes of social behaviour recorded by these authors in fact indicate little concerning the level of aggression of individuals, and in most cases investigators studying the level of aggression have recorded a smaller number of categories of behaviour and restricted the number of categories in the subsequent analysis still further. Sadleir (1965) recorded eight different categories of behaviour in Peromyscus but analysed only six aggressive elements, whilst Healey (1967), working on the same species, recorded nine elements but reported that only two were good indicators of aggression. Krebs (1970) recorded six broad categories of social behaviour in Microtus but included only five of these in his subsequent discriminant analysis and Turner and Iverson (1973) used only four aggressive elements out of the ten recorded, to calculate an 'Index of Aggression'.

In the present case the size of the event recorder restricted the number of elements recorded to a maximum of six for each animal. As the purpose of the analysis was to determine the level of aggression rather than an analytical study, and in view of the experiences of previous investigators, it was considered that this number would prove ample for the purpose. The choice of elements to be recorded was determined from observations of the most common elements during the

preliminary experiments. Terminology was derived from that of Oldfield (1968) and Ashworth (1973), as in some cases more than one element, as defined by Oldfield (1968), was included in a category. A description of the elements, together with an indication of their presumed motivation and derivation is given below, and the elements are illustrated in Figure 3.1.

α Approach

Approach is an introductory element (Grant and Mackintosh 1963) involving movement directed towards another individual. The approacher assumes an elongated posture with whiskers and ears forward and tail extended. This broad category of behaviour was used by Ashworth (1973) but was subdivided by Oldfield (1968) into Approach or Aggressive Posture depending on whether the fur on the nose was raised or not. This distinction was not made in the present study as a clear difference between the two extremes was not obvious.

β Investigate

This category comprises the introductory elements Nose, Investigate and Sniff as defined by Grant and Mackintosh (1963) and described any close appraisal of one animal by another. In Clethrionomys the animals are usually face to face with noses and whiskers in contact. This element of behaviour is usually of short duration, often mutual and generally follows an approach by one animal.

γ Defence Posture

This category includes the upright and sideways postures which have both offensive and defensive subdivisions in many rodents (Grant and Mackintosh 1963). In Clethrionomys only the defensive sub-division

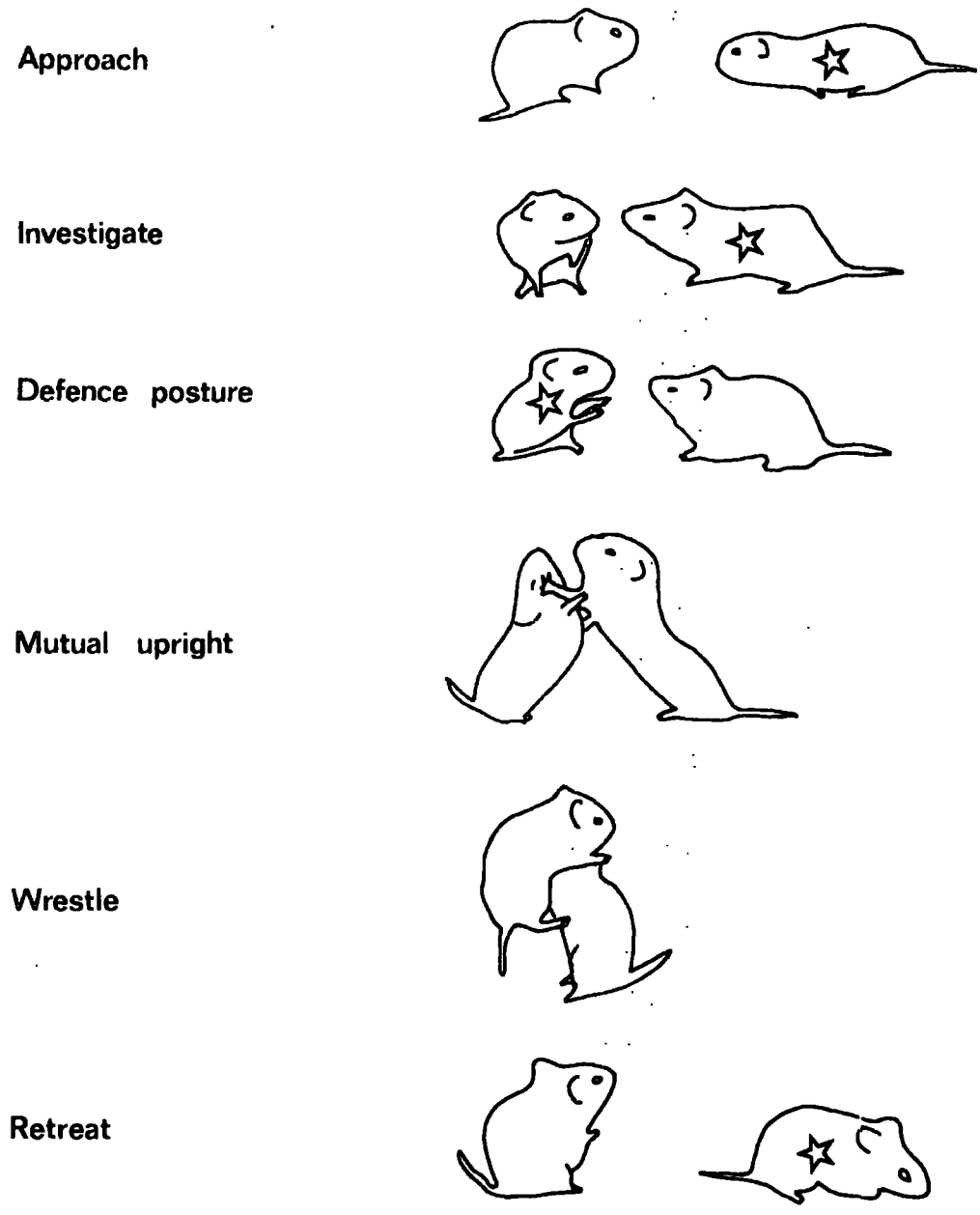


FIGURE 3.1 Behavioural acts recorded. (after Johst 1967) In cases where the description refers to only one of the protagonists, the subject is starred.

was common, the offensive subdivision occurring only as part of a Mutual Upright. Defence Posture is the most common response of a subject to an Approach or Investigation by its opponent (see page 141). The subject stands on its hind legs and one front leg in the sideways posture, or on its hind legs in the upright posture, and pushes out at its opponent with one or both forepaws. Oldfield (1968) recognised two similar elements which have both been included in this category. Thrust, he suggested initially was a defensive act but concluded that it was shown by animals which had both aggressive and flight drives activated, whilst Upright Posture was a closely associated posture with similar motivation. The behaviour sequence analysis of the present study (page 137) suggests that Upright Posture does contain an aggressive component as the response of the opponent is either Retreat or a further aggressive element.

§ Mutual Upright

For this element which has been described by Clarke (1956), Getz (1962) and Turner and Iverson (1973), both contestants stand on their hind legs a short distance apart and strike out at each other with their forepaws. The head is generally drawn back and the eyes closed. Grant and Mackintosh (1963) separated this category into an Offensive Upright Posture, shown by the animal which initiated the interaction, and a Defensive Upright Posture by its opponent, but as the Offensive Upright Posture, a common element in rats (Grant and Mackintosh 1963) never occurred except during a Mutual Upright, the distinction has not been made here. Clarke(1956b) and Getz (1962) considered this act to be most common among voles of approximately equal social status. The act has also been called Boxing by Allin and Banks (1968), Skirrow (1969), Colvin (1970) and Ashworth (1973, and Fighting by Oldfield

(1968) although other authors have used the latter name in a more general sense to cover a wide range of agonostic behaviours.

e. Wrestle

This element, which was rarely observed, is the most overt form of aggressive behaviour (Grant and Mackintosh 1963). The animals are locked together and roll about on the ground until one turns and flees.

f Retreat

In the present case Retreat is used as a general term for any movement away from another individual. Grant and Mackintosh (1963) described two withdrawal elements, Retreat, which did not involve rapid movement, and Flee, which was a rapid form of Retreat. Retreat was the common response of a subject to a Defence Posture by its opponent.

5 Analysis of Results

Whatever experimental procedure is adopted at the end of an encounter experiment, the investigator is left with a record of the timing, duration and frequency of all the behavioural acts recorded. Previous investigators have quantified their results by several different techniques. Sadleir (1965), Tamura (1966), Healey (1967) and others totalled the number of aggressive acts shown by both subjects and assumed that this total gave some indication of the level of aggression of the subjects. The latency of particular aggressive acts, as indicated by the time elapsing before their first occurrence in an encounter, has also been measured and related to aggression (King 1957, Catlett 1961). Turner and Iverson (1973) have shown that, in general, the frequency and latency of aggressive acts are negatively

correlated, suggesting that both are covariables of the same parameter. Krebs (1970) gave the frequencies of the aggressive acts recorded and related them to the frequency of approaches on the basis that each approach is followed by an attack, a retaliation, a submission an avoidance or a combination of these. The level of aggression in a particular encounter was then defined in terms of the ratio of attacks to approaches. Turner and Iverson (1973) recorded both the frequency and latency of aggressive acts. They then calculated an 'Index of Aggression' by multiplying the grand means of their four aggressive acts by a factor to make them all numerically equal. The weighted occurrence of each act in each encounter was then subjected to principal component analysis to give a further multiplicative factor. For each encounter the weighted occurrence of each act was multiplied by the principal components factor and the results summed to give the 'Index of Aggression'.

In the present study the total number of interactions observed was rather small, making the results unsuitable for calculating either an approach/attack ratio(Krebs 1970) or an 'Index of Aggression' (Turner and Iverson 1973) as both these methods rely on statistical treatment of the act frequencies. In this study almost every Investigate was followed by an aggressive act making these two variables highly correlated ($r = 0.83$, $p<0.001$) so an approach/attack ratio would have been of little value. For these reasons it was decided to compare aggressive behaviour by considering the total number of aggressive acts (Defence Posture, Mutual Upright and Wrestle) observed in each encounter and also the proportion of encounters in any one month in which any aggression was observed.

C. Results

1) General

In over a quarter of the encounters observed, the subjects showed no activity and remained in opposite corners of the arena. Mutual Upright and Wrestle occurred in only 21% of encounters. This lack of overt aggression together with the restricted number of males available from the trapping areas has meant that in many cases samples for individual months were too small for detailed statistical analysis, and the results for several months had to be combined to provide adequate sample sizes.

Most previous investigators have used laboratory populations of Clethrionomys for behavioural studies and have reported a considerable amount of interaction and few problems caused by the presence of an observer (Oldfield 1968, Ashworth 1973). As Clethrionomys adapts rapidly to captivity this difference in technique is a likely explanation for the differences in behaviour observed (see page 124). Investigators studying the behaviour of other species of small mammals captured in the field have reported no difficulty in observing aggressive behaviour (Krebs 1970; Turner and Iverson 1973) so it is possible that the lack of interaction observed is peculiar either to Clethrionomys or to the techniques employed.

2 Interrelationship of Acts

The behaviour patterns shown by Clethrionomys in the laboratory were rather stereotyped, with a small number of behavioural elements accounting for the greater part of the activity observed. Although the aims of this project were not primarily ethological, this section provides a short description of the common behavioural elements observed and the relationship between them in order that 'typical' behaviour sequences may be defined. As no differences in the relative frequencies of behavioural acts were observed between animals from

Behaviour of opponent	Response of subject	Frequency as % of total transitions
Approach	Defence posture	5.4
Approach	Mutual upright	2.7
Approach	Retreat	1.3
Approach	Wrestle	0.4
Investigate	Defence posture	25.6
Investigate	Investigate	10.8
Investigate	Mutual upright	6.3
Investigate	Retreat	5.0
Investigate	Wrestle	1.8
Defence posture	Retreat	26.5
Defence posture	Mutual upright	1.3
Defence posture	Defence posture	0.4
Mutual upright	Retreat	6.3
Mutual upright	Mutual upright	2.7
Wrestle	Retreat	1.8
Wrestle	Defence posture	0.4
Retreat	Retreat	0.4

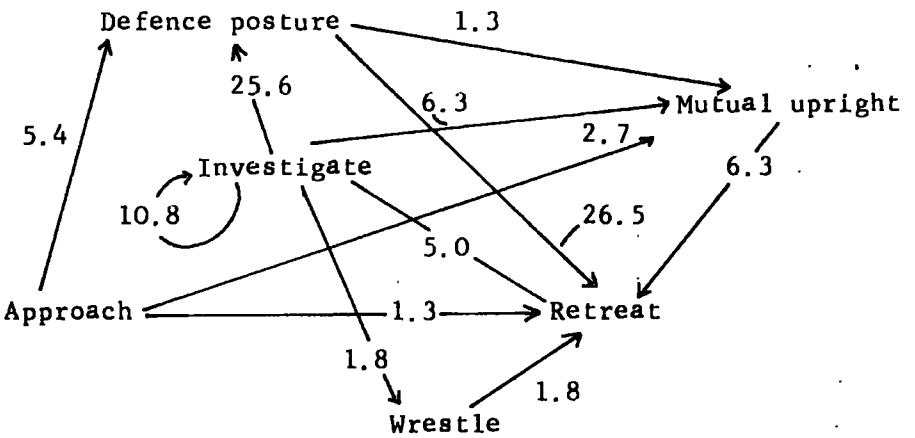


TABLE 3.3 + FIGURE 3.2 — Response of individual Clethrionomys to an act or posture by an opponent during aggression tests.

Figures on Figure 3.2. are percentages.

Behavioural transition			Frequency as % of total transitions
Approach	→	Investigate	38.6
Approach	→	Retreat	13.1
Approach	→	Defence posture	1.6
Approach	→	Mutual upright	1.6
Approach	→	Wrestle	0.4
Investigate	→	Retreat	23.5
Investigate	→	Mutual upright	6.4
Investigate	→	Defence posture	4.8
Defence posture	→	Mutual upright	1.2
Defence posture	→	Retreat	1.6
Mutual upright	→	Retreat	5.6
Mutual upright	→	Investigate	0.4
Wrestle	→	Mutual upright	0.4
Wrestle	→	Defence posture	0.4
Retreat	→	Defence posture	0.4

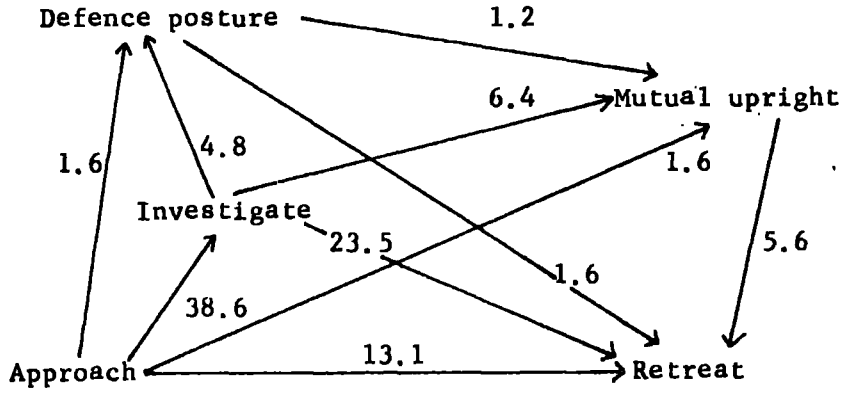


TABLE 3.4 + Figure 3.3 — Changes in behaviour by individual Clethrionomys during aggression tests.

Figures on Figure 3.3. are percentages.

Houghall Woods and Castle Eden Dene the results for the two sites have been combined to give larger sample sizes. Although the absolute frequency of all behavioural elements altered seasonally there was no detectable seasonal variation in the relative frequency of the elements, so the analysis includes results for the whole study period. Sequence of interactions between two animals may be described either in terms of the response of an animal to an action by its opponent, or as a temporal sequence of actions by a single animal, or both approaches may be combined to give a complete description of any social interaction. All these methods of analysis are presented in the following sections.

a) Behavioural transitions by a single animal

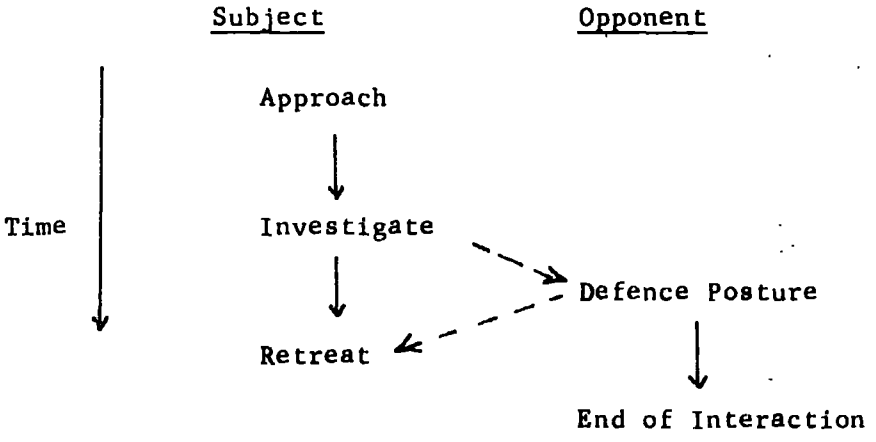
An analysis of behavioural transitions by an animal documents the frequency with which the subject changes its behaviour from one type of act or posture to another. In the present study two transitions predominated; Approach $\longrightarrow$ Investigate, which usually started any interaction, and Investigate $\longrightarrow$ Retreat which ended a high proportion of interactions. The results of this behavioural analysis are shown in Table 3.3 and Figure 3.2 Transitions which accounted for less than 1% of the total have been omitted from the latter in order to clarify the figure.

b) Behavioural transitions between animals

Behavioural transitions between animals are the response of one animal to an act performed by its opponent. Here again two transitions predominated; Investigate $\Rightarrow$ Upright Posture, the usual response of a subject to an Investigation by its opponent and Upright Posture $\Longrightarrow$ Retreat the usual response of the Investigating animal. The results,

as a percentage of the total transitions are shown in Table 3.4 and Figure 3.3. Behavioural transitions which accounted for less than 1% of the total have again been omitted from the figure.

