Individual and seasonal variation in aggression in long-tailed field mice (apodemus sylvaticus) and bank voles (clethrionomys glareolus)

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Individual and seasonal variation in aggression in long-tailed field mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*).

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- being a dissertation submitted in partial fulfilment of the regulations for the degree of M.Sc. Ecology.

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CONTENTS

INTRODUCTION AND AIMS.

Year to year fluctuations in population density of small mammals have been reported by many authors. An annual peak in numbers has been described for field populations of *Apodemus sylvaticus* (e.g. Tanton, 1965; Brown, 1966, 1969; Ashby, 1967, and Watts, 1969) and peaks at longer than annual intervals with dramatic "crashes" in numbers in populations of *Clethrionomys glareolus* (Ashby 1967). Ashby postulates a four year cycle of abundance for *Clethrionomys* in the populations occurring in Houghall Wood, Co. Durham. The present study was also carried out in this wood.

Intraspecific competition and social strife have often been invoked as the causes of fluctuations in populations of small mammals. Work on the short-tailed field vole, *Microtus agrestis*, by Chitty (1952) and Clarke (1955) suggests that these factors may be the most important in limiting population size and growth.

The classic work of Sadleir (1965), later substantiated by Healey (1966) conclusively demonstrates that the level of aggression of adult male deer mice, *Peromyscus maniculatus*, changes seasonally. The level of aggressive behaviour is related to the seasonal changes in the survival of juveniles, which in turn gives rise to an annual cycle in density. A similar mechanism has been postulated for fluctuations in *Apodemus* populations. (Brown 1966, 1969). Ashby (1967) found that the low recruitment operating throughout the main part of the breeding season was always preceded by a rise in adult male aggression in spring. (He assessed the degree of aggression by observing their behaviour when handled.)

Brown (1966, 1969) claims that population structure in *Apodemus* is based on social units or "super families". The stability of these units is supposed to be maintained by a social hierarchy similar to that found in *Peromyscus* (Sadleir 1965) and *Mus musculus* (Crowcroft 1963). At the head of the hierarchy a dominant male maintains its position by aggressive behaviour towards males lower in the order. Brown (1966) further suggests that adult males are the main cause of juvenile mortality in *Apodemus*, because their aggression forces the young to keep out of the way or disperse. Thus the high level of aggression shown by the adults in spring is claimed to be the direct cause of the low summer numbers. By this social mechanism *Apodemus* populations are believed to avoid the peak and crash type of fluctuations that are found in voles.

At the present time, despite the repeated demonstrations of population fluctuations there is little or no experimental evidence to support the hypothetical role of social behaviour in the population dynamics of *Apodemus* and *Clethrionomys.*

AIMS.

The aims of the present study were to adopt the procedure used by Sadleir and Healey in an effort to find some factual basis for the hypotheses mentioned in the introduction. By laboratory and field observation and experimentation it was hoped to elucidate the form of social structure existing in Apodemus and Clethrionomys populations and to establish the existence of a social hierarchy. An attempt was made to demonstrate an annual cycle in aggressiveness of adults, similar to that found in Peromyscus. The social implications of this cycle were also examined. By combined field and laboratory studies a correlation between hierarchical position and an empirical estimate of territory size was sought.

METHODS AND MATERIALS.

1. Field Work.

Apodemus sylvaticus and Clethrionomys glareolus were studied on two sites (Areas A and B) in mixed woodland in Houghall Wood, Co. Durham. (Grid Reference: NZ 278408) The vegetation has been described.

Animals were trapped with Longworth live traps

In Area A the main population parameters under investigation were sexual condition and aggressive behaviour. Thirty traps were distributed in such a way that at least one trap was in every ten yard square. Traps were bedded with hay and baited with wheat. Prebaiting was carried out for two or three days before the traps were set. Traps were left in position from March to May and trapping was carried out at weekly or fortnightly intervals throughout this period.

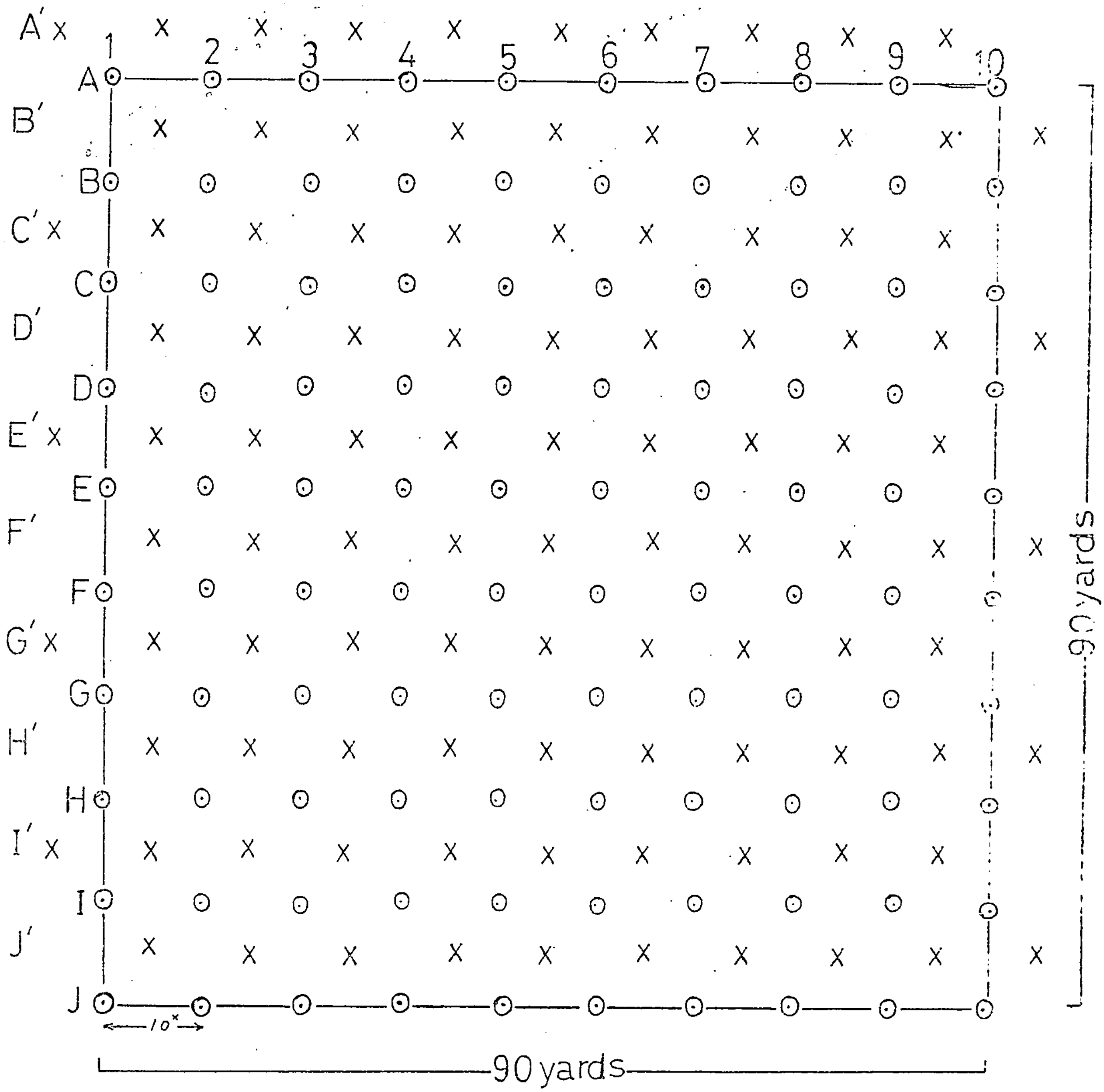
In Area B, a grid 90 yds. x 90 yds. was laid down with 100 traps, each at the corner of a ten yard square. The traps were in ten lines, each of ten traps as shown in Fig. III.