Because such a small number of behavioural transitions predominated, the frequency of these may be used to describe the most frequent interaction between two voles. Only four behavioural elements are involved, one vole Approaches the other and Investigates it, the second vole responds with a Defence Posture causing the first vole to Retreat. This short sequence was observed many times during the course of the study and is illustrated diagrammatically below



3. Variation in the Level of Aggressive Behaviour

a) Between the two study areas

Figure 3.4 shows the total number of aggressive acts performed by each pair of animals throughout the study period. There was considerable variation in the numbers of aggressive acts performed per encounter in any one month with little suggestion that there was any difference in the level of aggressive behaviour of animals from the two study areas. As the aggressive tests from the two areas contained equal numbers of encounters, it was possible to test statistically for any significant difference in the distribution of the numbers of aggressive acts by comparing distributions using a Mann-Whitney

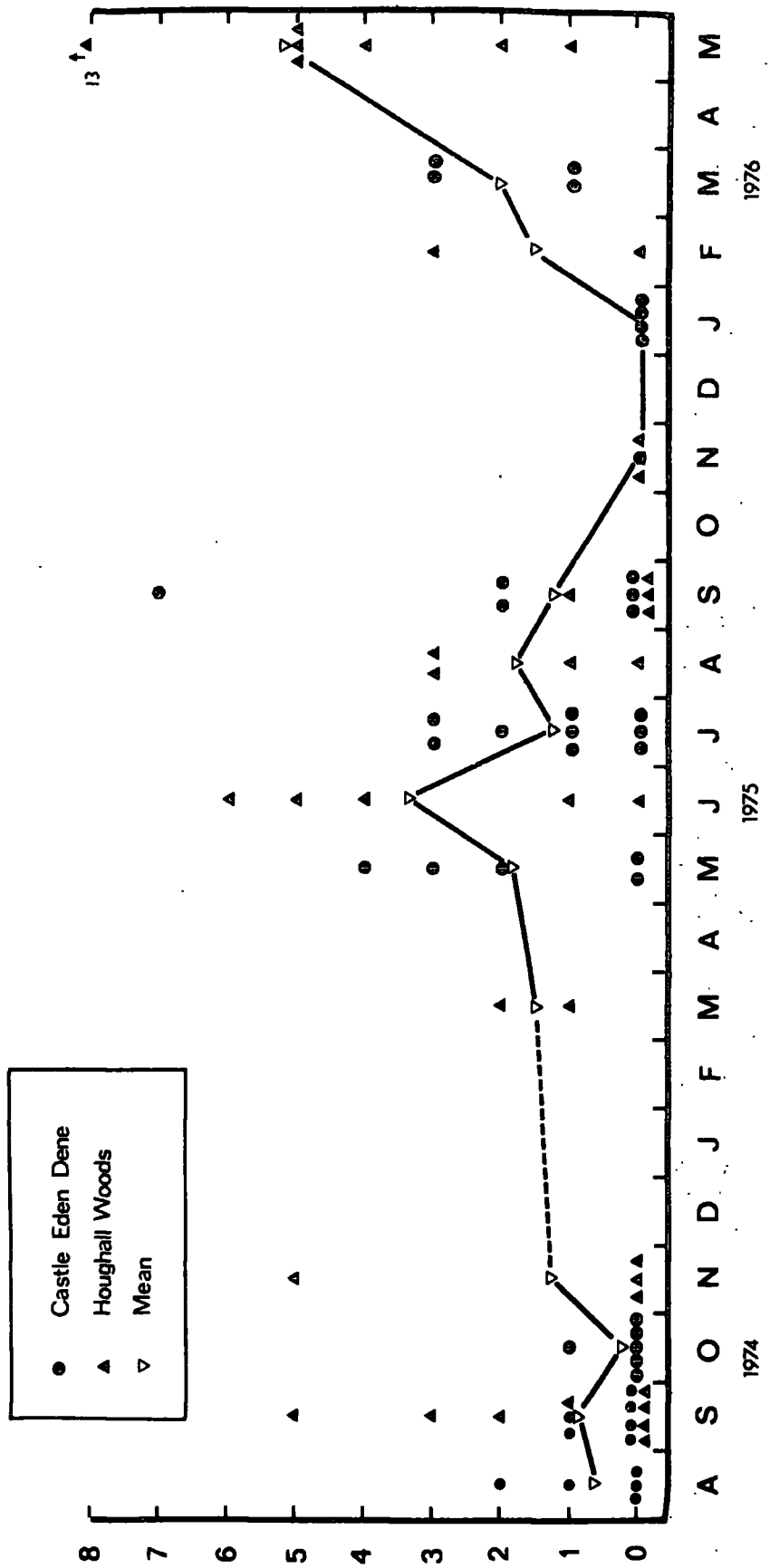


FIGURE 3.4 The number of aggressive acts in each encounter throughout the study period.
Aggressive acts are Defence Posture, Mutual Upright & Wrestle. Each encounter lasted 5 mins.

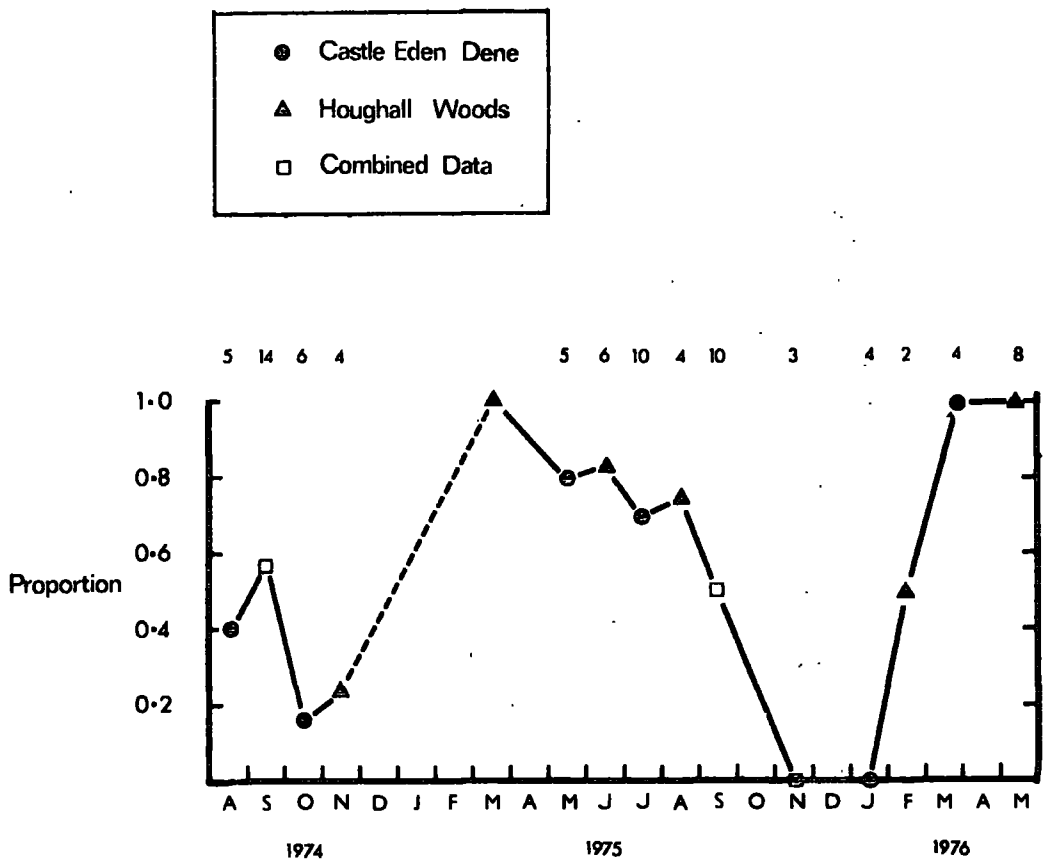


FIGURE 3.5 Proportion of encounters containing any aggressive acts in each month throughout the study period. Sample sizes are shown above each point.

U test, an appropriate non-parametric procedure. There was no significant difference between the distributions (U = 275, p 0.10) confirming that results for both sites may be combined to provide larger sample sizes for the remainder of the analysis.

b) Annual variation in aggression

The data were examined to see if there was any difference in the levels of aggression between 1975 and 1976. The numbers of aggressive acts in May 1975 were compared with those in May 1976 using the Mann-Whitney U-test and a comparison was also made between the combined data for August-November 1974 and August-November 1975. No significant differences were observed (U = 19, $p < 0.05$ for the May comparison; U = 166.5, $p < 0.10$ for the August-November comparison). It was concluded that there was no demonstrable difference in the levels of aggression between years and that data from different years could therefore be combined if required.

c) Seasonal variation in aggression

The proportion of encounters in which there was any interaction at all between the two subjects is shown in Figure 3.5. The overall pattern is one of a high level of aggressive behaviour during the spring and early summer which decreases gradually.

In order to test the significance of the difference in the level of aggression between the breeding and non-breeding seasons, the frequency distributions of aggressive acts (Figure 3.4) were compared for the two periods using a Mann-Whitney U-test. Ideally the breeding season should be defined as the period during which 50% or more of the males are in breeding condition. In the present study all the

trapping sessions from the beginning of March till the end of August are included in this definition as in September only 27% of males were in breeding condition. The frequency of aggressive acts was significantly higher during the breeding season both for the combined data ($U = 321$, $p < 0.001$) and for the two sites when considered separately; (Houghall Woods $U = 315$; $p < 0.005$. Castle Eden Dene $U = 326$, $p < 0.001$). The data may also be analysed by considering the decline in the mean number of aggressive acts from May to November when data from the two years are combined. This decline is significant ($r = -0.45$, $t = 4.19$, $p < 0.001$). The decline over this period in the proportion of encounters showing any aggressive acts represents a linear trend which may be analysed by the method of Yates (Snedecor and Cochran 1967); the fall in proportions is significant at the 0.1% level ($b = 0.128$, $z = 5.12$) showing that there is a significant decline in the proportion of encounters containing aggressive acts.

d) The relationship between age and dominance

The relationship between age and aggression was tested by observing dominance relationships between pairs of animals from different year classes. The dominant animal was considered to be the one which initiated all the social interactions. If both animals initiated interactions, or if there were no interactions at all, the outcome was scored as a draw. Positive associations between activity and aggression have been reported by Healey (1967) in Peromyscus, Lagerspetz (1964) in Mus, and Payne and Swanson 1970 in Mesocricetus. A similar characteristic of dominance has been found by Colvin (1970) and Turner and Iverson (1973), and is consistent with the findings of Brown (1966, 1969) that dominant Apodemus were bolder and showed more exploratory behaviour than subordinates.

The majority of individuals could be classified as overwintered

animals or young of the year on the basis of weight (see p. 51) or their previous trapping record. Those which could not be categorized were omitted from the analysis. Out of 21 encounters between overwintered and recently matured males, the former class were dominant in 10 cases and the latter in 1 case. If both classes of adult are assumed to be equally likely to be dominant the probability of such a result occurring by chance is less than 2% ($\chi^2 = 6.23$, D.f = 1), so it may be concluded that overwintered adults are generally dominant over those which mature in the year of their birth. In the one case in which a young adult was dominant over an old adult, the encounter took place in September, the end of the breeding season, and the young animal was one of the oldest recruits of that season.

D. Discussion

Some of the increase in aggressiveness of individual *Clethrionomys* with time after capture (see page 126) may be ascribed to a general habituation to captivity, but other factors are involved. Brain (1970) has shown that isolation prior to testing is one such factor. Isolated as opposed to grouped male house mice have a decreased adrenal gland weight and an increased level of aggressive behaviour, suggesting that the conditions of captivity have a profound effect on the hormonal state and behaviour of small mammals. Animals in captivity are generally subjected to a higher average temperature and an assured nutritionally adequate food supply. These factors, though less important than day length, have both been shown to induce testicular growth in juvenile or overwintering voles and to maintain testicular function at times of decreasing day length (Clarke 1977). If individuals are to be retained in the laboratory for some time before testing, as in the study of Gipps (1977), then the effect of these

factors on the level of aggressive behaviour must be considered. The behaviour of individuals retained in captivity for long periods may ultimately bear little quantitative relationship to that they would have shown in the wild. If results are to be compared between seasons there is clearly a requirement for a strict standardisation of the conditions and time for which animals are kept in captivity. Because few investigators have studied the behaviour of wild small mammals in the laboratory, standard procedures have not been generally agreed and comparisons between studies must therefore be performed with caution.

The patterns of behaviour recorded during this study are similar to those reported by Ashworth (1973) although her terminology was slightly different. She considered that in encounters between two voles the individual which initiated any social interactions was dominant, and reported that an Approach by one individual was frequently followed by a Defence Posture (which she termed Ambivalent Posture) from its opponent. Because attacks were rare she considered that most aggression was defensive. Oldfield (1968) found Clethrionomys to be much more aggressive than Apodemus and reported that non-aggressive interactions were rare with little contact between individuals except during fighting. Mice, on the other hand, would often behave amicably towards each other with few signs of overt aggression. The latter observation was also reported by Flowerdew (1971). This considerable difference in intraspecific behaviour is not reflected in the behaviour of the two species when handled, Apodemus being generally much more ready to bite than Clethrionomys. As Apodemus may be dominant to Clethrionomys (see page 108) there may be a distinction between intra- and inter-specific behaviour.

The avoidance shown between individual voles in the laboratory

may reflect their social behaviour in the wild, a view supported by the results of the few observational studies available. Kikkawa's (1964) observations at a bait point in Marley Wood showed that whereas up to four Apodemus were seen feeding together, visits by Clethrionomys were generally solitary and some individuals, presumably dominant, chased others if they encountered them. In a similar study Greenwood (1978) reported that there were few encounters between Clethrionomys and that the general response of a feeding vole was to retreat when it detected the approach of another. Bullock (1977) recorded few interactions between voles observed at bait point as there was little overlap between the visiting times of individuals; at no time were two or more voles seen feeding together. Further evidence that mutual avoidance may be an important component of vole social behaviour is apparent from the observations of Oldfield (1968). He reported that in laboratory colonies of between three and five male voles, members initially showed considerable antagonism to one another which slowly died down as a dominance hierarchy was established. The hierarchy, though leading to a suppression of overt aggression, was however easily upset either by the removal and subsequent re-introduction of a colony member or by the introduction of a strange vole, when overt aggression, involving all individuals, reappeared for a time. All the members of a colony shared a nest but organised their periods of activity to avoid one another so generally only one individual was active at a time.

To suggest that all individuals avoid each other at all times except for mating, would be a gross oversimplification and the observational studies referred to above show that on occasion individuals do interact. Some idea of the complexity of individual relationships can be gained from the double-trap studies of Kolodziej, Pomianowska

and Rajska (1972) and Rajska-Jurgiel (1976) where an individual confined in one part of the trap either increased or decreased the probability of capturing an individual in the other part of the trap. These studies have suggested that there is a complex series of relationships between individuals of different ages, reproductive state and dominance status and that individual recognition is an important aspect of social behaviour.

Cyclical changes in social behaviour, with particular emphasis on aggression, have been implicated both in 3 to 4 year cycles of abundance and in seasonal changes in numbers (see Introduction). The study of cyclical changes in aggression of the type proposed by Chitty (1967) has little relevance in the present study as in Britain Clethrionomys does not have the density cycles of large amplitude reported widely in Microtine species and in Clethrionomys at high latitudes (see page 1). At both Castle Eden Dene and Houghall Woods the difference in peak density between the two years of the study was only of the order of 15-20% and there was little difference in the estimated absolute density at the two sites. The only studies which have reported significant changes in aggressive behaviour correlated with changes in density are those of Krebs (1970) and Christian (1971), both of whom worked on populations of Microtus species which showed clearly defined population crashes during their studies. Because of the relatively small change in peak population density during the present study it is not unexpected that changes in the level of aggressive behaviour from year to year were not detected.

The seasonal changes in aggressive behaviour of Clethrionomys reported in this study are in general agreement with those found by Sadleir (1965), Healey (1967) and Turner and Iverson (1973). The

mean level of aggression was low during the non-breeding season, increased rapidly during the spring and decreased gradually during the summer and more rapidly during the autumn. This pattern of aggression would support the hypothesis of Sadleir (1965) and the findings of Watts (1969) that behavioural regulation of recruitment is most likely to occur early during the breeding season when the apparent aggression of overwintered adults reduces the survival of juveniles. The increase in aggression during the spring is coincident with the start of breeding activity and seems likely to be the result of the spring increase in the circulating level of testosterone (see pp. 194-9). The gradual decline in the general level of aggressive behaviour during the breeding season, as measured by the number of fights in which any interaction occurred, is similar to that recorded by Sadleir (1965) for Peromyscus and Turner and Iverson (1973) for Microtus. This decline is coincident with a decline in the number of overwintered adults surviving in the population and a consequent increase in the proportion of young of the year used for aggression tests. As overwintered adults have been shown to be dominant to young of the year (p.145) it is suggested that the latter class may be less aggressive. It follows that if the survival of juveniles is adversely affected by the aggressive behaviour of breeding residents, then overwintered adults would have a more adverse effect on survival than recently matured animals. Ashby (1967) reported that in Apodemus, and to some extent Clethrionomys low density in late spring and early summer was often associated with high recruitment rates subsequently. This was often followed by a lesser deviation than usual of sex ratios from 1:1 the following winter, suggesting that there was decreased intraspecific competition. The situation was complicated however by immigration. This observation would support the suggestions of Chitty and Phipps

(1966) and Wilson (1973) that the mortality of overwintered adults is an important prerequisite of the good survival of juvenile voles (Microtus agrestis). Flowerdew (1978) has suggested that the presumed tolerance of recently matured Apodemus towards juveniles may account for the observation that in some years juvenile survival improves during the autumn despite the continuation of breeding. The results of this study confirm the observations of Ashby (1967) and others, that by September of most years few overwintered Apodemus or Clethrionomys remained, and consequently that the majority of breeding animals were young of the year, so the suggestion of Flowerdew (1978) may be equally applicable to both species.

Whilst this study has been able to show a clear relationship between age, as defined by year-class, and dominance it has not been possible to investigate fully any relationship between weight and dominance because of the small sample sizes and great individual variation in behaviour. The present evidence would suggest that there is no clear relationship, a conclusion supported by the studies of Hall and Klein (1942), Healey (1967), Krebs (1970) and Gipps (1977). Turner and Iverson (1973) reported that in their study heavier animals were usually dominant, but they did not distinguish individuals from different year classes and as weight is not a good indicator of age in Microtus, were therefore unable to separate age and size effects. A number of studies on laboratory-bred rodent species have shown that heavier animals are usually dominant (Ginsberg and Allee 1942; Payne and Swanson 1970), but the applicability of these results to the situation in the wild must be questioned as laboratory conditions provide little opportunity for normal social development.

If dominance is independent of weight in the wild then other factors must be responsible for the observed dominance of overwintered

adults over young of the year. The effect of previous fighting experience on the aggressive behaviour of small rodents is well documented (Scott 1966), and it has been shown that winning or losing a fight can have profound and long lasting endrocrinological effects (reviewed by Bronson and Desjardins 1971). Dominant animals have smaller adrenal glands and larger sex accessory organs than subordinates, suggesting that the pituitary-adrenal system is less active and the pituitary-gonadal system more active than in subordinates (Brain 1971). In encounter experiments, animals which have previously been dominant are more likely to win than animals which have previously been defeated (Ginsberg and Allee 1942; Lagerspetz 1964; Oldfield 1968), so it would appear that both behaviour patterns are self-reinforcing. As overwintered adults must have been successful at establishing a home-range in order to survive, it is suggested that this greater social experience is the basis of their dominance.

The marked spring increase in intermale aggression took place 3 months before the appearance of the first juveniles. At both sites this time of year was characterised by reduced survival and increased recruitment of adults (see Chapter 2) suggesting that many individuals were shifting their home ranges. Similar changes in demography have been recorded by other workers (Sadleir 1965; Healey 1967; Turner and Iverson 1973; Gurnell 1978), and suggest that the increase in aggression may be the immediate cause of changes in movement patterns and home range size (Crawley 1965, 1969; Randolph 1976). In the case of Clethrionomys, where adult males are antagonistic to one another throughout the year, such changes might be expected to be less marked than with species such as Apodemus, where males behave amicably to one another except during the breeding

season (Gurnell 1978b). Any tendency for spring movement patterns to be unresponsive to changes in social behaviour in Clethrionomys may, however, be opposed by changes in movement patterns as a response to the spring growth of new vegetation. As has been shown in Section 1D such changes permit a wider distribution of the species in summer than winter.