Trapping was commenced on 20th June and after three days' prebaiting the traps were set. Traps were visited once a day thereafter for a total of 4 days. All animals captured in the first two days were weighed and measured. Subsequently only the male animals (i.e. those to be marked) were weighed and measured. Marking was carried out by toe clipping so that individuals could be recognised, as described by Southern (1964). On the fourth day the traps were emptied of bedding and bait, closed and left in position.

Trapping on this grid was recommenced in August after food and bedding had been placed in the traps. A prebaiting period of three days was allowed before the traps were set. The traps were visited once a day for five days. All animals captured were weighed and measured except on the fifth day when only previously marked animals were measured after they had been brought back to the laboratory. (All animals marked in June were brought into the laboratory).

Tracking of individually marked animals was carried out in the period between their marking in June and their final recapture in August. Tracking cylinders consisted of 80 aluminium tubes closed at one end. These tubes were 5.2 cm. (2") in diameter and 17.8 cm. (7") in length. A further 20

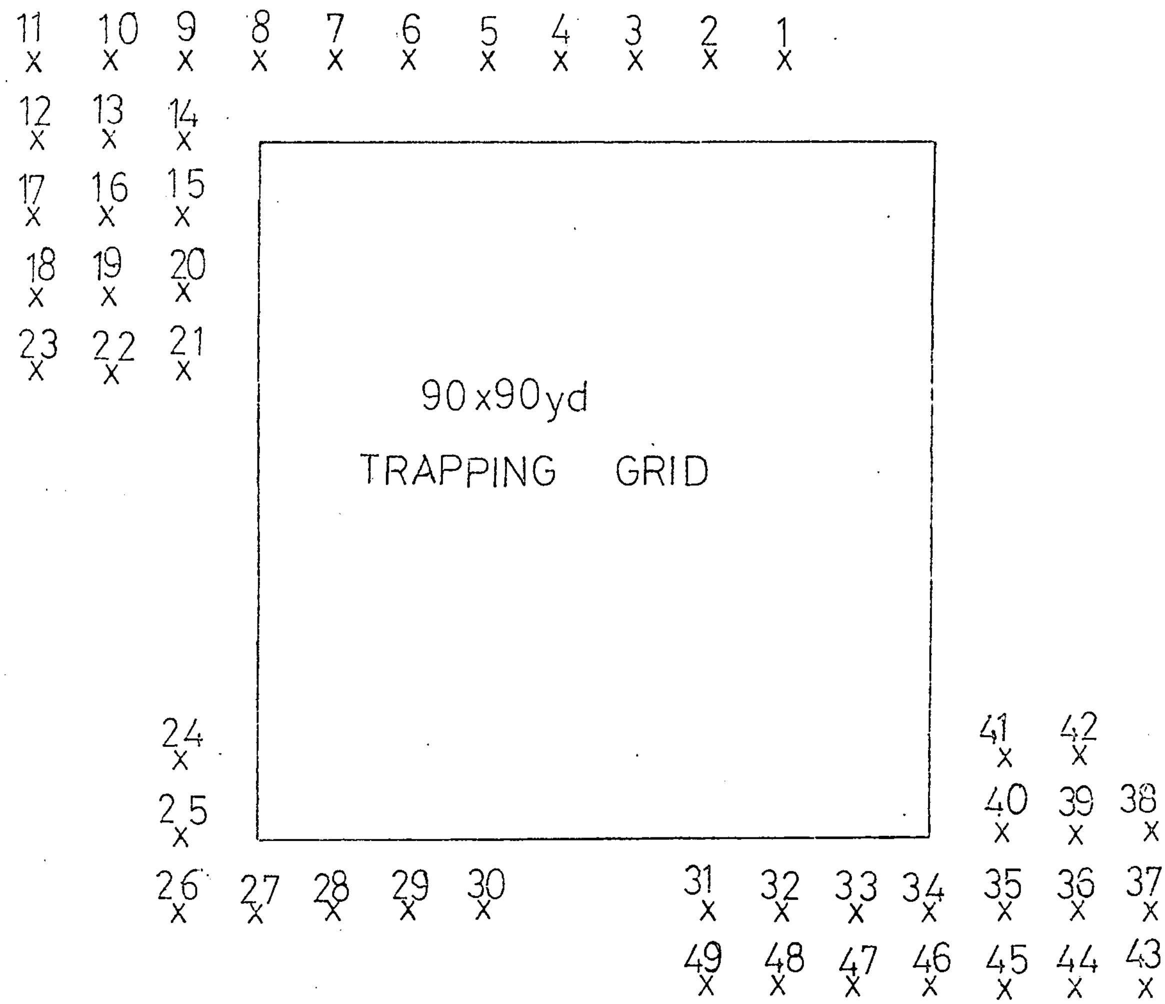
Fig. 3.
DESIGN OF TRAPPING/ TRACKING GRID



⊙ site of trap
x site of tracking cylinder

Fig. 2. (PLOT B)

MODIFICATION OF TRACKING GRID (last week in July)



grey plastic tubes open at both ends 5.8 cm. ($2\frac{1}{4}$") in diameter and 11.5 cm. ($8\frac{1}{2}$") in length were also used. Both types of cylinders had a shiny surface. These tracking cylinders were initially laid down on June 26th within the tracking grid as shown in figure II. Smoked kymograph paper 14.5 cm. x 18.5 cm. was fitted into the tubes prior to their transportation to the wood in order to protect the sensitive tracking surface.

Every day for a week the tracking surface was examined in all the tubes. Marked papers were taken out, replaced by freshly smoked ones, and taken back to the laboratory for closer examination.

Difficulties were experienced with this method, and so, after experimentation, a new tracking surface was adopted. Thick, black, mat-surfaced art-paper was cut to the same dimensions as the kymograph paper. White petroleum jelly was spread over the paper with a spatula to give an even surface, which was then sprinkled with white (unperfumed) talcum powder. This new tracking surface was placed in the cylinders and found to be very sensitive to the movement of animals over it. Further details on tracking techniques are given in Appendix I.