In colonising species such as small rodents (Lewontin 1974), the spring increase in aggression and simultaneous changes in distribution may be important in dispersing individuals into areas of seasonally available habitat, where they are able to exploit previously unavailable resources.

CHAPTER 4

Population Genetics

A. Introduction

Since the first application of electrophoresis to genetic analysis (Harris 1966, Hubby and Lewontin 1966), considerable effort has been directed towards determining the amount of electrophoretically detectable variation in a wide range of organisms. The extent of the variation discovered has proved to be very great, and the results of a number of studies suggest that for any population about 30% of loci will appear polymorphic and that about 10% of loci in any individual will appear heterozygous (Lewontin 1974). These figures will be under-estimates of the total genetic variation as only those alleles that have different electrophoretic mobilities will be detected. It has been calculated that about 74% of all possible amino acid substitutions are not distinguishable by electrophoresis, so it follows that about 66% of loci will be polymorphic in any species and that individuals will be heterozygous at 29% of loci (Lewontin 1974).

In their attempts to explain this previously unsuspected abundance of variation, most population genticists became polarised into one of two schools of thought. The 'neutralist' school (Kimura and Ohta 1971) stemmed from the classical theory that the vast majority of mutations were deleterious and that natural selection served mainly to remove them (Muller 1950). Its adherents proposed that most of the biochemical variation detected by electrophoresis was biologically irrelevant and neutral in the sense that it was not directly subject to selection. The 'balance' or 'selectionist' school took the opposite view, that all the alleles found in a population were there as the result of natural selection. They saw selection as maintaining the genetic variability of populations rather than constantly removing

it. Most adherents of the two schools now hold less extreme views than formerly, the neutralists accepting that many alleles may be subject to weak selection rather than being strictly neutral (King 1976, Crow 1976) and the selectionists accepting that random drift, chance and 'founder effects' may play a part in determining the frequency of alleles in a population. Much of the evidence used to support the views outlined above is derived from mathematical models and theoretical considerations which have proved to be virtually impossible to test in real populations. All the experiments that have been performed to date have failed to resolve the question, mainly perhaps, because the forces acting on individual loci are small and variable, so that the number of individuals involved in any experiment must be very large to yield statistically valid results (Lewontin 1974).

Despite the inability of genetical theory to account for the observed variation, electrophoresis has proved to be a useful research tool in ecological studies. Even though the neutralist-selectionist controversy remains unresolved, enzyme polymorphisms may be used as markers to detect genetic changes within or between populations. This is possible because loci are not inherited independently but interact with the loci around them to form gene complexes or 'supergenes' (Ford 1964) which are likely to prove the real 'unit of inheritance' (Lewontin 1974). The neutralist-selectionist controversy will not affect the conclusions of studies in ecological genetics as, even though a 'neutral mutation' will in the long term be independent of the loci around it, the number of generations required to reach equilibrium has been shown to be of the same order as the effective population size (Kimura and Ohta 1971). Its immediate evolutionary fate will therefore be determined by the action of selection on nearby

loci, and it will appear to be under selection.

In the majority of ecological studies on small mammals, enzyme polymorphisms have been employed as genetic markers without regard for the biological function of the enzyme. The few exceptions include those of Berry and Peters (1976) and Leigh-Brown (1976), where biochemical differences in the protein variants under consideration were considered to have a direct effect on the survival of the animal. Previous ecological studies may be divided into two groups with, admittedly, a little overlap: those concerned with geographical variation in allele distribution, which have attempted to elucidate the taxonomic relationships either between species and subspecies or groups within species (Selander, Smith, Young, Johnson and Gentry 1971), Hunt and Selander 1973, Berry 1970, Berry and Peters 1977), and those which have attempted to follow temporal or spatial changes in allele frequency within a population and relate the observed changes to environmental factors and demographic events. (Krebs and Myers 1974). The present study may be classified with the latter group.

Chitty (1967; 1970) was the first to suggest that a balanced polymorphism between two behavioural morphs, one tolerant of high densities but poor at breeding and one intolerant of crowding but successful at breeding, could be responsible for the three to four year cycle of abundance typical of populations of some small rodents. Consequences of this hypothesis would be that changes in the frequency of genetic markers for the two behavioural morphs would be in phase with the population cycle and that animals dispersing from high density populations would probably not be a genetically random sample of that population. Genetic changes of this type have been found in Microtus species by Semeonoff and Robertson (1968), Tamarin and Krebs (1969) and Gaines and Krebs (1971), who were able to show that significant changes in the

frequency of certain alleles were correlated with phases of the population cycle. The interpretation of the latter authors, that their results supported Chitty's hypothesis, has been questioned by Charlesworth and Giesel (1972) who constructed a mathematical model of a fluctuating population. This indicated that changes in gene frequency in numerically fluctuating populations could be the result of changes in the age structure of the population if different genotypes began reproduction at different ages. The observed changes in gene frequency would then be a consequence of demographic events rather than selection. Krebs and Myers (1974) however, have pointed out that the changes in gene frequencies observed in their natural populations were both too large and too rapid to be accounted for by the Charlesworth and Giesel (1972) model, and claimed that the data suggested that the changes in gene frequency could be accounted for only by the differential survival of genotypes. A further criticism of the selection hypothesis made by Charlesworth and Giesel (1972) was that all the genetic markers so far examined in cycling populations have shown a correlation with phase of the population cycle, suggesting that, if the loci studied were a random sample of the genome, then a very large number of loci must be showing cyclical changes in allele frequency. This criticism has also been countered by Krebs and Myers (1974) who have pointed out that if large density changes are times of strong selection then great changes in the genome would be expected.

If it is accepted that the observed changes in allele frequency are the result of selection via differential survival and fecundity, the problem still remains of whether the genetic changes are the cause or consequence of the population cycle. This question cannot be answered by simply observing changes in natural populations but requires an experimental approach. Some progress in this direction has been made by Myers and Krebs (1971), Pickering Getz and Whitt (1974)

and Krebs, Wingate, Redfield, Taitt and Hilborn (1976) who all trapped voles dispersing into uninhabited areas and showed that these were not a genetically random sample of the surrounding population. The experimental analysis of differential fitness of genotypes is, however, extremely difficult,as was shown by a study by Gaines, Myers and Krebs (1971). They established three enclosed populations of Microtus with different genotypes which had previously been shown to have different survival rates in natural populations. They failed to show any difference in growth, fecundity or survival in the three populations and suggested that perhaps intraspecific competition between the morphs was important in natural populations.

Whilst the studies of Krebs and his co-workers (reviewed in Krebs and Myers 1974) have demonstrated that cyclical changes in allele frequencies are a feature of 3 - 4 year cycling populations, the significance of these changes and their relevance to population processes is far from clear. Attempts to distinguish between cause and effect have so far met with little success, the only definite findings being that in some species particular alleles may be under-or over-represented in dispersing animals.

The difficulties of interpreting the results of the genetic studies and in showing that directional selection exists have caused Krebs (pers.comm.) to abandon electrophoresis and concentrate on the detection of behavioural polymorphisms by more direct means.

Although no genetic analysis has been done on the ten year cycle of the snowshoe hare, demographic analysis has suggested that this cycle can be explained in terms of an interaction between hares and their food resources (Keith 1974; Keith and Windberg 1978). This interaction results in periodic declines in hare numbers as they overeat the most nutritive parts of their winter food plants. The decline is lengthened and increased in size by the presence of

predators which have a marked effect at that period of the cycle. Large areas of northern Canada are kept in phase by the periodic effects of mild winters.

The population processes involved in vole and hare cycles have much in common (Keith and Windberg 1978). If the vole cycle is the result of similar interactions between the voles and their environment then there would be good reason for believing that the observed genetic changes are a consequence of the cycle rather than its cause. There is limited evidence to support such a theory of vole population cycles (Canham 1969). However much remains uncertain and the subject must await further research (for review see Krebs and Myers 1974).

Although much of the research on the population genetics of small rodents has been concentrated on species that show large perennial cycles, there are many species or populations which show only a well defined annual density cycle,with relatively little difference between peak numbers in successive years. Whilst much of the work on these species has been concerned with geographical variation and speciation (Selander, Young and Hunt 1969; Berry 1970) a number of studies have followed the frequency of genetic markers over a period of time. One of the most complete studies of this type is that of Gill (1977a, b) who followed the frequency of a buffy coat colour variant in a Microtus californicus population introduced onto a small island. Although M.californicus populations on the mainland exhibit population cycles, the Brooks Island population showed only annual changes in numbers (Lidicker 1973) possibly because of the absence of predators. The frequency of the buffy phenotype, which was recessive to agouti, the normal coat colour, showed annual changes out of phase with the changes in population size (Lidicker 1973). These suggested that it was at a seasonal disadvantage. From the

results of breeding experiments Gill (1977a, b) was able to show that, under laboratory conditions, the heterozygotes had greater reproductive success because of both behavioural and physiological factors. She suggested that the polymorphism was maintained by heterosis together with a seasonal reduction in the numbers of one of the homozygotes. Although this study may be criticised on the grounds that a heterozygote superiority under laboratory conditions may not be so under natural conditions, it is one of the few attempts to estimate partial fitnesses in small rodents. Whilst not explaining why the buffy allele is much more common on the island than the mainland or considering the possibility that this allele is in linkage disequilibrium with the rest of the genome, Gill (1977a, b) has suggested a plausible mechanism for the maintenance of this polymorphism.

Another attempt to measure one component of fitness has been made by Leigh Brown (1977) who observed that the proportion of a population of Apodemus sylvaticus homozygous for a phosphoglucomutase allele declined during one winter. Laboratory experiments suggested that such individuals were less able to mobilise liver glycogen reserves than individuals homozygous for the other allele, with the heterozygotes falling midway between. He suggested that food shortage, which may occur during the winter (Watts 1969), was responsible for the differential survival of genotypes. The high winter mortality of this genotype must have been balanced by opposing selection as the polymorphism was widespread, but insufficient information was available to postulate a likely mechanism. The approach of this study differed from that of Gill (1977a, b) as the polymorphism examined was assumed to have a direct effect on fitness, rather than acting simply as a genetic marker.

The studies outlined above are the only two which have attempted

to measure partial fitness in small rodents using laboratory techniques. The remaining studies have sought to follow seasonal changes in selection pressure or differential survival of genotypes under natural conditions. Berry and his co-workers (Berry and Murphy 1970; Berry and Jakobson 1975; Berry and Peters 1977) have studied the variability, both biochemical and skeletal, of a population of house mice (Mus musculus) on the island of Skokholm in considerable detail. They have reported a number of enzyme polymorphisms which show seasonal changes in either the proportion of heterozygotes or the frequency of a particular allele, which they have attributed to selection. Reviewing these studies, Berry (1977) has pointed out that a genetic change which occurs during one year and appears to be correlated with environmental conditions may not be repeated the following year. He concluded that the key to understanding the apparently random changes in gene frequencies is to recognise that selection pressures are not constant and that different polymorphisms may only be subject to selection spasmodically.

In the past, population genetics has been characterised by a great deal of theory, with little practical evidence to support it (Lewontin 1974). The field of ecological genetics, pioneered by Ford (1964), has attempted to measure selection and evolution in natural populations where data about both the ecology and genetics of a species must be collected. For some species genetical information is more plentiful than ecological information whilst for others, including Clethrionomys, the converse is true.

The present study was undertaken with the object of adding some genetical information to our considerable knowledge of the ecology of this species and perhaps point to differences between cycling and non-cycling populations of small rodents. In a small scale study

it was not expected that the balancing mechanism of any polymorphism would be explained as to do so required considerable resources and has been done successfully in few cases.

Blood samples were also collected from Apodemus during the study as little extra effort was involved and little is known about the biochemical genetics of this species.

B. Methods

1. Collection of blood samples.

Blood samples were collected in the field from the cavernous sinus of voles and mice (Semeonoff and Robertson 1968) into heparinised haematocrit tubes (Capilets, Dade), one end of the tube was then sealed with plastic sealer (Miniseal, Dada) and a label identifying the individual was attached. In the laboratory the sample tubes were centrifuged at $4^{o}C$ in a haematocrit centrifuge and frozen at $-20^{o}C$ until required for electrophoresis. Samples were stored for up to 6 months without any observable change in the electrophoretic pattern.

A blood sample was taken from each vole at its first capture unless the animal weighed less than 10g. or was in a weak condition. In these cases the identity of the animal was noted and a sample taken if it was captured again. Samples were taken from about 90% of voles at first capture.

2. Electrophoresis.

An initial attempt was made to use acrylamide-gel electrophoresis but this medium was abandoned in favour of starch-gel because of the limitation in the number of samples that could be run at once and the difficulty of comparing individual samples. On starch-gel up to 20 samples could be inserted into one gel and, after staining, any

variation in electrophoretic mobilities was immediately apparent.

The buffer system employed was a Tris-EDTA-Borate solution which was used for both the gel and electrode buffers (Smithies 1955). The concentrated buffer solution was prepared from -

Tris	109g	(0.9M)
Na_2 EDTA	7.6g	(0.02M)
Boric acid	30.9g	(0.5M)
Water to 1 Litre		

The pH of this solution was adjusted to 8.0 using concentrated boric acid solution. A 1:7 dilution of this solution was used for the electrode buffer tanks and a 1:20 dilution for preparing the gel.

Starch gels were prepared from partially hydolysed starch (Connought Laboratories) using the method described by Smith (1968). Each gel contained:-

25g	Starch
12.5ml	T.E.B. buffer pH8.0
237.5ml	H_2O

Initially attempts were made to use other makes of starch (B.D.H.,Sigma) but these resulted in much more fragile gels which were difficult to handle. Gel size was 150 x 180 x 5mm. Gels were used only on the day of preparation to avoid ageing effects (Smith 1968).

Samples were applied to the gel by removing 5µl of clear plasma from the unfrozen blood sample with a microsyringe and applying this to a 5mm square of filter paper. The plasma-soaked piece of filter paper was then inserted into a slit cut in the gel. Electrophoresis was carried out in a cold room at a temperature of about $5^{o}C$, thus obviating the need for any further cooling. Gels were run overnight for about 16 hours at a constant current of 8mA until the albumin band had moved about 60mm from the origin. After the run, gels were sliced

through the 5mm dimension with a fine wire to expose surfaces for staining.

3. Staining

Esterase activity was detected by incubating a gel slice in a solution containing an esterase substrate (α-naphthyl acetate) and an azo dye. Naphthol released by enzymatic hydrolysis combined with the dye to form an insoluble purple band in areas of enzymatic activity. The stain solution contained

1 ml of a solution of 10% α-naphthyl acetate in acetone

25 mg Fast Garnet or Fast Blue RR

50 ml Tris-HCL buffer 0.05M pH 7.0

After slicing, gels were incubated in stain solution for between 30 mins and 1 hour at room temperature with occasional agitation. After the esterase bands had appeared the gel slice was transferred, using a sheet of stiff plastic, to a destaining solution consisting of water, ethanol, acetic acid and glycerol. (2:1:1:1). After 24 hours in this solution gels were preserved by sealing in plastic bags, the glycerol in the destaining solution preventing them from drying up for several months.

The other half of the gel slice was stained for general proteins using Brilliant Blue (1% in 7% acetic acid). After about 30 mins in the stain solution the gel was washed in tap water and destained for 24 hours. The albumin and transferrin bands were the major proteins detected in this way.

C. Results

1 Polymorphisms detected

a) General proteins

In both species the fastest moving albumin bands were not resolved

by the buffer system employed but consisted of a long heavily staining region. In Apodemus this region can be resolved into 7 bands using suitable buffer solutions (Pantelouris and Arnason 1967). No individual variation was detected in Apodemus or Clethrionomys from either study site. The transferrin band was placed some distance behind the albumin band. It showed no variation in Apodemus but in Clethrionomys a small number of double banded individuals were detected. Because of the rarity of this variant this polymorphism was not studied.

b) Esterases

The esterase pattern of Apodemus consisted of a complex series of bands and heavily staining regions similar to that reported by Arnason and Pantelouris (1966) and Leigh Brown (1977). Whilst there were differences between the patterns of individuals, none of these appeared to be inherited in a simple manner, and breeding experiments would have been required to elucidate the inheritance of these differences. As Apodemus is difficult to breed in the laboratory the matter was not pursued further.

The esterase pattern in Clethrionomys consisted of an invariable fast band, an extended area which stained with variable intensity and was inhibited by eserine treatment (Semeonoff and Robertson 1968), and a series of variable slow bands which were eserine resistant. The variation in the mobility of the slow bands appeared to be a genetically-determined polymorphism. Three presumed genotypes were detected; one with a single slow band, a second with a single fast band and the third with a broad band of intermediate mobility. The three phenotypes are illustrated in Plate 1. In some cases individuals showed both a fast and a slow band but eserine treatment demonstrated that these were slow banded individuals as the fast band dis-

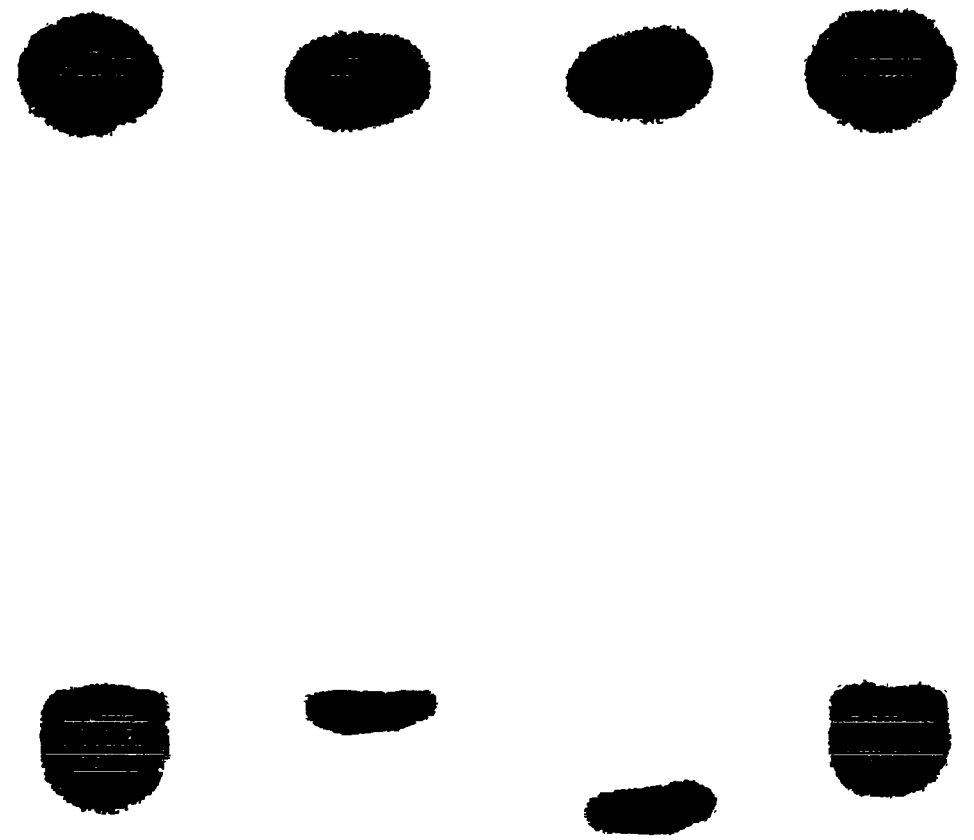


PLATE 1

THE ESTERASE POLYMORPHISM

appeared after treatment. The nature of the three phenotypes suggested that the individuals with either a fast or a slow band were homozygous for fast or slow alleles whilst those with a broad band of intermediate mobility were heterozygotes. This simple Mendelian inheritance has since been confirmed by R.Semeonoff (Pers.comm).