Tracking by this second method was carried out for 7 days in the third week of July. The cylinders were examined once every day for the footprints of marked animals. Where these occurred, the location of the tracking cylinder was recorded and the tracking surface smoothed over with a spatula (with the addition of more petroleum jelly where necessary). The surface was then repowdered and replaced in the cylinder.

In the last week of July 50 more cylinders were placed outside the perimeter of the grid in the positions shown in Figure II. Tracking continued throughout the retrapping period.

2. Laboratory Methods.

Twenty-four animals were brought into the laboratory in March. Three *Apodemus* males came from Area A and nine *Apodemus* males, together with twelve *Clethrionomys* males came from another part of the wood. Also from this other piece of woodland, six females and three males of each species were brought into the laboratory in April. The animals were kept individually in wire cages. Most of the cages measured 37 x 21 x 16 cm. but a few measured 41 x 26 x 21 cm. Each cage had an ample supply of bedding of hay or cotton-wool. Water was supplied in jars and food of oats, wheat or commercial food pellets in a metal dish. The cages had a mesh floor which was underlain by a metal tray containing sawdust, which was changed once a week. The cages were kept as far as possible insulated against noise. The laboratory temperature was not controlled and fluctuated between 19^{o} and $25^{o}C$, but was usually at 23^{o}.

The light regime was maintained as that of the natural environment for the period from March to mid-May. Five male animals were then subjected to a reduced photoperiod which consisted of one week of 10 hours light (0600 - 1600 hrs):

14 hrs. dark and subsequently 8 hrs. light (0800 - 1600): 16 hrs. dark. Other male animals were kept as controls under the natural photoperiod for the particular time of year. Studies on the effect of the reduced photoperiod were carried out in July and August.

In August, animals from Area B were brought into the laboratory. These comprised two marked male *Apodemus*, two unmarked male *Apodemus* and two *Apodemus* females. Nine marked male *Clethrionomys*, seven unmarked male *Clethrionomys*, five female *Clethrionomys* and six juveniles were also brought in. These were kept under similar laboratory conditions under a natural photoperiod, to those previously described.

The animals kept in the laboratory participated in various tests. Observation of behaviour took place through a slit in a black cloth screen erected across one corner of the laboratory. The observation platform was illuminated by the normal laboratory light. It seemed that noises made during normal movement of the observer did not disturb the animals.

In encounter experiments between two animals, both participants were weighed and measured 24 hrs. before the encounter. In experiments where one of the animals was on home territory, i.e. in its own cage, and another was introduced, the food and water containers were removed three hours before the encounter. Where encounter experiments were carried out on neutral ground, i.e. an empty unused cage, both participants to the contest were introduced simultaneously to the cage.

In all encounter experiments the observation period was ten minutes. During this period the behaviour of both subjects was noted and tabulated using a shorthand notation. Ten second intervals were used to record the temporal pattern of behaviour. Thus, every different behavioural act that occurred in each 10 second interval was noted, but if a particular act occurred more than once in that interval a score of one still prevailed. This method was used by Sadleir (1965) and Healey (1965 and 1966). The different categories of behaviour and the various elements or units that constitute them are described in the results.

3. Organisation of Tests.

(1) In April laboratory males were divided into two randomly chosen batches of five animals. Encounters between these two groups were then organised so that no one animal met another of the opposing group more than once. A total of three encounters for each animal was arranged.

In August animals recently trapped in that month were similarly tested.

In mid May five male experimental animals were subjected to a reduced photoperiod after they had reached full fecundity. This experiment was an attempt to simulate the onset of autumn and to test related behavioural and physiological changes. Tests were carried out in July and again in August with the same experimental procedure employed previously.

The same procedure was employed when marked animals were brought into the laboratory in August. These experimental animals were tested against a batch of control laboratory animals.

(2) In May tests between the sexes and between females were organised. An attempt was made to elucidate the sex of the aggressor. Male animals were known to be aggressive but it was not known if this category of behaviour was exclusive to that sex.

(3) Further tests in May were organised to investigate a possible increase in the level of aggression due to a "home cage factor". Intruders were introduced into the home cage of individuals which had been in residence from the time they had been brought into the laboratory (i.e. four weeks).

(4) In the first week in July colonies were established which contained one male and one female. (Three vole and two mouse colonies were so formed). The progress of these colonies was observed over subsequent weeks.

In August the effect of introduction of strange animals of both sexes into the colonies was investigated. A juvenile colony was also set up in August with animals trapped from Area B. The progress of this colony was observed and recorded.

After two weeks animals were reweighed and their condition noted. The effect of the introduction of a strange, adult male into the colony was then observed. This male was left in the colony to observe the longer term effects of its presence.

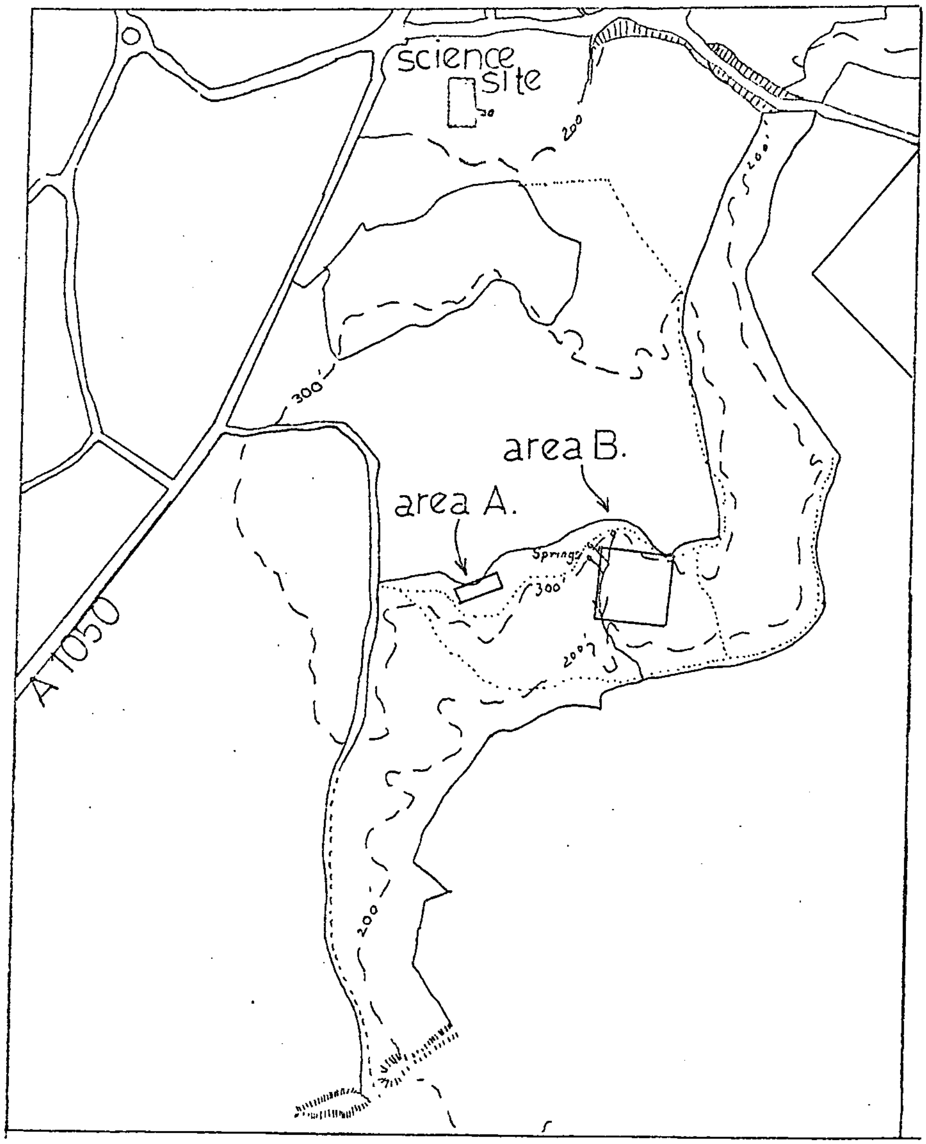
Two similar colonies of adult males and juveniles of both sexes were also established at this time. Progress in these colonies was also monitored.

Some encounters between juveniles of both sexes and adults of both sexes were organised to investigate any possible differences in behaviour of adults in these encounters.

Fig. I.

STUDY AREAS: Houghall Wood and southern outskirts of Durham.

(Grid Ref.: NZ 278408.)



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100 yds.

THE STUDY AREAS.

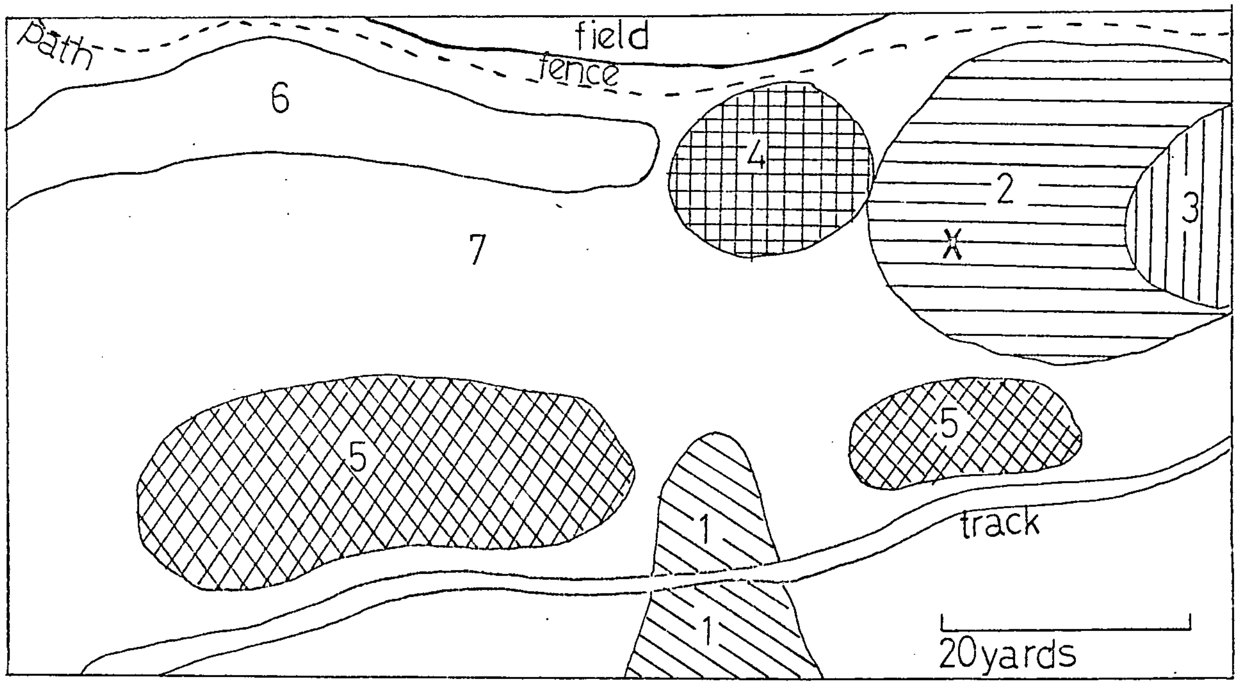
The location of the study areas is seen in Figure 1. Houghall Wood is an area of mixed woodland a mile south of Durham City, situated on sloping ground west of the Flood plain of the River Wear. The parent rock is boulder clay with locally substantial sandy fractions.

Area A (See Figure 4.)

Area A is an open mixed Oak (*Quercus petraea*) and Sycamore (*Acer pseudoplatanus*) woodland. Hawthorn (*Crataegus monogyna*)

Fig. 4.

PLOT A : VEGETATION (herb and shrub layer)



X : position of Badger set.

PHOTOGRAPHS OF WOODLAND AREA A.

1.

Area A.

View from eastern edge of area. Showing Oak woodland, and herb layer of bracken and willow herb. Track in left foreground.

2.

Area A.

View up the slope. Showing Oak and Sycamore. woodland. Bracken and bramble bank in background, and willow herb, bracken and nettles inthe foreground. Holly thicket on the right.

Sweet Chestnut (Castana sativa) and Wych Elm (Ulmus glabra) occur infrequently.

The herb layer is predominated by Bracken (Pteridium aquilinum) and Bramble (Rubus fruticosus). There is some Fern (Dryopteris dilitata) and a little grass (mainly the Common Bent: Agrostis tenuis). Some rushes (Soft Rush: Juncus effusus) and nettles (Urtica dioica) occur occasionally. Alongside the track in the drier areas Wood Sage (Teucrium scorodonia) and Hemp Nettle (Galeopsis tetrahit) occur infrequently.

Where the herb and shrub layer differs significantly from this general pattern has been noted in the map of Area A (Figure 4). These sub-areas have been designated 1 - 7 and are described below.

1. Wet, marshy area. Predominated by: Juncus effusus, Agrostis tenuis, Epilobium hirsutum (Great Hairy Willow Herb), Dryopteris dilitata (Broad buckler Fern), Angelica sylvatica (Angelica)

2. Bramble bank. Predominated by: Rubus fruticosus, Pteridium aquilinum. These form a very dense cover.

3. Holly Thicket. No herb layer, but thick litter layer. (Ilex aquifolium)

4. Ivy Bank. Complete ground cover of Hedera helix.

5. Dry Heath Area. Predominated by: Epilobium angustifolium (Rose Bay Willow Herb), Urtica Dioica. Some:

Rubus fruticosus and Pteridium aquilinum.