As Clethrionomys appears to be unusually monomorphic (Bathgate 1978) and this polymorphism appeared in many respects analagous to that studied by Semeonoff and Robertson (1968), it was decided to monitor the frequency of alleles at this locus in Clethrionomys from both study areas. In discussing this polymorphism those individuals with the slow band are assumed to be of genotype SS, those with the fast band FF and the heterozygotes FS.

2. Variation in esterase allele frequency

A total of 183 voles were scored for esterase genotype. At Castle Eden Dene 77% of the population, totalling 101 individuals, were scored and at Houghall Woods 71% of the population,totalling 82 animals. The proportion of the total population scored is lower than the proportion sampled because of breakages in the centrifuge or losses during storage and electrophoresis. As many individuals were present for more than one trapping session,the proportion of the population with a known genotype at any one time was generally higher than 75%.

The numbers of individuals of each genotype present at each trapping session are shown in Tables 4.1A and 4.1B for the two study areas,together with the frequency of the fast allele (F) which was less common than the slow allele. The frequency of the former allele is presented graphically in Figures 4.1A and 4.1B. In general the proportion of heterogygotes at both sites was rather lower than would

a. Castle Eden Dene

Trapping period	Frequency of 'F' allele (± s.e.)	Individuals of genotype: SS	FS	FF	Total Scored
Sept.'74	.289±.074	11	5	3	18
Oct.	.232±.056	17	9	2	28
Jan.'75	.230±.082	8	4	1	13
May	.250±.068	12	6	2	20
June	.214±.063	14	5	2	21
July	.212±.050	21	10	2	33
Sept.	.182±.058	14	8	0	22
Nov.	.333±.078	7	10	1	18
Jan.'76	.308±.090	7	4	2	13

b. Houghall Woods

Trapping period	Frequency of 'F' allele (±s.e.)	Individuals of genotype: SS	FS	FF	Total Scored
Sept.'74	.368±.074	7	10	2	19
Nov.	.382±.083	8	5	4	17
March'75	.166±.076	9	2	1	12
May	.154±.070	10	2	1	13
June	.156±.064	12	3	1	16
July	.147±.060	13	3	1	17
Sept.	.277±.074	10	6	2	18
Oct.	.321±.088	7	5	2	14
Nov.	.434±.073	10	6	7	23
Feb.'76	.417±.100	6	2	4	12
May	.500±.133	3	1	3	7

TABLE 4.1. Clethrionomys esterase allele frequencies at each trapping session.

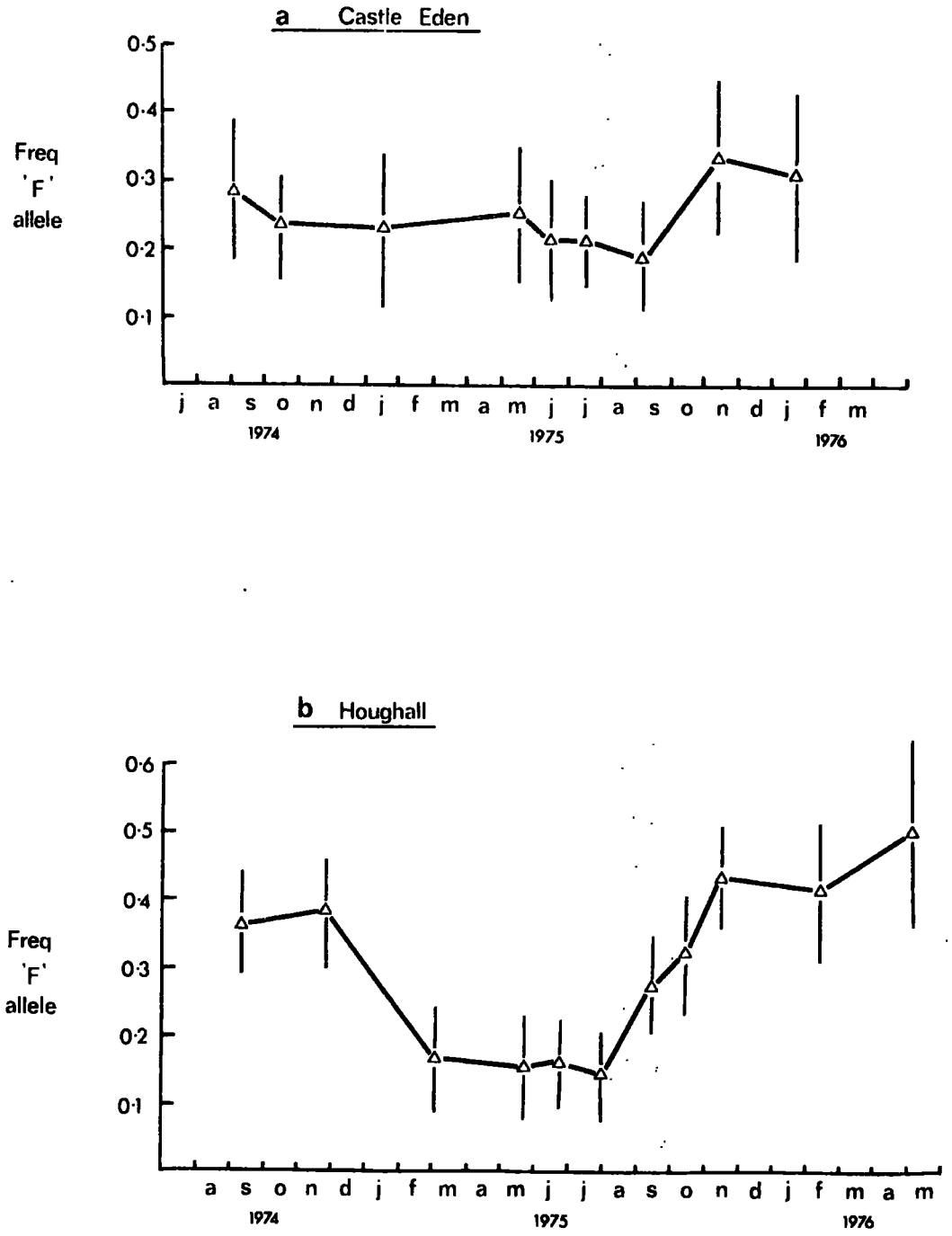


FIGURE 4.1 Seasonal variation in the frequency of the esterase F allele at Castle Eden and Houghall. Vertical bars are 1 s.e.

TABLE 4.2

Genotypes	SS	FS	FF	Freq. of F alleles
Castle Eden	59	33	9	.252
Houghall	43	27	12	.311

The frequency of each genotype at the two study areas.

be expected from the Hardy-Wienberg equilibrium (though the deficit is not significant for any one trapping session) and the proportion of FF individuals was greater than would be expected. The distribution of genotypes totalled over the whole study period is shown in Table 4.2 above. The proportions do not differ significantly from the binomial expectation at Castle Eden ($\chi^2 = 1.84$, $p < 0.10$) although there was a marked deficiency of heterozygotes at Houghall ($\chi^2 = 4.42$ $0.05 > p > 0.02$).

At Castle Eden Dene there was little change in the frequency of the F allele during the study period and the slight rise in the frequency of the allele during November 1975 was not significant. At Houghall Woods, however, there was a more marked change in gene frequencies with a decline in the frequency of the F allele during the winter of 1974-75 and the mean frequency of this allele over the whole study period was close to that for Castle Eden Dene. Whilst the decline in the frequency of this allele during the winter of 1974-75 was statistically insignificant (χ^2 between November and March = 2.22, $.20 > p > .10$), the rise in its frequency, which appeared to be the result of an increase in the proportion of both SF and FF individuals (cf. Leigh-Brown (1977) where only the frequency of one homozygote altered) during the 1975 breeding season was significant at the 1% level ($Z = 2.76$ $p = .0058$) when analysed by the linear trend method of Yates

(Snedecor and Cochran 1967). The apparent decline in the proportion of the F allele during the winter of 1974-75 was not repeated in 1975-76 and the frequency of this allele appeared to remain high throughout the winter, though sample sizes were rather small. A much later sample of animals from Houghall Woods taken in May 1978 suggested that the frequency of the F allele had declined once more as 14 SS, 4 SF and 2FF individuals were captured, giving a frequency of 0.22 for this allele.

The method of sampling gene frequencies used in this study means that, particularly during the winter when survival is high, one individual will contribute to the estimations of gene frequencies on more than one occasion, depending on its trapping record, and that therefore the samples are not independent. This, together with the fact that voles have overlapping generations, means that statistical treatment of changes in allele frequencies and estimates of selection coefficients is impracticable (Tamarin and Krebs 1969, 1973). The use of Tate's test for linear changes in proportion during 1975 is, however, justifiable, as the period of changing gene frequencies is also a period of rapid population turnover. One way of avoiding the interdependence of samples would be to consider only the genotypes of recruits but sample sizes are too small at any one time to permit this.

Changes in gene frequency in a population must be either the result of differential survival or fecundity of genotypes, or differential migration. Whilst it is extremely difficult to examine differential fecundity in wild populations, it is sometimes possible to examine the differential survival of genotypes. This may be done either by following the survival of a cohort over a period of time or by examining the gene frequencies in groups of animals of different ages

(Semeonoff and Robertson 1968). This method is more sensitive than comparing population gene frequencies as the gross gene frequency of all age groups may conceal variability amongst different age groups (Berry and Peters 1975), and selection in different directions in different age groups of the population may appear as a constant gene frequency in the whole population.

At Castle Eden it proved possible to divide the population into two age groups during the summer of 1975. The ratio of genotypes of mature adults recruited before September was compared with that of the immature late-born young of the year recruited between September and November. Although the difference is not significant ($\chi^2 = 2.26$, $p > 0.10$) there is some suggestion that the F allele was more common amongst the later born young of that year. If this is so, the change would be in the same direction as that observed at Houghall during the same period. A comparison of the same type at Houghall was not possible as the proportion of overwintered and early born young still surviving in September was low.

In general, observing the differential survival of genotypes in cohorts of marked animals has not proved to be a useful method of detecting selection because of the small number of animals surviving from one trapping session to the next. Times of high numbers and high survival were also times of low recruitment so analysing the differential survival of cohorts would have added no information to that available from allele frequency changes as the majority of overwintering animals were of a similar age.

Previous investigators (Tamarin and Krebs 1969; Gaines and Krebs 1971) have reported differences between males and females in the frequency of certain alleles in cycling populations of Microtus, though the same phenomena has not been recorded for non-cycling populations. During the present study, monthly samples were too small to treat the sexes separately but over the study period as a whole there was no

evidence for heterogeneity between the sexes. (At Houghall Woods; χ^2 for heterogeneity = 0.64, $p>0.30$. At Castle Eden Dene; $\chi^2 = 2.01$, $p>0.10$).

D. Discussion

A number of Clethrionomys enzyme systems have been surveyed by Bathgate (1978) who reported an unusual lack of variability compared with other rodent species. She found biochemical polymorphisms at only a peptidase locus and at the esterase locus described here. The plasma esterases appear to be amongst the most variable enzymes (Powell 1975), probably because they are not required to bind with one specific substrate but have a general detoxification function (Levin 1976). The presence of this polymorphism in Clethrionomys populations throughout Britain (Bathgate 1978; R.Semeonoff pers. comm.) suggests that it is balanced rather than transient, though in Scotland an additional allele is present which produces no enzyme activity. Whilst nothing is known about the biological importance of this enzyme, its non-specificity suggests that it may not be subject to strong selection per se but may be associated with other loci subject to strong and fluctuating selection pressures. A similar situation for the Es-2 locus in house mice has been suggested by Bellamy, Berry, Jakobson, Lidicker, Morgan and Murphy (1973). These authors were able to separate genotypes with 85% accuracy by considering phenotypic traits such as size and bone composition. Berry and Peters (1977) suggested that such loci function as switches between a range of phenotypic traits and hence may be subject to selection because of their associated rather than primary effects.

The changes in allele frequency at the esterase locus reported in this study are in many respects similar to those reported by Berry and his co-workers for Mus musculus (Berry and Murphy 1970; Berry and

Jakobson 1975; Berry and Peters 1977). There does not appear to be any continuous repeatable association between any obvious social, environmental or seasonal factors such as those reported for cycling populations of Microtus (Krebs and Myers 1974), or the coat colour variant reported by Gill (1976a, b). The fact that parallel changes did not take place in two study areas only 11 miles apart lends weight to the suggestion that the observed changes were not a synchronised response to external factors such as the weather, but were a localised response to conditions prevailing in one piece of woodland. Berry's studies of biochemical and morphological variation in the Skokholm population of house mice (reviewed in Berry 1977a, b), in which traits are only subject to selection spasmodically rather than cyclically, have led him to emphasise the inconsistancy, both in time and space, of the selection pressures which determine the genetical composition of a population. This conclusion is well illustrated by changes at the Hbb locus in the Skokholm mice (Berry and Peters 1977). For two years the frequency of genotypes at this locus showed an increase in the proportion of heterozygotes during the breeding season and a decrease during the winter. This pattern however was not repeated in one particular winter, a fact the authors attributed to milder than usual winter weather. The frequency of alleles also showed spatial heterogeneity as the cyclical selection only occurred on the cliffs of the island and not in the centre during some years.

In the case of the present study it might be possible to explain the changes observed in allele frequencies at Houghall Woods in terms of different environmental and ecological factors during the two years of trapping. However as Lewontin (1974) has pointed out, a post facto search for factors correlated with changes in gene frequency is almost certain to find some statistically significant correlation because of the large number of factors, or combinations of factors, available to

the investigator. Because of the probability of finding some correlation is so high, Lewontin (1974) has suggested that such an analysis may often be unable to distinguish the true cause of the gene frequency changes. An example of such an analysis is provided by the calculation of Bryant (1974) who showed that 83% of the allelic variation in a number of studies of house mice could be accounted for by the co-efficient of variation of mean monthly rainfall. As most of the data came from house mouse populations living in barns and protected from the weather, it is difficult to see how rainfall could exert such direct selective pressure on these populations.

The widespread occurrence of the esterase polymorphism in Great Britain suggests that is it balanced. If this is so then the question arises of how it is maintained. Simple heterosis, the 'classical' explanation for polymorphisms, would suggest that ideally there ought to be an excess of heterozygotes, as the heterozygote has a fitness greater than either of the two homozygotes. However this is certainly an oversimplification of a very complex situation and there are a number of reasons why a deficiency of heterozygotes, such as that seen in the present study, does not rule out heterosis.

Although for heterosis the net fitness of the heterozygotes must be greater than that of the homozygotes, this total fitness is divisible into a number of components, notably fecundity and survival, not all of which need be greater in the homozygote. Prout (1971a, b) has shown that in determining overall fitness the fertility component in both males and females is of much greater importance than viability, so it is unnecessary for the heterozygote to appear at a selective advantage throughout the life cycle. A deficiency of heterozygotes can also result from the subdivision of the population into small inbreeding sub-units or demes, a phenomenon known as the 'Walhund' effect (Li 1955). Although little is known about the

breeding structure of Clethrionomys populations, a subdivision into demes is well documented for other rodent species (Anderson 1970, Rasmussen 1970) and may also occur in Clethrionomys.

The size of the deficiency of heterozygotes has been used as a quantitative measure of the amount of inbreeding (Rasmussen 1964, Petras 1967). This approach may be questioned,as the proportion of heterozygotes can be influenced by factors such as heterosis, directional selection, sexual variation in allele frequencies and other factors which are not easily measured (Selander 1970).

Whilst simple heterosis cannot be ruled out as the mechanism maintaining this polymorphism several factors argue against such an explanation. The deficiency of heterozygotes, the apparently variable directional selection and the differences in gene frequencies at the two sites should not occur with simple heterosis (Li 1955), and there is increasing evidence that simple heterosis may not be very important in natural populations as few polymorphisms have been shown to be maintained in this way (Bryant 1974).

If simple heterosis, in which the heterozygote is constantly fitter than the homozygotes, proves to be uncommon in natural populations what other mechanisms would result in a stable polymorphism? Recent theoretical models (Haldane and Jayakar 1963, Bryant 1974, Hedrick Ginevan and Ewing 1976 (review)) have emphasised environmental heterogeneity, both temporal and spatial, as an important way in which polymorphisms might be maintained, though at present there is little practical evidence to support this idea. In terms of allowing stability over a wide range of allele frequencies, temporal heterogeneity has been shown to be more restrictive than spatial heterogeneity (Hedrick Ginevan and Ewing 1976). This conclusion has however been questioned by Bryant (1974). A combination of temporal and environ-

mental heterogeneity may lead to a stable polymorphism under a wide range of environmental conditions and the subdivision of a population into a number of partially inbreeding demes with limited migration may be particularly effective in maintaining a global polymorphism (Maynard Smith 1970, Gillespie 1973, 1974). All these factors, environmental 'graininess', perennial unpredictable changes in climatic or micro-climatic conditions, and local migration, have been shown to be important in the ecology of Clethrionomys so it would appear that this variability may in itself, be sufficient to maintain a polymorphism.

CHAPTER 5

The Measurement of Plasma Testosterone

A Introduction: Testosterone and Aggression

The effects of castration on male sexual and aggressive behaviour have been known for centuries and the androgen dependence of male sexual behaviour was one of the first endocrinological phenomena to be investigated scientifically (Berthold 1849), yet many aspects of this relationship are still unclear.

A number of studies on inbred strains of the house mouse (reviewed by Gipps 1977) have shown that, depending on the strain, castration either reduces or eliminates the display of sexual and aggressive behaviour. Prepubertal castration is particularly effective in this respect, suggesting that once these behaviours have developed they are never completely suppressed and that experience may maintain them in the absence of circulating androgens. Testosterone injections are effective at restoring sexual and agonistic behaviour in postpubertally castrated mice and rats. In prepubertal castrates however the lack of androgens at the critical age of puberty, means that later injections have no effect.

In postpubertally castrated mammals, the level of testosterone replacement required to restore and maintain sexual and aggressive behaviours at an 'intact' level may be less than the normal circulating hormone level. Damassa, Smith Tennent and Davidson (1977) reported that in castrated rats the plasma testosterone level needed to be restored to only one third of normal in order to completely maintain sexual behaviour. A similar situation may apply to the rhesus monkey (Michael and Wilson 1975) and man (Kraemer, Becker, Brodie, Doering, Moos and Hamburgh 1976).