6. Sandy Bank. Generally a sparse herb layer. A little: Rubus fruticosus, Oxalis acetosella and some grasses.

The area is sited near the edge of the wood, bordering arable land. The whole area slopes up towards the woodland-edge. (a slope of about 50 ft. in 50 yds.) Just below the fence there is a pronounced bank. Towards the right of the area this bank becomes exaggerated into a steep hill. The area is crossed in its lower quarter by a cinder-track.

Area B (See Figure 5)

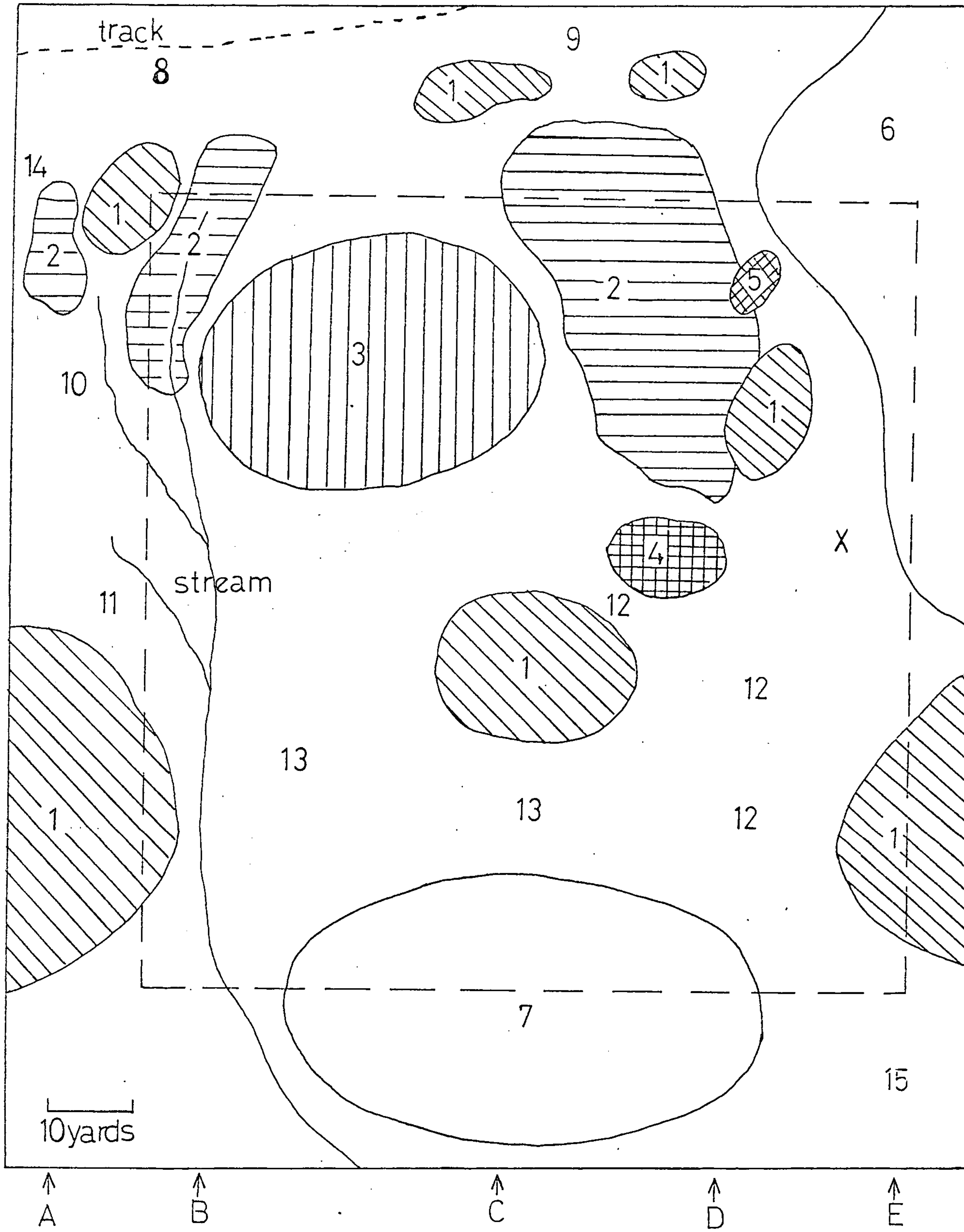
Area B is again on sloping ground. The whole area has an approximate slope of about 100 ft. in 100 yds. In places this shope is exaggerated into almost vertical banks. Profiles of the area were obtained using a rough siting method with canes. These are seen in Figure 6.

The vegetation of the area consists of open woodland with Sycamore predominating over most of the area with some Oak. The Sycamore gives way to increasing Oak towards the east of the area, till only Oak occurs in sub-area 6. Some scattered elms (Ulmus glabra) occur.

The shrub layer consists of occasional holly thickets and birch saplings (Betula pubescens), some hazel bushes (Corylus avellana) and rowan (Sorbus aucuparia)

The herb layer consists mainly of bracken with some brambles and a little fern. Where the herb layer differs

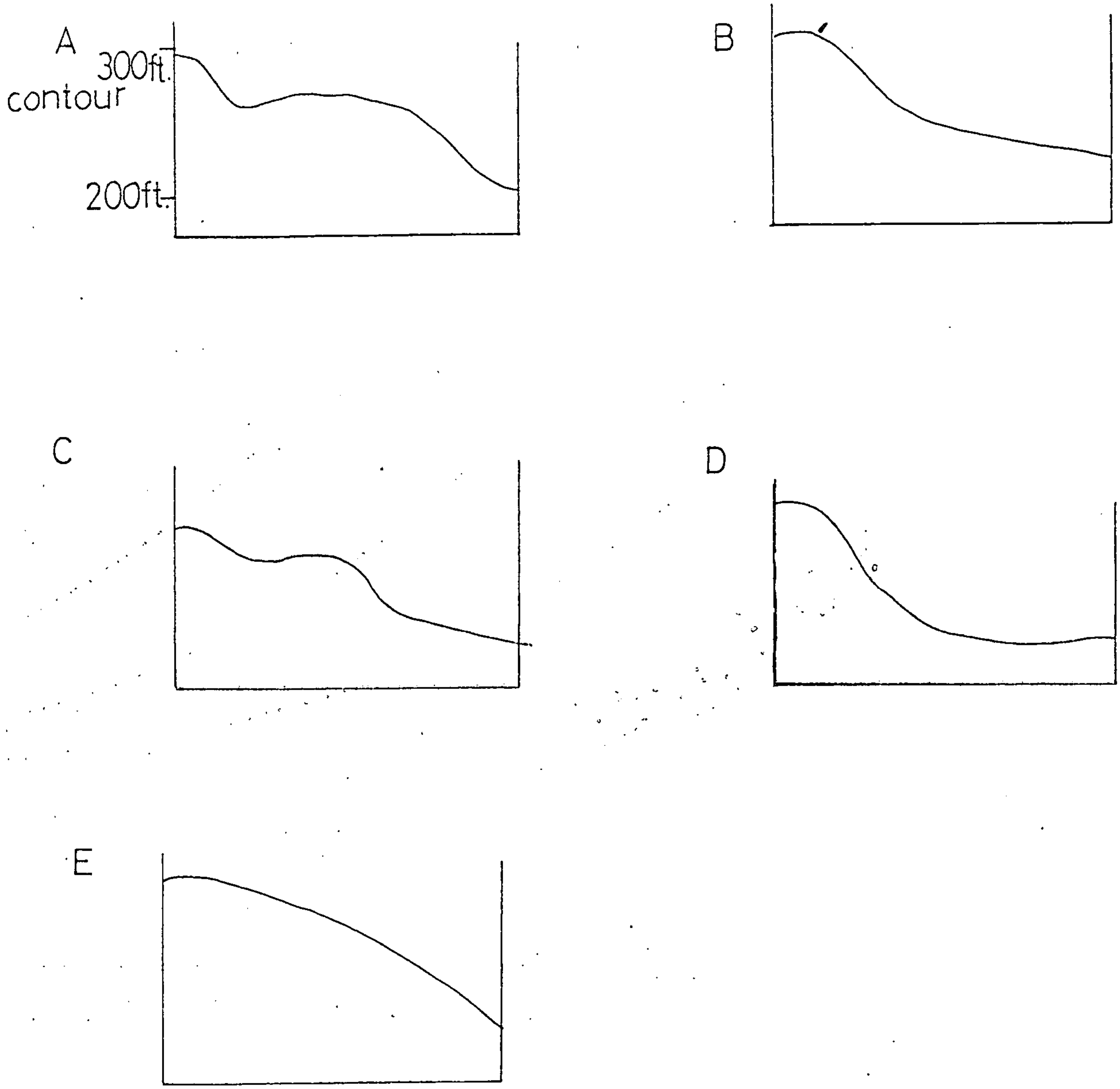
Fig. 5. PLOT B : VEGETATION (shrub layer)