In the Cricetidae, which includes *Clethrionomys*, sexual and agg-

ressive behaviour may be less dependent on the presence of testicular androgens than in the Muridae. Payne and Swanson (1971) reported that the level of aggressive behaviour in castrated golden hamsters (Mesocricetus auratus) was over 60% of that of their intact opponents, and in a later study (Payne and Swanson 1972) found that whilst castrates initiated fewer aggressive interactions, their level of response once an interaction was initiated was not altered. In similar studies Vandenbergh (1971) reported that the level of attacking by castrates was over 70% of that of their intact opponents and Tiefer (1970) and Whitsett (1975) found no differences between the aggressive behaviour of castrated and intact animals. In Mongolian gerbils (Meriones unguiculatus), another cricetid, castration has been reported as actually increasing aggressive behaviour (Anisko, Christenson and Buchler 1973) although an earlier study reported a decrease (Sayler 1970). In the latter study the subjects were socially naive juveniles which were kept in isolation for over a month after castration, whilst in the former the subjects were adults which had previously been housed together. Possibly the different results of the two studies reflects a difference in social experience. Gipps (1977) studied the effects of castration on the aggressive behaviour of male Clethrionomys glareolus during the breeding season by observing interactions in the laboratory between castrates, intact males and sexually immature juveniles. He concluded that the aggressive behaviour of castrates was rather similar to that of juveniles as both groups showed much social and investigative behaviour but little aggression. Intact males on the other hand, were less willing to approach one another but were invariably aggressive when they did so. It would appear from Gipps' (1977) study that in this member of the Cricetidae, androgens are important in maintaining the normal agonistic behaviour

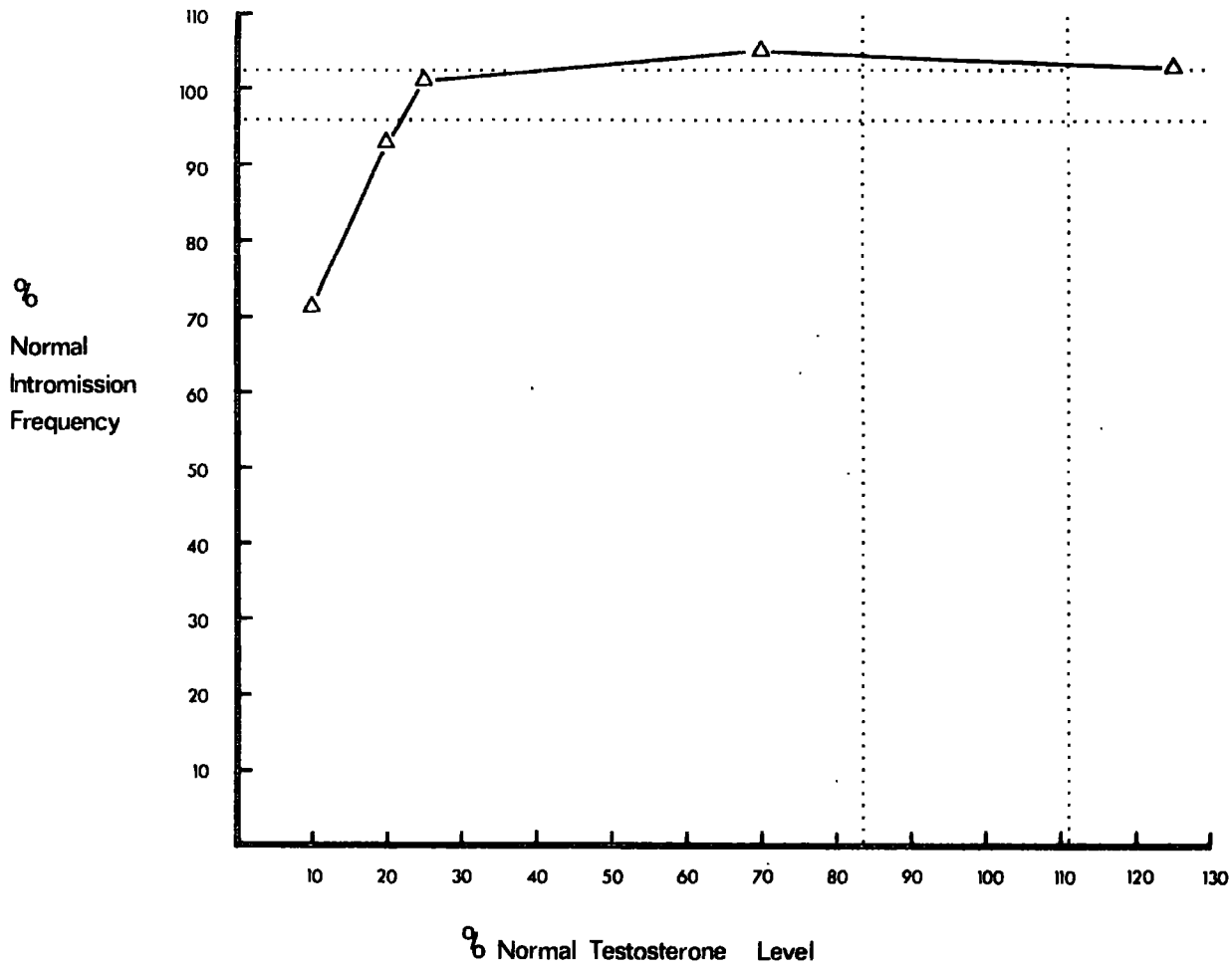


FIGURE 5.1 Relation between circulating testosterone level and the amount of sexual behaviour shown by castrated male rats with testosterone implants. (redrawn from Damassa et al 1977). Dotted lines show range (mean ± 1 s.e.) for intact males.

of adult males, although castration does not lead to the complete suppression of aggressive behaviour.

Species specific differences have also been found in the degree of androgen dependence of scent glands and scent-marking behaviour by male rodents. Price (1975) reported that scent-marking behaviour by male rats ceased completely after castration, whereas Whitsett (1975) found that castration made no difference to the amount of marking behaviour exhibited by golden hamsters, although since the flank gland did not develop the marks could have contained little pheromone. In the gerbil (Blum and Thiessen 1971) and rabbit (Mykytowycz 1970) scent-marking is androgen dependent, though it does not disappear completely after castration and the levels of pre- and post-castration marking are correlated, showing that other factors are involved.

Although castration and replacement studies have implicated androgens in the control of sexual, aggressive and scent-marking behaviours in a number of species, few researchers have attempted to measure the circulating testosterone titres resulting from hormone replacement injections and relate these to natural levels of the hormone. The only studies which have successfully examined the behavioural consequences of constant and measurable levels of plasma testosterone are those of Damassa et al (1977) and Barkley and Goldman (1977b). The former authors implanted controlled release capsules of testosterone in castrated rats and, after showing that the resulting plasma testosterone level was stable over several weeks and was linearly related to the size of the implant, reported that even a plasma testosterone titre of less than one third of normal was able to maintain a range of sexual behaviour variables with normal limits (see Figure 5.1). With the proviso that testosterone released from an implant may have a different physiological effect to that released periodically from the testes (Damassa,

Kobashigawa, Smith and Davidson 1976 – see page 182) these authors concluded that"differences in circulating androgen are not an important factor in determining the variance in sexual performance among individual male rats ". The results of this study were confirmed for mice by Barkley and Goldman (1977b) who were also able to show that, whilst sex accessory organ weights were linearly related to the size of the testosterone implant over a range of dose levels (see also Selmanoff, Abreu, Goldman and Ginsburg 1977), behaviour was maintained with an implant too small to maintain the sex accessory organs. Thus, with respect to behaviour, there appears to be considerable redundancy in the amount of testosterone found in normal males.

Whilst the studies referred to above utilised artificially maintained testosterone levels, other workers have measured testosterone titres in intact males and attempted to relate these to behavioural variables. Rose, Holoday and Bernstein (1971) reported a positive correlation between dominance, rank, frequency of aggressive behaviour and plasma testosterone titre in an all-male group of rhesus monkeys (Macaca mulatta), but this accounted for only 20-25% of the variance between individuals and further studies on free-ranging (Eaton and Resko 1974) or captive (Gordon, Rose and Bernstein 1976) bisexual groups have not confirmed this correlation. Sensitive assays have now enabled this technique to be applied to small mammals. Selmanoff, Goldman and Ginsburgh (1977) have examined the relationship between serum testosterone titre and social dominance, as measured by body scarring or encounter experiments, in inbred mice. They failed to find any consistent relationship between testosterone level and any behavioural variable in either long term or short term experiments. This conclusion was supported by the findings of Barkley and Goldman (1977a, b) who performed similar experiments. Batty (1978a) reported that there was no relationship between individual levels of sexual

behaviour and plasma testosterone titre within a strain of inbred mice although there was a negative correlation between mean plasma testosterone titre and the level of sexual behaviour between a number of inbred strains. All these authors have reported considerable individual variation in plasma testosterone levels amongst animals of the same strain housed under identical conditions. Similar variability has been reported by Bartke, Musto, Caldwell and Behrmem (1973) who found 111— fold differences between individual mouse testosterone levels.

As well as great intrinsic variability in testosterone levels between individuals many factors have been shown to result in fluctuations in circulating testosterone titres, in a range of species. These include diurnal rhythms (Plant and Michael 1971; Kinson and Liu 1973; Rowe, Lincoln, Racey, Lehance, Stephenson, Shenton and Glover 1974), exposure to females or copulation (Saginor and Horton 1968; Herz, Folman and Drori 1969; Kamel, Mock, Wright and Frankel 1975; Batty 1978b) and stress (Brain 1970; Bliss, Frischat and Samuels 1972; Kreuz, Rose and Jennings 1972). There is also evidence that testosterone release from the gonads may be pulsatile rather than continuous (Bartke et al 1973; Murray and Corker 1973; Katongole, Naftolin and Short 1974; Bartke and Dalbero 1975) so that the use of a single determination may be a poor index of androgen metabolism.

It has become increasingly clear that since plasma testosterone titres may show rapid and transient responses to certain social or environmental conditions, a single determination of plasma testosterone level is unlikely to be related to an individuals level of sexual or aggressive behaviour. As, in the majority of species studied, both sexual and aggressive behaviour are, to a greater or lesser extent, responsive to androgens, it may be that testosterone plays only a permissive role in the expression of these behaviours, so that as long

as the hormone is present above a 'threshold' level the behaviours will appear at a normal frequency. Although few studies have examined this suggestion in detail, there is some evidence from the work of Damassa et al (1977) and Barkley and Goldman (1977b) already referred to, that in laboratory rats and mice this may be the case. Only the study of Blum and Thiessen (1971) has reported a relationship between presumed plasma testosterone levels and behaviour. In this case gerbils were castrated and given hormome replacement weekly by injection. The authors reported a correlation between testosterone dose and the level of scent-marking behaviour, but it is worth noting that even their largest replacement dose, which restored scent-marking behaviour to a normal level, was insufficient to maintain the weights of sex accessory organs within normal limits. This suggested that this dose had a physiological effect similar to a very low titre of plasma testosterone and that their smaller doses had physiological effects far below the range of normal plasma testosterone levels.

Although the relationship between behaviour and plasma testosterone level does not appear to be quantitative in animals in breeding condition, there is evidence that behaviour patterns associated with seasonal breeding require testosterone for their induction and maintenance. Lincoln, Guinness and Short (1972) showed that the display of both social aggression and rutting behaviour in the red deer stag required the presence of testosterone either from the testes or from controlled-release implants, although the presence of testosterone per se was insufficient to cause rutting behaviour at an inappropriate time of the year. Lincoln (1974) reported that the commencement of reproductive behaviour or 'March madness' in brown hares (Lepus europaeus) was associated with rapid testicular growth and a sharp rise in the total testosterone content of the testes. At the close

of the mating season there was a marked reduction in both testis size and its testosterone content.

Whilst there are no published reports of the testosterone levels in wild small rodents, the factors influencing the size and spermatogenic activity of the testes, and by implication the level of plasma testosterone, have been studied in some detail in voles. In non-breeding individuals during the winter the testes are small and abdominal and few mature sperm cells are present,due to the failure of the later stages of spermatogenisis, although the early stages are not deficient (Clarke and Forsyth 1964; Grieg 1968). Winter populations consist of a mixture of autumn-born juveniles, which have not matured, and older animals which showed a regression of the testes during the autumn (Clarke 1977). The change to summer breeding condition appears to be controlled largely by the increasing day length during the spring (Baker and Ranson 1932; 1933; Clarke and Kennedy 1967) although nutritional state, ambient temperature, social influences and genotype may also be involved (Grocock 1972; Clarke 1977). These external influences appear to act by mediating an increase in the level of pituitary gonadotrophins (Grieg 1968; Worth, Charlton and Mackinnon 1973) which stimulate the growth of the testes, the production of mature sperm and, presumably, an increase in the production of testicular androgens. During the autumn the decreasing day length generally causes a reduction in the level of gonadotrophins resulting in a regression of the testes of breeding animals. At this time of the year the day-length is insufficient to stimulate the pituitaries of juvenile animals so these remain in an immature condition until the following spring. In some years breeding continues throughout the winter and animals which matured during the late summer do not show testicular regression. Ashby (1967) has concluded that for Clethrionomys in N.E.England such years are characterised

as having a warm dry autumn with presumably a plentiful supply of food. Thus the length of the breeding season in the wild is controlled not solely by day length but also by prevailing environmental conditions.

As studies published since this project was undertaken have confirmed that even under the most strictly controlled experimental conditions it is impossible to relate individual testosterone titres to levels of sexual, marking or aggressive behaviour, it was decided that investigating such a relationship should be outside the scope of the present work. The development of the radioimmuno-assay technique, which proved to require considerable skill in dealing with the small volumes and close tolerances required, and its application to the determination of plasma testosterone levels in both voles and mice captured in the field was, however, considered worthwhile. It was hoped to provide data to support the assumption that in these species plasma testosterone levels are high in breeding individuals and low in non-breeders. The technique, if feasible with wild small rodents, could also be applied to other plasma hormones such as the corticosteroids, pituitary hormones and hormones of pregnancy, and may in the future prove to be a valuable aid to our understanding of the hormonal background to individual and seasonal differences in behaviour.

B. The Measurement of Plasma Testosterone

1 Introduction

A number of methods have been used to assay plasma testosterone. These include gas-liquid chromatography (Brownie, Van der Molen,

Nishizawa and Eik-Nes 1964), double isotope methods (Riondel, Tait, Gut, Tait, Joachim and Little 1963), fluorimetric methods (Finkelstein, Forchielli and Dorfman 1961) and competitive protein binding assays (Horton, Kato and Sherins 1967). All these methods are capable of detecting nanogram quantities of testosterone but suffer from one or more practical drawbacks. Testosterone is only one of a number of 17-ketosteroids and others, such as aldosterone and cortisol, must generally be removed as they interfere with the detection technique. This requires the use of one or more purification steps, usually chromatographic, which can be tedious and time consuming as well as reducing the sensitivity of the assay. A further disadvantage is the comparatively large quantity of plasma required for a determination; this can be as much as 5ml. and is invariably more than 1ml., a quantity which cannot be removed from a vole without killing it.

The sensitivity of the radioimmuno assay described by Furuyama, Mayes and Nugent (1970) suggested an answer to these problems. The specificity of the assay is such that no purification steps are necessary as the only steroid that interferes to a marked degree, dihydrotestosterone, does not occur in significant quantities in male mice (Lucas and Abraham 1972). The assay will detect as little as 25pg. of testosterone which means that only 25-50µl. of plasma is required. This amount can be readily obtained from a small rodent without sacrificing it.

Although not itself antigenic, testosterone forms a complex with bovine serum albumin (BSA) to which antibodies can be raised in sheep or rabbits. The antibodies, which are very specific, are then purified and used in the radioimmuno assay, which is a competitive reaction. Testosterone extracted from the plasma sample and ^{3}H-testosterone are first bound to an excess of BSA. The two types of complex, one of which is radioactively labelled, then compete for binding sites on

a limited amount of the anti-testosterone antibody. After incubation, a dynamic equilibrium is established between the two types of testosterone-BSA complex so the more testosterone there was in the plasma sample the less ^{3}H-testosterone will be bound to the antibody. The free and antibody bound phases of testosterone can then be separated using dextran-coated activated charcoal and an estimation made of the proportion of ^{3}H-testosterone in each phase. ^{3}H-testosterone is detected by liquid scintillation counting, a technique which is responsible for the great sensitivity of the assay. As the method is comparative it is necessary to construct a standard curve by performing the assay with known amounts of testosterone. The proportion of ^{3}H-testosterone bound to the antibody is regressed on the amount of unlabelled testosterone added. The amount of testosterone in an unknown sample can then be found by reference to this standard curve. Details of the technique were adapted from the methods of Verjan, Cooke, De Jong, De Jong and Van Der Molen (1973) and Williams, Horth and Palmer (1974).

2 Materials

a) Standards

1, 2, 6, 7 (n) - ^{3}H-testosterone, S.A. 91 Ci/mMol. was obtained from the Radiochemicals Centre, Amersham. A stock solution in toluene-ethanol (9:1 V/V) containing approximately 20,000 dpm/50µl. was used. Testosterone B.P. was obtained from B.D.H. and standards prepared by serial dilution in n-hexane-ether (4:1).

b) Solvents and reagents

Ethanol 'Specially purified for the determination of 17-ketosteroids', toluene 'Aristar', diethyl ether 'Aristar' and n-hexane 'Analar' were obtained from B.D.H. Dextran coated charcoal was prepared by

dissolving 25mg. dextran (Sigma) in 100ml. of 0.05M borate buffer, pH 8.0, and adding 250mg. activated charcoal (B.D.H.);

3. Glassware

Assays were performed in conical glass centrifuge tubes which were siliconised with a solution of dimethyl-dichloro-silane in toluene.

4. Antiserum

Freeze-dried rabbit anti-testosterone antiserum (Searle), obtained by immunization of a rabbit with testosterone-3-BSA, was diluted to working strength with 0.05M borate buffer pH 8.0 containing 0.1% BSA (Sigma) and 0.1% NaN_3 as an antibacterial. This solution had a shelf life of six weeks at $4^{o}C$.

5. Tritium detection

Samples were dissolved in 5 or 10ml. of NE250 Scintillation Fluid (Nuclear Enterprises) and counted for 10 minutes in a Nuclear Enterprises automatic scintillation counter. Counting efficiency was 36.2%

C) Procedure

Plasma from male Clethrionomys and Apodemus was obtained as detailed on page 162. Samples of 25µl. for individuals or 50µl. for pooled samples were extracted by shaking with 1.5ml n-hexane-ether (4:1 V/V) for 60 seconds using a vortex mixer, and then centrifuged at 3000rpm for 5 minutes. In order to prepare the standard curve, known amounts of testosterone in the range 0-200pg. were added to

1.5ml. n-hexane-ether and treated in the same way. After centrifugation, 1ml. aliquots of the n-hexane-ether phase were transferred to clean tubes containing 100µl. (approx. 40,000dpm) of the ^{3}H-testosterone solution and evaporated to dryness under a stream of pure nitrogen; 450µl. of antiserum was then added to each tube. After mixing on a vortex mixer for 60 seconds the tubes were incubated overnight for 16 hours at 4°C to equilibrate the competition reaction. The following day 50µl. of the incubation solution was removed into a counting vial to estimate the total amount of ^{3}H-testosterone present and 500µl. of dextran coated charcoal was added to the remainder to separate the free and antibody bound testosterone. Following incubation at 4°C for 15 minutes, the tubes were centrifuged at 3000rpm for 10 minutes and 500µl. of the supernatant containing the antibody-bound testosterone removed into a counting vial. 5ml. of NE250 scintillator were added to the 'total estimation' vials and 10ml to the 'antibody-bound' vials and all were counted for 10 minutes.