— — : extent of grid (90x90yds)

X : position of Badger set.

Fig.6. PLOT B : PROFILES.



(slope :100ft. in~100 yd.)

substantially from this general pattern has been noted on the map as sub-areas 1 - 15. These are described below:

1. Holly thickets. No shrub layer - thick litter layer.
2. Wet, marshy areas. Predominated by: Angelica, Broad Buckler Fern, Meadowsweet (Filipendula ulmaria), Raspberry (Rubus idaeus), Great Hairy Willow Herb; some: buttercup (Ranunculus spp.), Woundwort (Stachys sylvatica), nettles (Urtica dioica); and a little Red Campion (Lachnis Dioica).
3. Open, grassy area. Predominated by: grasses (Agrostis tenuis and others). A little fern and willow herb.
4. Honey-suckle bank. Forms a dense mat over the ground (Lonicera periclymenum). Some bramble incorporated into this mat.
5. Broom thicket. Broom (Cytiscus scoparius) on a dry bank. Some Wood Sage and a little grass (WavyyHairgrass Deschampsia flexuosa).
6. Dry bank and Dry Sandy Spur. Open Oak woodland. Some regenerating oak seedlings and a little coppiced oak. Also some Rowan - both trees and regenerating shrub. Herb layer consists mainly of Bilberry (Vaccinium myrtilus) which forms a dense ground cover, with some Deschampsia flexuosa. A little Hard Fern (Blechnum spicant) occurs, and a little Wood Rush (Luzula campestris) lower down in the more shaded parts of the bank. A little Common Cow-wheat (Melampyrum pratense)

occurs in more open, sunny places.

7. Beech woodland. Large beech trees and consequent little shrub layer. A little bramble, bluebell (Endymion non-scriptus) and Wood Sorrel occurs.

8. Steep bank with dense, high bramble thicket. Bank very dry and sandy with some grasses. Lower down is some coppiced hazel and a little willow (Salix spp.)

9. Steep bank, very shaded. Sparse herb layer. Some grasses, ferns and ivy occur. Occasional Rowan bush and Yew (Taxus baccata).

10. Damp area of woodland, very shaded due to some beech trees. Bramble thickets and great deal of fern (Dryopteris dilitata).

11. Dry bank with very dense birch thickets (Betula pubescens) and generally less dense herb layer.

12. Sparse herb layer predominated by ferns, and a little bramble. Mostly the Broad Buckler Fern (Dryopteris Dilitata), but much male Fern (D. Felix-mas), and some Scaly Male Fern (D. Borreri).

13. Very dense and high herb layer of bramble thickets and bracken.

14. More open, flat woodland area with young trees and open grassy patches. Some birch and larch (Larix spp.), brambles, nettles, Wood Sorrel, honeysuckle, willow herb, rushes and a little hemp nettle. Some hazel and willow.

15. Beech woodland (*Fagus sylvatica*). Generally open with much less shade than sub-area 7. Bracken and bramble predominate, with some birch thickets. Some willow herb, nettles and grasses. A little foxglove (*Digitalis purpurea*).

PHOTOGRAPHS OF WOODLAND AREA B.

1.

Area B.

Looking from the top of the grid. Bramble bank in the foreground. Open Sycamore woodland.,Wet area in the left centre. Holly thicket in centre background.

2.

Area B.

Open Oak woodland on the eastern side of the grid. Rowan, rejuvenating Oak, and Bilberry and Deschampsia can be seen.

3.

Area B.

View at centre of grid area. Fern in foreground. Honeysuckle bank top right.

4.

Area B.

Same position as 3, looking towards the top right of the grid. Bracken and bramble herb layer and open sycamore wood can be seen.

5.

Area B.

Beech woodland in the foreground, looking across to holly thicket in the left background.

6.

Area B.

Bottom western side of the grid. Looking across stream towards a birch sapling thicket. Bramble and bracken in the foreground.

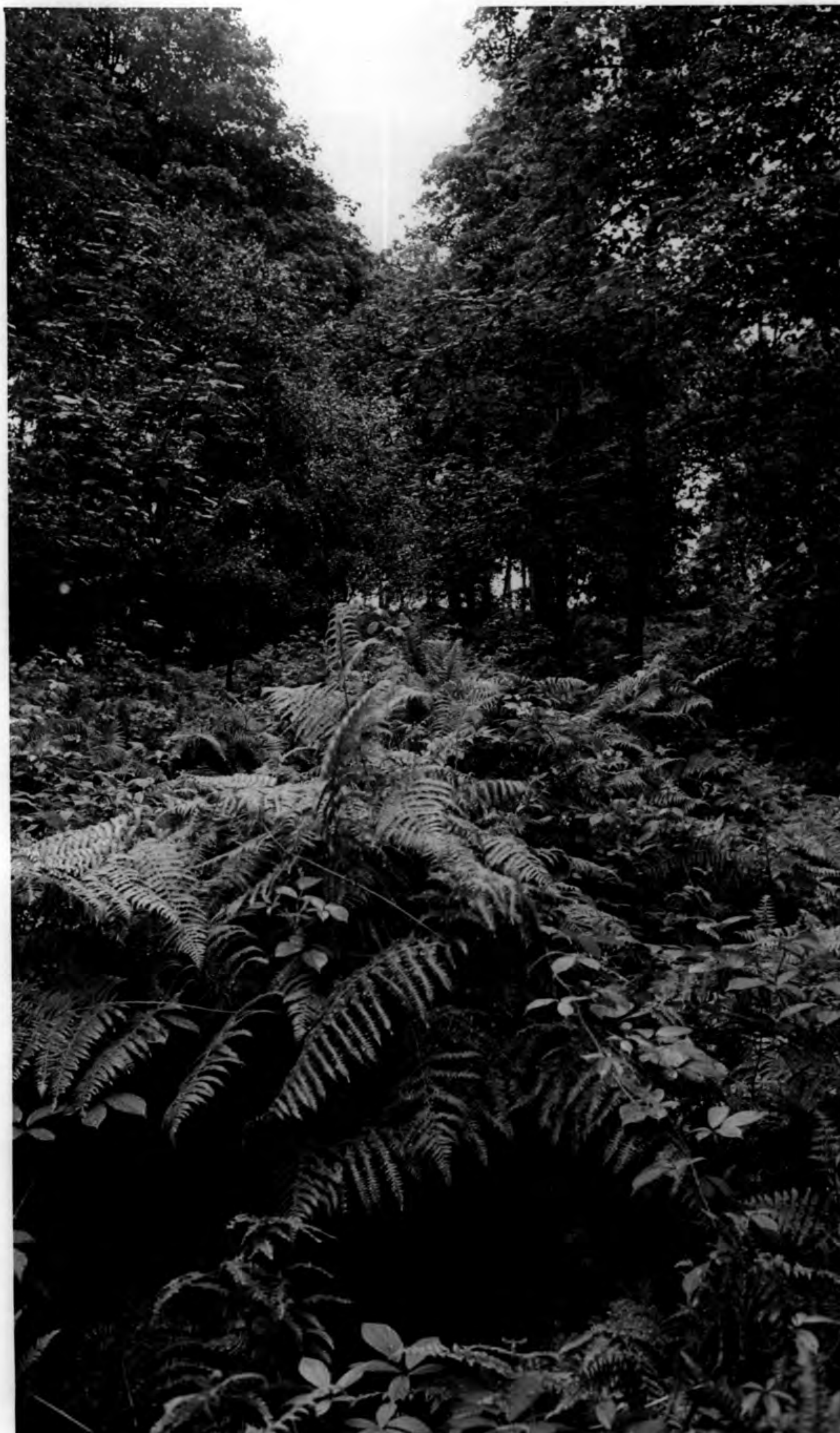
7.

Area B.

Looking from the bottom western corner of the grid.

Stream on the left; holly thicket at the right.

Dense bracken and bramble thicket in the foreground



OBSERVATIONS AND RESULTS

Preliminary Field work and a subjective index of aggression.

All animals trapped in Area A were handled and examined. Weights and lengths were measured, and sexual condition and aggression were assessed. These parameters were monitored throughout spring to early summer.

As Ashby (1967) suggested, handling provided an important indication of overall activeness of animals, and also of any aggressive tendencies. In conjunction with stimulation of sexual condition, a subjective assessment of aggressiveness was made and an arbitrary index of aggression devised.

Male fecundity (= degree of sexual maturity) can be estimated once experience has been gained of the sexual condition of animals throughout their reproductive cycle. During early spring the testes begin to drop from the abdominal position which prevails during winter. In late spring or early summer the full extent of testes development in the scrotum is reached. By this time a large bulge can be seen below the abdomen and the scrotum is prominent. In *Apodemus* observation of this development is facilitated by loss of hair from the scrotum - the latter forming prominent bulges beneath the tail. The pes epididymi are located here, the main part of the testes being located beneath the abdomen in much larger bulges. In *Clethrionomys* testes development is not so accentuated as in *Apodemus*. The bulge of the testes is not so pronounced and no loss of hair in the perineal region occurs. The protuberant scrotum is never developed to any visible extent either. However, knowledge of the absolute positions of testes, as mentioned above, enables a good estimate to be made of fecundity. There is, perhaps, more of a subjective element, here, than in Apodemus.

An arbitrary scale can be devised with a notation from non-fecund to full fecundity, with degrees of $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ between these limits, to describe sexual condition in males. This scale is used by many workers. Arbitrary classification is, however, always accompanied by the obvious subjective limitations and cannot be an absolute guide. Some work was done to relate this classification to the absolute physiological state of animals. Testes from $\frac{3}{4}$ and fully-fecund animals were sectioned and spermatozoa were being actively produced (and, presumably, testosterone; which is known to effect male behaviour). (cf. Healey (1966)). No comparable data for other, lower positions on the scale were obtained.

Female sexual conditions were noted as being either perforate or imperforate. Sometimes the perforate vulva was either swollen or secreting fluid. Animals in this condition were judged as being in oestrous. Later in the season, when breeding had commenced, conditions of 'pregnant' and/or 'lactating' were also recorded.

The concurrent development of aggressive behaviour when handled was also classified. The subjective index of aggression had four divisions: 0→3. These divisions are based on behaviour of animals when handled, and when stimulated in the hand. There are basic behavioural differences between the two species which complicate classification and prevent, to some extent, collation between the species. Apodemus is never so inactive as some Clethrionomys are in winter. Even at their most inactive periods mice struggle and will readily escape if handled carelessly. Voles, on the other hand, are often torpid in winter and inactive enough to be held in the open hand. Voles also have a greater tendency towards vociferous display, whereas mice rarely squeal unless very aggressive or hurt in some way.

The divisions of the index are described below:

3. Animals are very aggressive; they struggle violently, turning the head and body round in an attempt to bite the handler. All the limbs are used to try to gain purchase with the feet to facilitate biting or escape. The mouth is open and biting of any article or any part of the handler's anatomy presented to the animal readily occurs. Actual bites are hard and persistent, the animal often clinging on whilst overall grip of its body is released. In this position the animal has to be shaken before its hold is loosened.

   Squealing invariably accompanies struggling, and also urination; and sometimes even ejaculation. Squealing in voles persists for the whole period of handling. Mice squeal less frequently.

Blowing on the animals, or mechanical stimulation with the fingers heightened struggling and squealing. Struggling, in both species, does not cease till the animal is released

2. The same behaviour occurs here as that noted in division 3, but is generally much less intense. Struggling is less persistent and violent, and squealing takes place much less readily - and not at all in mice. Animals are also less persistent in their efforts to turn round in attempts to bite the handler. They usually quiesce if held still and no further movement occurs till stimulation is applied.

1. Animals are quiescent in the hand till stimulated. A little intermittent struggling then takes place, but soon ceases. No squealing is heard. Very rough handling may educe some weak squeals from voles.

When held by the scruff of the neck voles hang limply down from the hand; whereas mice bring their hind legs up against the hand and close their eyes - assuming a very hunched posture. In both animals these positions persist till release.