In order to estimate the efficiency of the n-hexane ether extraction, aliquots of the ^{3}H-testosterone standards were added to pooled samples of rat plasma and treated as unknown samples.

D. Results and Discussion

1) Calculations

As this method is comparative it is not necessary to make an allowance for the efficiency of the counting system used. Quench correction is also unnecessary as the experimental and standard tubes all contain the same amounts of solvents and are thus quenched to the same extent.

The total amount, in cpm, of ^{3}H-testosterone in an assay tube is calculated from the count of the 50µl. sample taken after incubation.

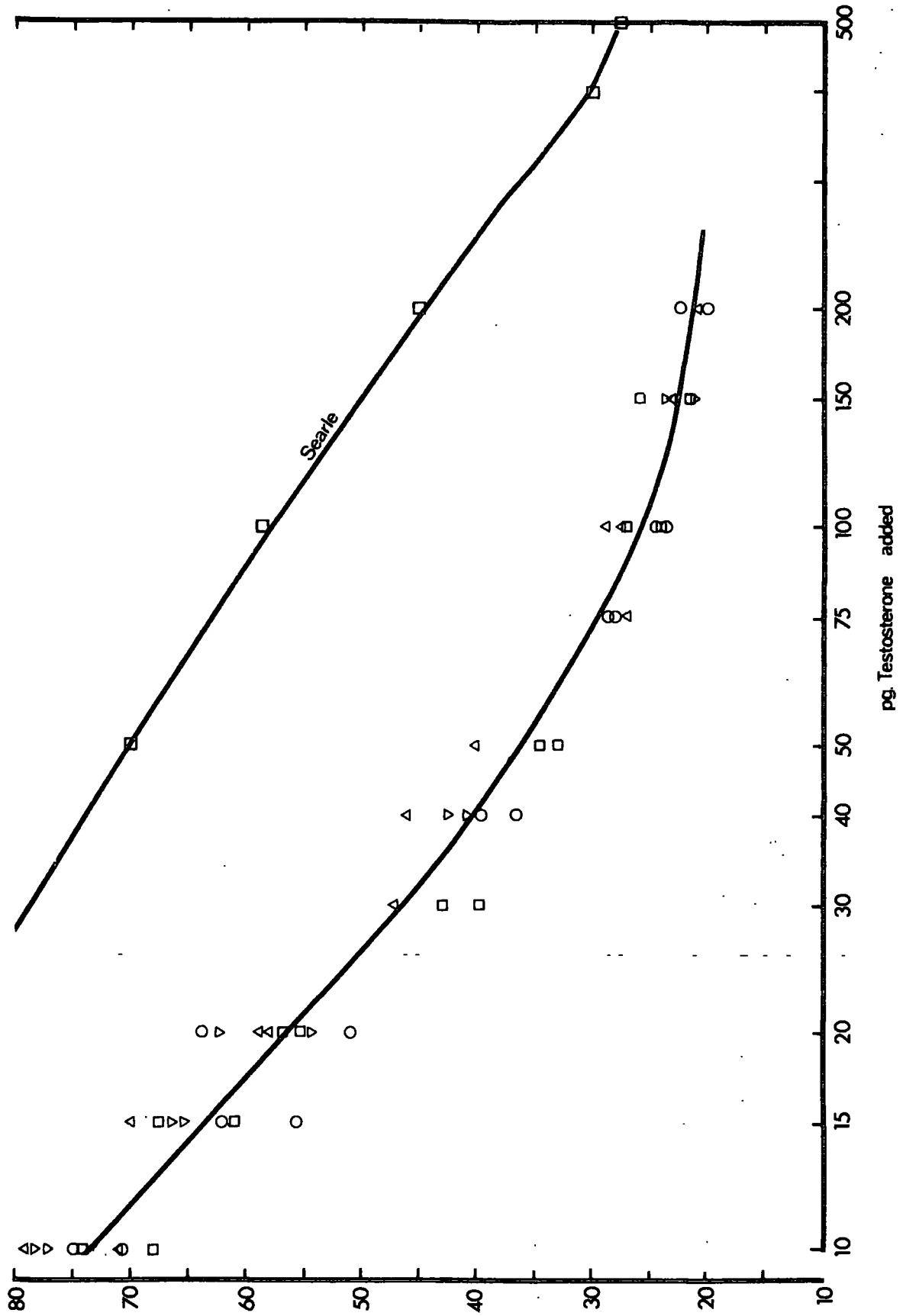


FIGURE 5.2 Testosterone assay standard curve. A curve supplied by the manufacturers of the antiserum is shown for comparison. Symbols indicate different experiments.

$$\text{Total } {}^{3}\text{H-T remaining} = \text{count of } 50\mu\text{l. sample} \times \frac{400 - 50}{50}$$

The amount of antibody-bound testosterone is calculated from the count of the second sample

$$\text{Total } {}^{3}\text{H-T antibody-bound} = \text{count of } 500\mu\text{l sample after incubation} \times \frac{350 + 500}{500}$$

From these two figures the absolute percentage of ^{3}H testosterone bound to antibody can be found

$$\text{Absolute \% bound} = \frac{\text{antibody bound } {}^{3}\text{H-T}}{\text{total } {}^{3}\text{H-T}} \times 100$$

The figure plotted on the standard curve is the relative % bound, found by equating the percentage bound when 0 pg. is added with 100%. The relative percentage bound is plotted against the logarithm of the amount of testosterone added. The quantity of testosterone in a sample of plasma is found by calculating the relative percentage of ^{3}H-testosterone bound and reading off the amount of testosterone present from the standard curve. This figure is then multiplied by a correction factor to account for the losses in the extraction procedure.

A typical standard curve is shown in Figure 5.2 together with a curve supplied by the manufacturers of the antiserum. There is some difference between the two as the result of the slightly different methods used. The curve obtained shows good sensitivity between 10 and 100 pg. although pipetting errors, which become sizeable when working with such small volumes, are responsible for the large increase in errors near the limit of sensitivity. For each experiment the standard curve was constructed using duplicate samples of each of the standards. The curve shown in the figure is a composite one containing the results of several different experiments and it can be seen that there is good agreement between the values obtained at different times.

^{3}H-T added µl	^{3}H-T added pg	No. of Observations	Mean proportion recovered(±s.e.)
25µl	40pg	6	.596±.021
50µl	82pg	6	.608±.029
100µl	165pg	6	.624±.029

Mean proportion recovered = 0.609 ± .016

TABLE 5.1 Proportion of testosterone extracted from plasma

a) Recovery Estimation

The efficiency of the solvent extraction was determined by adding either 25, 50 or 100µl. of ^{3}H-testosterone to an assay tube, evaporating the solvent and dissolving the testosterone in 25 or 50 µl. of laboratory rat plasma. The testosterone was then extracted from the plasma in the usual way and the proportion of ^{3}H-testosterone recovered estimated by counting a sample of the n-hexane-ether phase. As the specific activity of the ^{3}H-testosterone solution and the counting efficiency of the system used were known, it was possible to equate a particular count (in dpm) with a particular amount of testosterone. The results shown in Table 5.1 were obtained. Mean recovery from the plasma was 60.9% so all values obtained were adjusted to account for this.

b) Precision

As only one 25µl. plasma sample was available for each wild animal it was not possible to estimate the precision of the assay by performing duplicate analyses. A plasma pool from two male laboratory rats in breeding condition was therefore used. The testosterone content of this pool was assayed a number of times to provide an estimate of the precision of the assay. In 14 estimations, using either 25 or 50µl. plasma samples the mean testosterone level, uncorrected for procedural losses was 1.98ng/ml. with a S.D. of 0.415 giving a coefficient of variation of 8.66%. 95% confidence limits were 1.15-2.81 ng/ml. The mean testosterone level, after correction for procedural losses was 3.26ng/ml. which is within the range reported by Frankel, Mock, Wright and Kamel (1975).

E. Plasma Testosterone in Voles and Mice

Individual estimates of plasma testosterone are given in Table 5.2 for Clethrionomys and Table 5.3 for Apodemus. For both species there was a clear difference between the values for individuals in breeding condition, defined as the possession of scrotal testes, and individuals not in breeding condition. In the latter case values of below 10pg. in the assay were below the level of detection as this was the smallest standard used. Animals with partially scrotal testes in general showed values intermediate between breeding and non-breeding titres, though there was considerable variation. There thus appears to be correspondence between breeding condition, as defined by the presence of scrotal testes, and high plasma testosterone level, a result which is in agreement with numerous other studies (Lincoln 1974; Gordon, Rose and Bernstein 1976; Bramley 1970; Lincoln, Youngson and Short 1970). For Clethrionomys the mean value for individuals in breeding condition was 4.34 $\pm$ 0.37 (s.e.) ng/ml and for Apodemus 5.12 $\pm$ 0.34ng/ml. Both these values are within the range reported for laboratory house mice (Batty 1978a) but are a little higher than those found in laboratory rats (Damassa et al 1977). There was no evidence of the extreme variation between individuals reported for mice (see page 182) as the range of values was 0-6.6ng/ml. for Clethrionomys and 0-5.9ng/ml. for Apodemus.

The breeding cycle of Clethrionomys has already been described on page 61. The data from this study would suggest that the circulating level of testosterone is related to the size, and consequently, state of maturation (Clarke 1977) of the testes. Such a conclusion is not unexpected as in all seasonally breeding mammalian species which have been studied, both testicular growth and testosterone production are mediated by the pituitary hormones.

Date/Site	Breeding Status	Uncorrected T level pg/25µl	Corrected T level ng/ml.
May 1975	TS	70	4.6
Houghall	TS	100	6.6
June 1975	TS	85	5.6
Houghall	TS	52	3.4
	TS	36	2.3
	TS	90	5.9
	TS	65	4.3
July 1975	TS	58	3.7
Castle Eden	$T\frac{1}{2}S$	44	2.9
	Juv	0	0
July 1975	Juv	22	1.4
Houghall	TS	85	5.6
	TS	65	4.3
	TS	65	4.3
	Juv	0	0
Sept. 1975	Juv	0	0
Castle Eden	Juv	0	0
	TS	50	3.3
Jan. 1976	TNS	0	0
Castle Eden	TNS	0	0
	TNS	0	0
Feb. 1976	TNS	0	0
Houghall	TNS	0	0

Mean for TS animals = 4.34±0.37ng/ml.
Mean for TNS + Juv. animals not calculable as value of 0 indicates only that the value was below the sensitivity of the assay (approx 0.65ng/ml).

TABLE 5.2 Plasma testosterone levels in Clethrionomys.

TS = Individuals with scrotal testes.
TNS = Individuals without scrotal testes.
T = Testosterone.

Date/Site	Breeding Status	Uncorrected T level pg/25µl	Corrected T level ng/ml
June 1975	TS	70	4.6
Castle Eden	TS	67	4.4
	TS	98	6.4
	TS	68	4.4
July 1975	TS	79	5.2
Houghall	TS	89	5.9
	$T\frac{1}{2}S$	48	3.1
Sept. 1975	TS	85	5.6
Houghall	TS	75	4.7
	$T\frac{1}{2}S$	10	0.65
	$T\frac{1}{2}S$	24	1.6
Sept.1975	Juv	20	1.3
Castle Eden	TS	68	4.4
	TS	37	2.5
Nov. 1975	TNS	14	0.9
Castle Eden	TNS	0	0
Jan.1976	TNS	0	0
Castle Eden	TNS	0	0
	$T\frac{1}{4}S$	0	0
Feb.1976	$T\frac{1}{2}S$	49	3.1
Houghall	$T\frac{1}{2}S$	22	1.44
March 1976	$T\frac{1}{2}S$	81	5.3
Castle Eden	$T\frac{1}{2}S$	38	2.5

Mean for TS animals = 5.12±0.34ng/ml.
Mean for TNS + Juv. animals not calculable as value of 0 indicates only that the value was below the sensitivity of the assay (Approx 0.65ng/ml).

TABLE 5.3 Plasma testosterone levels in Apodemus.

TS = individuals with scrotal testes.
TNS = individuals without scrotal testes.
T = Testosterone.

Lincoln (1974) reported that in brown hares the testicular content of testosterone increased to a peak in March or April, some time after the testes had reached their maximum size and rate of sperm production. The time of this increase was well correlated with the onset of intense breeding activity or 'March madness'. After April the testosterone level decreased to about one third of its former value but sexual activity continued, albeit at a lesser intensity. The rate of spermatogenisis and the weights of the testes and sex accessory organs were maintained at this lower level until July or August. These findings suggest that a testosterone level even less than one third maximum was sufficient to maintain full breeding condition and that the spring peak in testosterone level was related to a behavioural phenomenon rather than a climatic one.

There is no evidence from the present study for a spring peak in testosterone levels in either species studied and the results available would suggest that the titre of testosterone rose concurrently with testis size. This difference between these species may be related to their different breeding strategies; hares showing a short peak of intense breeding behaviour over one or two months and small rodents a longer period of sustained breeding activity.

The April peak in hare testosterone levels reported by Lincoln (1970) may have been a consequence, rather than a cause of 'March madness', as it has been shown for several species (see Introduction to this chapter) that testosterone levels can be influenced, at least in the short term, by the social environment. The onset of testicular growth and sexual behaviour may be initiated by more central mechanisms such as changes in the pituitary or central nervous system. Such an interpretation is supported by the study of Lincoln, Guiness and Short (1972) who showed that testosterone played only a permissive role in the rutting behaviour of the red deer stag. The

administration of testosterone at an inappropriate time of the year failed to induce sexual behaviour although it had an effect on social aggression.

The results of the experiments described both here and in the Introduction suggest a dual role for testosterone in seasonally breeding small mammals. Firstly, the correspondence between the maturity of the testes and the secretion of testosterone may enable the pituitary to monitor the state of these organs (Damassa et al 1976) and initiate sexual and sexually-associated behaviour at an appropriate time. Secondly, testosterone has a directly stimulating effect on secondary sexual characteristics, particularly the growth of the sex accessory organs. This effect may by quantitative to some degree. Thus the maturation of the testes and onset of spermatogenesis is accompanied by the growth of these organs to the size required for successful breeding.

These observations suggest that the administration of testosterone at a natural level to a small mammal with regressed testes will fail to initiate both the growth of the testes and the appearance of sexual behaviour. There would however be growth of the sex accessory organs. Such an experiment does not appear to have been performed as all testosterone administration studies have used laboratory animals which breed throughout the year.

Although the presence or absence of a measurable level of circulating testosterone may provide a good guide to the breeding condition of an individual, there appears from previous studies (see Introduction) to be no relationship between individual titres of testosterone and any form of sexual or aggressive behaviour. Because of the unknown precision of the testosterone estimates and small range of values encountered during the present study, a comparison of

individual testosterone levels with individual aggression scores could have yielded no statistically satisfactory conclusions. As has already been pointed out on page 182 a single determination of plasma testosterone titre may be a poor index of the mean physiologically effective level of this hormone. For this reason as well as the fact that plasma testosterone levels are responsive to short term environmental factors, it seems unlikely that field experiments on small rodents, in which conditions must remain uncontrolled and unmeasurable, will provide much information about any relationship between hormone level and behaviour at the individual level.

CHAPTER 6

CONCLUSIONS

Watts (1969), after an analysis of 18 years trapping data from Wytham Woods, Oxford (Newson 1960; Smyth 1963; Watts 1966; Southern and Lowe 1968) suggested that several different mechanisms, some of them density dependent, were involved in the regulation of Apodemus populations. These conclusions were later extended to include Clethrionomys by Flowerdew (1971) though in this species the situation was complicated by the use of buffer habitats which were only occupied seasonally.

Both these authors and others (Bergstedt 1965; Hansson 1971; Flowerdew and Gardner 1978) have concluded that during the winter, survival is well correlated with the size of the autumn tree seed crop, a good crop resulting in high winter survival and an early start to breeding the following spring (Flowerdew 1973). Whilst this may be true in woodland where the food supply is dominated by favoured tree seeds such as oak, ash or beech, it may not be so in mixed sycamore woodland where the total seed crop is much smaller. Ashby (1967) found that sycamore seed was not a favoured food of voles or mice, being generally eaten in quantity only during winters when other foods were scarce in relation to rodent abundance. He concluded that the demand for seeds of this type was determined by a complex series of interactions including the availability of alternative foods, population density, interspecific competition and weather conditions during the winter. The occurrence together in mixed woodland of a wide variety of foods of varying palatability may make the overwinter survival of small rodents in this habitat less sensitive to annual variation in the availability of any one resource than is the case in largely monotypic woodland. This does

not rule out the possibility that food is limiting during the winter, but suggests that annual variation in the availability of any single food may be poorly correlated with overwinter survival. Ashby (1967) considered that the weather during the autumn had an influence on the length of the breeding season in both species, though the effect was more marked with Apodemus, warm dry autumns resulting in a prolongation of breeding. He suggested that such autumns were particularly favourable because they both reduced the demand for food and increased its availability. The overwinter survival of these species may therefore be influenced by an interaction between weather, food resources and the type of habitat.

Previous authors (Watts 1969; Flowerdew 1971; Flowerdew and Gardner 1978) have calculated overwintering success by comparing numbers caught in November or December with numbers caught in the following May or June. In many cases, for example the Apodemus population in Castle Eden during 1975-76, this leads to very high estimates of survival, sometimes greater than 1, despite the fact that the survival of marked animals may be rather poor. Overwinter success calculated in this way contains three separate components, winter survival, spring survival, and winter and spring immigration. Data from this and other studies have shown that winter and spring survival rates may be very different as there is often a marked decline in numbers during the spring, particularly in Apodemus. Winter and spring movements though not always detectable by trapping (Crawley 1965, 1969; Flowerdew 1976) may lead to considerable recruitment of unmarked individuals even in the absence of winter breeding. In mixed woodland, such as the two study sites, the winter distribution of food may be heterogeneous, encouraging individuals to move in order to take advantage of favoured food sources

as and when they become available.

Spring declines in numbers, though not common in Clethrionomys, are a feature of many Apodemus populations and have been attributed by Flowerdew (1978) to a combination of predation, starvation and dispersal. At Houghall much of the spring decline of Apodemus in 1975 could be attributed to emigration into the nearby fields. At Castle Eden there was not a particularly marked decline although Crawley (1965, 1970) reported a sharp drop in numbers associated with poor spring survival, suggesting that Apodemus were emigrating from the trapping area. A decline in the amount of arable land around the Dene has been suggested as the probable reason for this change in population dynamics.

Watts (1969, for Apodemus) and Flowerdew (1971, for Clethrionomys) concluded that the recruitment of juveniles during the summer was density-dependent so that high numbers of adults during the breeding season resulted in poor juvenile recruitment and vica versa. Other factors must also be involved, particularly in Clethrionomys, as in some years juvenile recruitment is insufficient to replace the number of old adults that disappear, resulting in a decline in density. The present study has been too short to investigate the problem of density dependence but the results of the distribution analyses have shown the importance of seasonally available buffer habitats in the population dynamics of Clethrionomys.

The very rapid increase in the numbers of Apodemus during the autumns of the present study has been attributed to immigration so that numbers at this time reflect breeding success and survival in this alternative habitat. Watts (1979) omitted woodland edge populations of Apodemus from his analysis of this species density regulation mechanisms in favour of populations 'living under more

natural conditions'. Whilst such migratory populations may only have become common since the advent of agriculture (Jeffries et al 1973) and large scale forest clearance they may now be as typical as populations living in continuous habitat. Since neolithic times the proportion of lowland Britain covered by trees has shrunk from 70 to 7 percent (Godwin 1956) and large areas are now covered by arable or grazing land interspersed with woods and hedgerows. Even in the remaining forests, large areas of continuous climax vegetation are rare, most woodland containing a mixture of natural and planted trees. Such a variety of trees will consequently provide a wide range of habitats and food resources within one piece of woodland.

The great mobility of Apodemus and its ability to exploit a wide range of habitats suggests that 'habitat-edge' migrations and movements may be a widespread feature of this species ecology. Movements of several hundred metres do not appear to be uncommmon (Watts 1970; Ashby unpubl.) so that the population dynamics of this species may be affected by migratory movements for some distance either side of a habitat discontinuity.

In Castle Eden Dene, Apodemus numbers appeared to be less influenced by migratory phenomena, though this has not always been the case (page 107). Changes in numbers at that site during 1974-75 were typical of those reported for continuous woodland or field habitats. The weight distribution of the young animals captured during September and October suggests that many of them were two or three months old, though few had been trapped previously. A similar age distribution is apparent from the work of Crawley (1965, 1970),; Watts (1969); Green (1978) and Gurnell (1978b), and suggests that the increase in numbers during the autumn is not solely the result of the improved survival of juveniles but can partially be attributed to an increase

in the willingness of subadults to enter the traps.

Though there is a little direct evidence for the behavioural regulation of juvenile recruitment in either Clethrionomys or Apodemus the annual cycle of aggression of male Clethrionomys reported in Chapter 3 shows that seasonal changes in behaviour do occur, with most intermale aggression being shown at the start of the breeding season. The greater aggressiveness in the laboratory of overwintered males of this species, than subadult individuals maturing in the year of their birth suggests that it is the disappearance of the former which permits an increase in juvenile and subadult recruitment during the autumn. Whether such a hypothesis applies to Apodemus is still uncertain as whilst Flowerdew (1971) was able to show that the presence of adults had an adverse effect on the growth of juveniles in the laboratory, he was unable to demonstrate any aggression between adults. More recently Gurnell (1978b) has reported that except for a short period at the start of the breeding season, male Apodemus usually behave amicably towards one another.

The type of agonistic behaviour which in the wild causes the majority of juveniles of both species to disperse from their place of birth, is unknown. The results of the few observational studies available suggest that the sort of overt aggression observed in the laboratory, particularly in Clethrionomys, may not be common in the wild, though it should be noted that nothing is known about the behaviour of either species in their burrow systems, which can be extensive (Ashby, unpubl.). Though few fights have been observed at artificial feeding stations (Kikkawa 1964; Greenwood 1974, 1978; Bullock 1977; Gipps 1977), wounded individuals, usually adult males (Rose and Gaines 1976), are not uncommon during the breeding season, so some fighting must occur. Whether juveniles are ever involved

in such fights is unknown but displacement from feeding sites by adults may be common. The stratification of times of emergence to feed, with dominant individuals appearing first (Gliwicz 1970; Garson 1975) suggests one way in which juveniles may be forced to disperse. They may be constrained to emerge at such an unfavourable time, or be displaced so often from favourable feeding sites, that they have insufficient time or opportunity to feed and are thus forced to migrate in an attempt to find an area where there is less intraspecific competition.

The results of the genetic analysis of Clethrionomys together with those of Berry and his co-workers (review: Berry 1977) have suggested that in rodent populations which shown only annual cycles of numbers, changes in allele frequency in many polymorphisms may be local and temporary responses to environmental heterogeneity. In this respect they differ from those reported by Krebs and his co-workers (reviewed Krebs and Myers 1974) who found changes in allele frequency at a number of loci to be in phase with the three to four years population cycle. Such changes have, however only been studied for the duration of one cycle. Although Krebs has been unable to ascertain whether the genetic changes are the cause or the consequence of the population cycle he has concluded that such changes are an integral part of the population ecology of these species. The size of these changes has been taken as an indication of the strong selection pressures presumed to be operating at times of rapid population density changes.

The relationship between genetic changes in annual and perennial population cycles is far from clear. Perhaps the non-cyclical nature of the genetic changes in annually fluctuating populations is a reflec-

tion of the relatively weak selection operating on such populations and the short time for which selection operates in one direction. There does not appear to be a fundamental genetic control of whether a species will undergo population cycles as some populations of a species may show perennial cycles whilst others do not (Lidicker 1973; Krebs and Myers 1974). Rasmuson, Rasmuson and Nygren (1977) claim to have found inherited differences in behaviour between cycling and non-cycling populations of Microtus agrestis from different parts of Sweden, but have not yet shown that these would be solely a consequence of the difference in population dynamics.

A number of ways in which a polymorphism might be maintained in a population have been discussed in Chapter 4. There is increasing theoretical evidence that environmental heterogeneity might be sufficient to maintain a polymorphism in the absence of heterosis, if the fitness of different morphs depends on their local environment. Gilpin (1975) has suggested that a situation in which extinction and recolonisation are frequent events, would enable group selective pressures to produce evolutionary change at an appreciable rate. The organisation of small mammal populations in which there may be a demic structure, limited migration, utilisation of buffer habitats and a short lifespan may be particularly effective at maintaining polymorphisms. Although Clethrionomys appears to have rather few detectable enzyme polymorphisms, Bathgate (1978) has shown that this species is morphologically rather variable so that its genome as a whole may not be deficient in variability.

The ease with which environmental heterogeneity can maintain a polymorphism may depend on the 'patchiness' of the environment as experienced by the individual (Weins 1976). A 'coarse grained' species, which exhibits patch selection, may be subject to different

selection pressures in different patches, and may occupy small patches where drift and founder effects become important. Under such conditions there should be a high degree of polymorphism (Maynard Smith 1970; Gillespie 1974a, b). For fine grained species, which react at random to environmental patchiness, there are two conflicting theories. Some investigators have suggested that, as all members of a species encounter the same average environment, a 'general purpose' genotype should be selected (Selander and Kaufman 1973), while others have maintained that high variability would be preserved to deal with all eventualities (Bryant 1973).

Since the present study has shown that Clethrionomys is not distributed at random with respect to its environment, it therefore tends towards being a coarse grained species. Such an interpretation is in agreement with the results of the genetic analysis which has suggested that this species may respond rapidly to short term environmental changes. Much more research is required on both the population structure and genetic constitution of small rodent species before the significance of such gene frequency changes can be fully understood.

The results of the endocrinological experiments reviewed in Chapter 5 appear to show that in small rodents testosterone plays only a permissive role in the display of sexual and aggressive behaviour. Although the present study has been unable to investigate the apparently unlikely possibility of a quantitative relationship between plasma testosterone levels and aggressive behaviour, it has shown that the spring increase in testosterone level is coincident with the growth of the testes and an increase in the level of male sexual behaviour. Other authors reaching a similar conclusion have been referred to in Chapter 5.

The results of two recent studies appear to support the view that testosterone stimulates the growth of the sex accessory organs but has only a permissive role in the control of behaviour. Krebs, Halpin and Smith (1977) implanted testosterone propionate pellets into intact male Microtus townsendii in an effort to increase their aggressive behaviour and perhaps influence their spring population dynamics. The pellets were implanted during January, some weeks before the start of the breeding season. As predicted by earlier studies (page 183) the increased level of testosterone failed to advance the onset of breeding or increase the level of aggressive behaviour, but there was some evidence that the growth of hip glands was accelerated. Morin, Fitzgerald, Rusak and Zucker (1976) reported that in castrated hamsters kept under short photoperiods, testosterone injections failed to increase the display of copulatory behaviour although it is known that under longer photoperiods testosterone is effective in this respect. As in the experiment of Krebs et al, the testosterone resulted in an increase in the size of the sex accessory organs, even under short photoperiods.

There is thus much evidence that testosterone, produced by the testes during spermatogenesis, is acting as a 'trigger' to initiate patterns of sexual and sexually-oriented aggressive behaviour at an appropriate time of the year. The evolutionary advantage of such a feedback loop is clear, as for an individual to exhibit these behaviours before spermatogenesis is complete would be a waste of resources and thus lead to a reduction in evolutionary fitness.

SUMMARY

1. The population dynamics, aggressive behaviour, population genetics and plasma testosterone levels of two populations of bank voles, Clethrionomys glareolus and the population dynamics and plasma testosterone levels of wood mice, Apodemus sylvaticus have been studied in mixed woodland in Castle Eden Dene and Houghall Woods, County Durham.

2. At Castle Eden there are large areas of perennial herbs, notably dog's mercury Mercurialis perennis, giving seasonal ground cover only, interspersed with small areas of permanent cover, while at Houghall seasonal changes in the degree of cover are smaller. Rodents were captured by live trapping at intervals of approximately 4 weeks during the summer and 8 weeks during the winter from July 1974 to May 1976. At Castle Eden a 90 x 90m. trapping grid, with adjacent traps 10m. apart, was laid out and trapped for 3 days after 2 days prebaiting. At Houghall the 3 transects laid out by Ashby (1967) were used, to maintain the continuity of his study. Each transect consisted of two parallel lines of 20 traps 9.14 metres. apart, adjacent traps being separated by 5.94 metres. The trapping period consisted of 2 days prebaiting followed by 2 days trapping.

3. The total number of individuals caught was 425 Clethrionomys and 272 Apodemus at Castle Eden and 388 Clethrionomys and 247 Apodemus at Houghall, giving a preponderance of Clethrionomys at both sites. Mean trap mortality of Clethrionomys was 13.3% at Houghall and 5.6% at Castle Eden. The high figure at Houghall is reduced to 10.4% if an allowance is made for delayed trap inspection during October 1975, but mortality at this site was still significantly higher than at Castle Eden, perhaps

because of local weather conditions. Trap mortality of Apodemus was negligible. The trap-revealed sex-ratio of Clethrionomys was 1.06 males per female at Castle Eden and 1.36:1 at Houghall. For Apodemus the ratios were 1.47:1 at Castle Eden and 2.19:1 at Houghall. The greater excess of males at Houghall may be the result of the trapping technique employed there.

4. Population size was estimated using the following capture-mark-recapture methods; the calendar of captures, Petersen estimator, Haynes regression and Jolly's method. An additional method assumed that a constant proportion of the population was seen at each trapping session. A comparison of results suggests that with large sample sizes and a high proportion of re-captures, Jolly's method applied over the whole study period yields estimates with acceptable confidence limits but that with small samples and relatively few recaptures this method fails. The results of all the methods should then be compared and any very high or low ones rejected.

5. Absolute densities were estimated by two methods at Castle Eden and one at Houghall. The first, applicable at both sites, adds a boundary strip equal in width to the mean radius of the home range, taken as 23m. for Clethrionomys and 26m. for Apodemus. The second, applicable only to grid trapping, relies on the theoretical decline in the probability of capture from the edge to the centre of the grid. This suggested a boundary strip of 10m. for Clethrionomys but did not yield an estimate for Apodemus as the probability of capture of this species did not decline. It is concluded that this latter method may not apply in the present instance. Densities

calculated by the home range method varied between 6 and 29 per hectare for Clethrionomys and between 0 and 29 per hectare for Apodemus.

6. Changes in numbers at the two study sites were similar to those described by other workers. The Clethrionomys populations were at a minimum during the first three months of the year and in 3 cases out of 4 reached a maximum during the autumn. At Houghall, the population of Apodemus disappeared almost completely during the summer then increased rapidly during the autumn, while at Castle Eden there was less variation between summer and autumn population sizes.

7. Weight data confirm that Clethrionomys do not grow during the winter but increase rapidly in weight during the spring. In contrast, Apodemus continue to grow throughout the winter with no evidence for an increased rate of growth during the spring. Large Clethrionomys lost weight during the autumn so that in January and February all individuals weighed between 11 and 15g. The growth of the young of both species appeared to be slower during the autumn than the early summer. The length distributions provided an unreliable index of the age structure of the population because of a change in measurement technique with experience.

8. Survival was calculated from the recapture of marked animals and converted to a monthly survival rate by a logarithmic transformation. Estimates varied between 0.43 and 0.94 per month for Clethrionomys and 0.24 and 0.89 per month for Apodemus. The weighted mean monthly survival at Castle Eden and Houghall respectively was 0.698 and 0.717 for Clethrionomys and 0.677 and 0.581 for Apodemus. Survival of both species was generally

better during the winter than the summer, with a spring decline in survival commencing before the recruitment of any young. At Houghall the poor trap-revealed spring survival of Apodemus was probably the result of emigration to nearby fields.

9. At both sites the continuous recruitment of unmarked adults of both species showed that many individuals shifted their home range from time to time. The autumn recruitment of Apodemus at Houghall was too large in both years to be attributable to breeding within the wood and in 1974 contained both overwintered adults and young of the year. It is concluded that at this site Apodemus migrate into the woods from the fields during September. At Castle Eden the autumn recruitment of this species was high in 1974 but not 1975 and in both years could be accounted for by reproduction in the trapping area. In 1975 the rate of recruitment of Clethrionomys at Castle Eden was high at the start of the breeding season then declined, whereas the reverse was true at Houghall. This difference is attributed to differences in vegetation between the two sites.

10. The distribution of captures of the two species was related to the density of vegetation around each trap position. At both sites the distribution of Clethrionomys was positively correlated with the density of vegetation so that at Castle Eden this species showed a markedly aggregated distribution, particularly during the winter. Apodemus, by contrast, was in general distributed at random with respect to the vegetation, though at Castle Eden it showed a tendency to avoid areas of thick cover during the summer. It is concluded that the use of seasonally available habitats plays an important role in the

distribution of Clethrionomys, allowing juveniles to avoid to some degree, competition with older animals. The dependence of this species on the availability of suitable cover may account for much of the variability from year to year in its population dynamics.

11. It is concluded from a discussion of the literature that there is much circumstantial evidence for the regulation of small rodent population densities by social behaviour. Direct evidence is, however, lacking, as these species social behaviour is not well documented. The aggressive behaviour of Clethrionomys was studied in the laboratory by observing neutral cage encounters between pairs of males removed temporarily from the trapping areas. Recently captured individuals showed little interaction, which experiments showed to be due to their unfamiliarity with the testing situation. An annual cycle in the level of aggressive behaviour was observed, with a maximum at the start of the breeding season declining to a minimum during the winter. Overwintered males were the more aggressive and were generally dominant to those which matured in the year of their birth. Though the results may be interpreted as supporting a hypothesis of the limitation of juvenile recruitment by adult aggression, the applicability of laboratory results to the field situation is questioned as previous studies have suggested that intraspecific avoidance may be as important as overt aggression.

12. From a review of previous studies on genetic changes in small rodent populations it is concluded that genetic changes in cycling and non-cycling populations may be related. A plasma esterase polymorphism of Clethrionomys was studied by starch-

gel electrophoresis. At Castle Eden estimated allele frequencies did not show any significant change during the study period but at Houghall the estimated frequency of the fast allele varied significantly between 0.15 and 0.43. This change took place during the exceptionally dry summer of 1975. There was no evidence for an annual cycle in the frequency of this allele and it is concluded that the genetic change was a localised response to temporary environmental conditions. Similar genetic changes have been reported by other workers.

13. From a survey of the literature it is concluded that testosterone plays only a permissive role in the maintenance of aggressive behaviour, with a threshold well below the range of values found in normal males. Individual variation in aggression appears to be controlled by more central mechanisms and is markedly influenced by experience. A radioimmunoassay was developed for assaying testosterone levels in small samples of rodent plasma. The results confirm that testosterone levels are high in breeding individuals and low in non-breeding ones. Mean levels for breeding individuals were 4.34ng/ml. for Clethrionomys and 5.12ng/ml for Apodemus. Levels in non-breeding individuals were below the sensitivity of the assay of 0.65ng/ml.

14. It is concluded that the ecological and behavioural data for Clethrionomys are compatable with a theory of intrinsic population regulation mediated via the limitation of juvenile recruitment by adult agonistic behaviour. For this species, however, the availability of suitable vegetational cover may be the proximate factor limiting population density in mixed woodland. The distribution of Apodemus, though relatively

independent of cover, appears to be markedly influenced by seasonal changes in the attractiveness of different habitat types, so the great mobility of this species must be considered when studying its demography. In mixed woodland of the present type the overwinter survival of both species is unlikely to be correlated with the availability of any single food resource as the tree seed crop is small.

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APPENDIX 1

Calendar of Captures

Trapping dates

Castle Eden Dene

21-23 August 1974
2- 4 September 1974
15-17 October 1974
15-17 January 1975
13-15 May 1975
12-14 June 1975
16-18 July 1975
4,5,9,10 September 1975
11-13 November 1975
21-23 January 1976
25-27 March 1976

Houghall Woods

10-11 July 1974
12-13 September 1974
29-30 November 1974
5- 6 March 1975
22-23 May 1975
26-27 June 1975
31 July - 1 August 1975
18-19 September 1975
16-17 October 1975
19-21 November 1975
19-20 February 1976
6- 7 May 1976.

Key to tables

Number - individual toeclipped numbers
S - Sex
G - Genotype
  S = slow banded
  F = fast banded
  H = heterozygote
x - Captured and released
D - Captured but dead.

Calendar of Captures Clethrionomys. Castle Eden Dene

No.	S	G	Aug'74 1 2 3	Sept'74 1 2 3 4	Oct'74 1 2 3	Jan'75 1 2 3	May'75 1 2 3	June 1 2 3	July 1 2 3	Sept 1 2 3	Nov
0001	M		x								
0003	F			x x x x	x x x	D					
0032	F			x							
0100	F		x	x x x x	x						
0101	F		x	x							
0102	M	S	x x								
0103	M	S	x x	x x x x	x x x						
0104	M	S	x	x x x							
0105	M		x								
0200	F		x x	x x x x		x					
0201	M		x	x x							
0202	M		x								
0203	F		x	x x	x x	D					
0204	M	H		x x x x	x						
0205	F	F		x x	x		x	x			
0210	M	S		x x							
0220	F			x x x x							
0220a	M	S		x x x	x x						
0230	F	S		x	x						
0240	M	H		x x x x	x x x						
0250	M			x							
0300	M	S		x x x			x	x	x x	x x	
0301	M	F		x x							
0302	F	H		x							
0303	F	S		x							
0304	F	S		x x x							
0305	F			x x x x							
0310	M	H		x x	x						
0320											
0330	F	S		x		x	x x x	x			
0340	M	H		x x x	x x x						
0350	M			x x							
0400	F	S		x x	x x						
0401	M	F		x x							
0402	F	S		x x x	x	x x x	x x x	x x x			
0403	F			x	x						
0404	M			x							
0405	M	S			x x x						
0410	F	S			x x						
0420	F				x x						
0430	M				x						
0440	M	S			x						
0450					x						
1000	F	H			x						
1001	F	S			x						
1002	F				x						

No.	S	G	Oct'74 1	2	3	Jan'75 1	2	3	May'75 1	2	3	June'75 1	2	3	July 1	2	3	Sept 1	2	3	Nov. 1	2	3	Jan'76 March 1	2	3
1003	M	S	x				x																			
1004	M	S	D																							
1005	F	S	x	D																						
1010	M	H	x																							
1020	M		x		x																					
1030	M	S	x						x																	
1040	M	H	x			x	x				x		x	x			x	x								
1050	F		x																							
1100	M	S	x	x																						
1200	F			x		x		x		x			x	x												
1300	M	H		x			x																			
1400	M			x							x															
2000	M			x	x																					
2000a	F	F		x	D																					
2001	M	S		x																						
2002	F	H			x		x	x			x															
2003	M				x	x	x	x																		
2004	F	S				x								x	x											
2005	F	H				x		x			x		x	x	x	x	x	x					x			
2010	M	S				x				x			x	x	x	x	x	x	x							
2020	F						x		x	x																
2030	M	S						x																		
2040																										
2050																										
2100																										
2200	M	S							x	x	x		x		x											
2300	M	H							x		x			x		x	x									
2400	M	H							x				x	D												
3000	F	S							x	x	x			x	x											
3001	M	S							x	x			x		x											
3002	M	S							x		x		x													
3003	F	H							x		x															
3004	M	S								x	x					x	x	x	x	x	x	x	x			
3005	M	S								x							x	x								
3010	F	F									x			x												
3020	F	H												x			x									
3030														x												
3040	M													x	x			x	x		x					
3050	M	S													x	x	x	x								
3100	F	S													x		x	x								
3200	F														x			x								
3300	F	S														x										
3400	M	H														x			x							
4000	F	S														x		x								
4001	F	F														x	x									
4002	F	S														x	x	x	x	D						

No.	S	G	July '75 1 2 3	Sept. 1 2 3	Nov. 1 2 3	Jan. 1 2 3	March 1 2 3
4003	F	H	x				
4004	M	S	x x	x			
4005	F	S	x x	x x	x x	x	
4010	M	H	x		x		
4020	M		x x				
4030	F	S	x x	x			
4040	M	S	x x x				
4050	M	S	x x				
4100	M	S	x				
4200	M	F	x x x				
4300	M	S	x x				
4400	M	H	x x	x			
0001	F	S	x				
0002	M	S	x x	x			
0003	M	H	x x				
0004	M		x				
0005	M	H	x				
0010	F	S	x	x			
0011	M	S	x	x			
0012			x				
0013	F	H		x			
0014	M	H		x x	D		
0015	M	H		x	x		
0020	M			x			
0021	M			x	x		x
0022	M	H		x	x		
0023	M	S		x			
0024	M	S		x			
0025	M			x			
0030	M	S		x	x	x	x
0031	M	S		x			
0032	F			x			
0033	M	H			x		
0034	M	H			x		x
0035	F	S			x x	x	
0040	F	H			x		
0041	M	F			x		x x
0042	F	S			x		
0043	M	S			x		
0044	F	H			x		D
0045	F	H			x		
0050	F	F				x	
0051	M	H				x	x
0052	M	H				x	
0053	F	S				x	
0054	M	S				x	
0055	F	S				x	
0100	F						x
0101	F						x
0102	F	H					x
0103	M	S					x
0104	F	S					x

Calendar of Captures, Clethrionomys, Houghall Woods

No.	S	G	July'74 1 2	Sept 1 2	Nov 1 2	Mar'75 1 2	May 1 2	June 1 2	July 1 2	Sept 1 2	Oct 1 2	Nov 1 2 3
0001	M		x x									
0002	M		x	x x	x x							
0010	M		x x									
0011	F		x x									
0015	M		x x	x								
0030	F			x x								
0031	M	H	x x									
0032	M	H										
0033	M	S	x									
0034												
0035												
0040	M			x								
0041	F	F	x	x								
0042	M	S	x			x x	x x					
0043	F		x									
0044	M		x	x x								
0045	F	H		x								
0050	F			x								
0051	M	H		x								
0052	F	S		x			x	x	x	x x	x	
0053												
0054	M			x								
0055	F	S		x								
0100	M	H		x								
0101	F	S		x								
0102	M	H		x		x						
0103	F	H		x								
0104	F	H		x								
0105	F	S		x								
0200	M			x								
0201	M			x								
0202	F	H		x								
0203	M			x								
0204	M	H		x	x		x					
0205	M	S		x	x	x	x	x			x	x x
0210	M			x								
0220	M	F		x	x x							
0230	F			x			x	x	x			
0240	M	H		x	x							
0250	F	H		x								
0300	M	S		x								
0301	M	F			x x							
0302	M	F			x		x x	x	x x			
0303	M	S			x	x	x x	x x				
0304	M	S			x x							

No.	S	G	Sept'74 1 2	Nov 1 2	March 1 2	May 1 2	June 1 2	July 1 2	Sept 1 2	Oct 1 2	Nov 1 2 3	Feb 1 2	May 1 2
0305	M	S		x									
0310	F		x	x x		x x							
0320	F	S		x				x	x		x		
0330				x		x							
0340	F	S			x								
0350	F	S			x								
0400	M	S			x x	x x	x	x					
0401													
0402													
0403	M	H				x	x x						
0404	M	S				x x		x					
0405	M					x x							
0410	M	S				x							
0420	M	S				x							
0430	F						x						
0440	F	S					x						
0450	M						x x	x					
1000	F	H					x						
1001	F						x x	x x			x		
1002	F	S					x x						
1003	F	S					xx						
1004	M	H					x	x x	x x				
1005	M	S					x				x		
1010	M						x						
1020	M						x	x					
1030	M	S					x	x					
1040													
1050	F						x						
1100	M	S						x					
1200	M							x x	x				
1300	M							x D					
1400	M	S						x					
2000	M	S						x	x				
2001	M	H						x					
2002	M	S						x	x				
2003	M	S						x x					
2004	F	S						x	D				
2005	F							x					
2010	F							x			x		
2020	F							x	x				
2030	F	F							x x		x		
2040	M	S							x				
2050	F	F							x				
2100	F								x				
2200	F	H							x				

No.	S	G	Sept'75 1	2	Oct 1	2	Nov 1	2	3	Feb'76 1	2	May 1	2
2300	F	S	x										
2400	M	S	x	x		x		x					
3000	F	S	x	x									
3001	F		x	x									
3002	F	H	x	x									
3003	M	S		x	x		x	x					
3004	M	H		x		x		x	x				
3005	F	H		x									
3010	M	H			x								
3020	M	S			x			x					
3030	M	F			x							x	x
3040	M				x		x	x	x	x			
3050	M	H				x							x
3100	M	S					x	x					
3200	F						x	x					
3300	F	S					x		x				
3400	M						x			D			
4000	M	S					x						
4001	F	F					x			D			
4002													
4003	M	F					x						
4004	M	F						x					
4005	F	S						x		x			
4010	M	H						x					
4020	F	F						x					
4030	M	F						x				x	x
4040	F	S							x				x
4050	M								x				
4100	F	F							x			x	
4200	F								x				
4300	M	H								x			
4400	M									x			
0001	M									x		x	
0002	F	S								x			
0003	F	S								x			
0004	M	S										x	
0005	M	S										x	

Calendar of Captures, Apodemus, Castle Eden Dene.

No.	S	Aug'74 1	2	3	Sept 1	2	3	4	Oct 1	2	3	Jan'75 1	2	3	May 1	2	3	June 1	2	3	July 1	2	3
0002	M			x			x																
0003	F						x																
0004	M					x																	
0005	F			x																			
0022	M	x																					
0041	M						x																
0100	F	x																					
0107	M	x		x																			
0102	F		x	x			x	x	x														
0103	M		x	x																			
0104	M		x							x	x												
0105	F		x	x	x						x		x										
0200	F		x		x		x																
0201																							
0202	M				x																		
0203	M				x		x	x															
0204	F				x	x			x	x	x	x	x	x									
0205	M				x	x																	
0210	M				x																		
0220	M				x			x															
0230	M				x			x						x	x			x	x				x
0240	M				x																		
0250																							
0300	M					x																	
0301	M					x	x	x															
0302	M					x	x																
0303	F					x	x																
0304	M						x			x	x												
0305	M						x																
0310																							
0320																							
0330																							
0340																							
0350																							
0400	M							x				x			x	x							
0401	M							x															
0402	M								x														
0403	F								x														
0404	M								x														
0405	F								x	x	x												
0410	M								x			x	x	x									
0420	M								x														
0430	F								x														
0440	M								x		x												
0450	M								x				x	x									
1000	M								x	x		x	x	x	x		x						

No.	S	Oct 1 2 3	Jan 1 2 3	May 1 2 3	June 1 2 3	July 1 2 3	Sept 1 2 3	Nov 1 2 3	Jan'76 1 2 3
1001	M	x x x							
1002	M	x x x							
1003	F	x x x							
1004	M	x x	x						
1005	F	x x	x x	x x x					
1010	M	x							
1020	F	x							
1030	M	x x							
1040	F	x x							
1050	M	x x x	x x	x x x					
1100	M	x	x x	x x					
1200	F	x x							
1300	M	x							
1400	F		x						
2000	M	x							
2001	M	x							
2002	M	x	x x x	x	x				
2003	M	x							
2004	F	x				x x x			
2005	M	x							
2010	M	x							
2020	M	x							
2030	M	x							
2040	M	x x	x x x						
2050	F	x x	x x x						
2100	F	x		x					
2200	F	x x							
2300	F	x							
2400	M	x	x x						
3000	F	x	x x x						
3001	F	x	x		x				
3002	F	x	x x	x	x x x		x		
3003	M	x	x x	x x	x x				
3004	M		x x						
3005	F		x x x	x	x x x	x	x x		
3010	F		x						
3020	M		x x x	x x	x x x	x x x			
3030	M		x						
3040	M		x x x						
3050	F		x						
3100	F		x x						
3200	M		x						
3300	F		x						
3400	M		x						
4000	M		x						
4001	M		x x						

No.	S	Jan'71 1 2 3	May 1 2 3	June 1 2 3	July 1 2 3	Sept 1 2 3	Nov 1 2 3	Jan'76 1 2 3	Mar 1 2 3
4002	M	x x	x x x	x					
4003	F	x x							
4004	F		x			x			
4005	F		x x	x	x				
4010	M		x x	x x x	x				
4020	M		x						
4030	F		x x		x x				
4040	F		x	x	x				
4050	M			x x					
4100	M				x				
4200	F				x x		x x		
4300	M				x				
4400	F				x				
0001	F				x	x x			
0002	M				x				
0003	M				x				
0004	M				x				
0005	M					x			
0010	M					x			
0011	M					x			
0012	M					x x x			
0013	M					x			
0014	M					x			
0015	M					x			
0020	F					x			
0021	M					x			
0022	M					x		x	
0023	F					x			
0024	M					x		x	x
0025	F					x			
0030	M					x			
0031	F					x	x x	x x x	
0032	M					x			
0033	F					x	x x		
0034	F					x	x x		x x
0035	M					x		x	x
0040	F						x	x	
0041	F						x x		
0042	M						x x		
0043	F						x x	x x	x
0044	F						x		
0045	M						x x	x x	x
0050	F						x	x	x
0051	M						x	x x	
0052	M						x		
0053	M						x x	x x	

No.	S	Nov. 1	Nov. 2	Nov. 3	Jan 1	Jan 2	Jan 3	March 1	March 2	March 3
0054	F		x							
0055	M			x	x					
0100	M			x						
0101	F				x				x	
0102	M				x					
0103	M				x				x	x
0104	M				x					
0104a	M				x		x		x	x
0105						x			x	x
0110	F					x				
0120	M						x			
0130	M						x		x	x
0140	F						x			
0150	F						x			
0200	F							x		
0201	M							x		
0202	F							x		
0203	M								x	
0204	M								x	
0205	M								x	x
0210	M								x	x
0220	M									x

Calendar of Captures, Apodemus, Houghall Woods.

No.	S	July'74 1	July'74 2	Sept 1	Sept 2	Nov 1	Nov 2	Mar'75 1	Mar'75 2	May 1	May 2	June 1	June 2
0050	F	x	x		x								
0051	M			x			x						
0052	F			x									
0053	F			x	x	x	x						
0054	M			x	x	x	x						
0055	M			x	D								
0100	M			x									
0101	F			x	x								
0102	F			x	x								
0103	F			x									
0104	F			x									
0105	M			x		x		x	x				
0110													
0120													
0130													
0140													
0150													
0200	M			x		x	x		x				
0201	M			x	x								
0202	M			x	x								
0203	F			x									
0204	F			x									
0205	M			x	x				x				
0210	M				x								
0220	M				x	x							
0230	M				x								
0240	F				x								
0250	M				x								
0300	M				x						x		
0301	F				x								
0302	M				x	x		x	x				
0303	M				x								
0304	M				x			x	x				
0305	F				x								
0310	F				x								
0320	M				x		x						
0330	M				x								
0340	M				x								
0350	M				x								
0400	F				x								
0401	M				x								
0402	F				x								
0403	F				x								
0404	M				x								
0405	M				x								
0410	M				x								

No.	S	Sept'74 1	2	Nov 1	2	Mar'75 1	2	May 1	2	June 1	2	July 1	2	Sept 1	2	Oct 1	2
0420	M		x														
0430	M		x														
0440	M		x														
0450	F		x														
1000	F		x														
1001	M		x														
1002	F		x														
1003	M			x													
1004	M			x													
1005	M			x	x												
1010	F			x													
1020	M			x		x	x										
1030	F			x	x												
1040	M			x		x	x										
1050	M			x		x											
1100	M			x	x		x	x									
1200	F			x													
1300	M			x													
1400	M			x	x												
2000	F			x	x												
2001	F			x													
2002	F			x													
2003	M			x													
2004	F			x	x		x		x	x				x			
2005	F			x	x	x											
2010	M			x	x												
2020	M			x		x											
2030	F				x												
2040	M				x												
2050	F				x												
2100	M				x	x											
2200	M				x												
2300	M					x	x										
2400	F					x											x
3000	F					x		x	x								
3001	M					x											
3002	M					x											
3003	M						x										
3004	M						x										
3005	F						x										
3010	F						x										
3020																	
3030																	
3040																	
3050																	
3100	M						x										

No.	S	May 1	May 2	June 1	June 2	July 1	July 2	Sept 1	Sept 2	Oct 1	Oct 2	Nov 1	Nov 2	Nov 3	Feb'76 1	Feb'76 2	May 1	May 2
3200	F	x	x															
3300	M	x	x															
3400	F			x														
4000	M							x					x		x			
4001	M							x	x	x	x							
4002	M							x	x									
4003	F							x		x	x							
4004	M							x										
4005	M							x			x							
4010	M							x		x		x					x	
4020	M							x			x							
4030	M							x		x	x							
4040	M							x										
4050	M								x		x							
4100	M								x			x		x			x	x
4200	M								x									
4300	M									x								
4400	M									x								
0001	M									x	x							
0002	F									x						x		
0003	M									x	x	x						
0004	M									x								
0005	F									x	x		x					
0010	M									x								
0011	M									x		x	x		x	x		x
0012	M									x	x	x						
0013	M									x	x							
0014	M										x							
0015	F										x							
0020	F										x							
0021	M										x							
0022	M										x							
0023	M										x							
0024	F										x							
0025	F										x							
0030	M										x							
0031	M											x			x			
0032	M											x						
0033	F											x						
0034	F											x		x				
0035	M											x						
0040	F											x						
0041	M											x						
0042	M											x						
0043	F											x						
0044														x				
0045	M												x					
0050	M												x					
0050	F												x					
0052																		
0053	F													x				
0054	M														x			
0055	M																x	x

Population estimates of Apodemus in Castle Eden Dene. Jolly's method using a computer program from Davies (1971).

Time (I)	Proportion Marked (ALPHA)	Total Marked (M)	Total Number (N)	Probability of Survival (PHI)	Number Joining (B)	S.E.(N)	S.E.(PHI)	S.E.(B)
Aug'74		0.0		0.7429			0.3380	
Sept'74	0.1667	7.43	44.57	0.4010	73.79	23.32	0.1475	31.59
Oct'74	0.1200	11.00	91.67	0.4571	3.35	34.92	0.0902	14.78
Jan'75	0.5556	25.14	45.26	1.0087	15.00	9.12	0.6026	12.43
May'75	0.6842	41.50	60.65	0.1504	33.74	37.61	0.1053	25.92
June'75	0.1667	7.14	42.86	1.0889	-9.33	27.98	0.5269	28.15
July'75	0.5000	18.67	37.33	0.2936	34.07	19.88	0.1869	21.32
Sept'75	0.1739	7.83	45.04	0.3602	24.86	25.87	0.1421	17.16
Nov'75	0.2353	9.67	41.08	0.5294	1.25	18.75	0.1211	8.52
Jan'76	0.5217	12.00	23.00			4.80		
Mar'76	0.5789							

Population estimates of Clethrionomys in Castle Eden Dene

Time (I)	Proportion Marked (ALPHA)	Total Marked (M)	Total Number (N)	Probability of Survival (PHI)	Number Joining (B)	S.E.(N)	S.E.(PHI)	S.E.(B)
Aug'74		0.0		0.3810			0.1060	
Sept'74	0.2353	8.00	34.00	0.8531	48.49	3.37	0.1765	12.76
Oct'74	0.3673	28.15	76.64	0.3939	10.89	18.87	0.1101	7.49
Jan'75	0.5455	21.33	39.11	0.4430	8.87	11.07	0.1127	3.42
May'75	0.5217	13.44	25.76	0.7658	15.21	5.53	0.1187	3.48
June'75	0.5357	18.71	34.93	0.5385	25.27	7.41	0.0978	1.91
July'75	0.3721	16.00	43.00	0.4101	18.45	6.55	0.1013	4.23
Sept'75	0.4828	17.22	35.67	0.3635	14.36	8.87	0.1154	4.69
Nov'75	0.4286	11.71	27.33	1.5197	93.50	8.20	1.0503	90.63
Jan'76	0.2500	33.00	132.00			111.77		
Mar'76	0.5000							

APPENDIX 3.

On several occasions the trapping routine described in Chapter 2 was extended. Allowance for this has been made on the figures showing the best estimate of population size by adjusting the estimates as follows:-

Castle Eden

August 1974 — Only half the grid was trapped.

The total numbers of individuals captured has been multiplied by two to give an estimate of the total population on the whole trapping area.

September 1974 — The grid was trapped for a total of four days.

The total numbers of individuals for three days was:-

Clethrionomys	35
Apodemus	22

No unmarked Clethrionomys were captured on the fourth day so no adjustment to the estimated population size was required. Two unmarked Apodemus were captured on the fourth day so the best estimate of population size has been reduced by one to 26 by applying the 'constant proportion seen' method.

Houghall

July 1974 — Only two transects were trapped but for three days.

The total numbers of individuals captured in two days was:-

Clethrionomys	18
Apodemus	1

The figure for Clethrionomys was adjusted to three transects using data from May and September 1974

$$\text{Adjustment factor} = \frac{\text{Individuals on all transects}}{\text{Individuals on transects 1\&2}} = \frac{62}{45}$$

Total number of Clethrionomys = $18 \times \frac{62}{45} = 25$

Best estimate of population size by 'constant proportion seen' method = 35.

November 1975 Transects trapped for three days.

Total numbers of individuals for two days:-

Clethrionomys	29
Apodemus	21

Best estimate for Clethrionomys from 'constant proportion seen' method = 41.

Best estimate for Apodemus is not altered from that given in Table 2.8 as no unmarked individuals were captured on the third day.

The survival of Clethrionomys given in Table 2.13 has been based on a two day trapping period.