0. Apodemus were never allocated to this division. Clethrionomys, in winter and early spring are mostly very inactive and torpid, and show no aggressive tendencies. In this state, voles can be held in the

open hand and will not attempt to escape till provoked by some form of stimulation. They do not attempt to bite, even if a finger (of the handler) is put in front of, or actually in, their mouths. Blowing on them has no stimulatory effect, and squealing can never be induced.

Sometimes, voles take on an almost moribund appearance. This may be due to exposure in traps, which may adversely effect lethargic overwintering animals more than animals in breeding conditions in summer.

Using the above index, a gradual increase in activity and aggression was recorded through March. (See Table I, Appendix 2). These changes accompany development towards breeding condition.

Sexual development occured late in this year, probably as a result of a late spring. Development was possibly initiated in late February. By mid-March animals were already quite active and quite advanced sexually. Males were on average $\frac{1}{4}$ to $\frac{1}{2}$ fecund - females were, of course, still imperforate. One male Apodemus in particular was very active and quite aggressive - being $\frac{3}{4}$ fecund (and index division 2). Clethrionomys males were generally less well developed, being on average non-fecund and non-aggressive. (index divisions 0 and 1).

In April animals approached breeding condition, and both mice and voles were now, on average, $\frac{1}{2}$ - $\frac{3}{4}$ fecund. A corresponding rise in the aggression index was also recorded. At this time care had to be taken when handling animals.

Whereas in March, careless handling might only be rewarded with, at the most, a slight nip, a painful bite would now ensue. In mid-May full breeding condition was achieved by all animals, though a few more advanced and very aggressive animals had reached sexual maturity at the beginning of the month. The first perforate females were seen in mid-May, but the majority seemed to achieve this state even later in the month.

From handling and classification of males by the subjective aggression index, a good idea is gained of position in the postulated social hierarchy. There are obviously severe limitations in the application of an index, based on reactions to humans, to the reaction of one animal to another of the same species. However, in the author's opinion, the index is of particular usefullness in singling out the most aggressive members of the population. These animals would have dominant or co-dominant social status. On several occasions, such field assessment was later substantiated by laboratory tests.

Females were generally noted as less active and aggressive than males, and thus scored correspondingly less high aggression indices. This general rule did not, however, apply to the breeding season when perforate females, especially those lactating or pregnant, were as aggressive towards the handler as the males. This was also seen in June and August in Area B. (See Tables 13 and 14, Appendix 2).

Another indication of hierarchical position is, the author believes, provided by the time of trapping of particular animals. The very aggressive male Apodemus were always amongst the first to be trapped. Invariably, they would be captured the first day after the traps were set. One particular animal in Area A was caught the same day the traps were put down. (There was no prebaiting period in this instance since the mechanism holding the trapdoor slipped and thus set the trap.) This animal was taken into the laboratory and later tested, when a dominant social status was recorded.

Similar observations were recorded from Area B in June and August, both in relation to behaviour towards traps and tracking cylinders. Very aggressive individuals were again amongst the first to be trapped, and were the first and most frequent visitors to tracking cylinders. These field observations were later substantiated by laboratory testing in some cases.

Similar differentiation could not be applied to Clethrionomys males. Dominants, very aggressive to other Clethrionomys, were not so obvious either from handling or from their behaviour in relation to traps or tracking cylinders.

These speculative observations do concur with Brown's (1966 and 1969) contention that the dominant male is more active and confident in its territory than subordinates, and is quick to investigate any new object in its range. Crowcroft (1955) records similar behaviour in dominant Mus musculus males.

In the present study, the presence of food in traps might be an overriding factor in determining exploratory behaviour; but this factor cannot apply to the tracking cylinders.

Preliminary Investigation into aggressive behaviour in the Laboratory.

Preliminary investigation into behaviour in the laboratory was made using both single animals and encounters between two animals. Periods of observation varied from minutes to hours according to the information sought and the activity of the subjects. Knowledge of the various classes of behaviour, recognition of behavioural elements within them, and also the temporal sequence of behavioural elements was gained. This knowledge was a necessary precursor to more formally organized tests.

Grant and Mackintosh (1963) have described the social postures of four laboratory rodents (Rattus, Cavia, Mus and Mesocricetus). In their study, they divided adult behavioural responses into several classes or categories. For each of these classes they assumed motivational similarity. The classification and terminology used in the present study is based on that used by these authors. Oldfield (1968), in a study of agonistic behaviour in Apodemus and Clethrionomys, also used this same classification.

Sadleir (1965) and Healey (1966), similarly, used a classification devised by Eisenburg (1962) in their work on <u>Peromyscus</u>.

The following classes of behaviour were recognised in this study: Introductory Elements (Approach; Nose; Investigate; and Sniff); Aggressive Elements (Aggressive Posture (Threat), Attack; Fight; Wrestle and Chase); Defence Elements (Thrust); Withdrawal Elements (Retreat; Flee; Defeat); Submissive Elements (Submit); Contactual Elements (Groom and Crawl); Ambivalent Elements (Upright Posture, and Parry); and Non-Social Elements (Scratch; Self-groom; Eat). These classes and elements have been described in detail by Oldfield (1968).

For the purposes of this study exploratory behaviour has been included in the Non-Social behavioural category. This provides a good indication of confidence and of activity which is not necessarily related to aggressive tendencies.

Aggressive Grooming was also recorded in this study as an aggressively motivated variant of the Contactual Element: Groom. Oldfield (1968) did not record such an element but Grant and Mackintosh (1963) have described this variant in their study.

Naming and classifying of behavioural elements is necessary, though the somewhat artificial nature of this procedure must be understood. Frequent transitions between named elements occur which cannot be identified with any certainty.

In presenting the results of encounters (See Tables 3 - 9) between animals, the number of elements of each of the above categories displayed by each participant in the encounter was tabulated. More importantly, for the purposes of the present study, the frequency of each aggressive element is also shown, - since there seems to be a variation in degree of intensity of motivation for these elements. Hence, Fight, Wrestle and Chase were of high aggressional intensity, but Threat, Attack and Aggressive Groom were of low intensity.

Distinct behavioural differences between the two species were observed during encounters. Voles were generally less active, making only brief sorties from a favourite corner of the cage. Mice displayed prolonged exploratory behaviour. Voles rarely groomed themselves, whereas mice groomed frequently, thoroughly and for prolonged periods. Also, voles were always vociferous in conflict situations, to a varying degree. Mice were never heard to squeal during encounters. These differences were substantiated by interspecific encounters between some males of each species.

Degrees of Aggression - the Dominance Hierarchy.

From organized encounters, the aggressiveness of participating male animals was measured. The mean of the total number of aggressive elements displayed by each animal for the three encounters was calculated and recorded. Thus designated, animals then constituted a series graded by aggression. (See Table 2.)

TABLE 2. Laboratory Record of Some Experimental Male Animals (April - May)

Laboratory identification number	APRIL Weight (grm.)	Length (cm.)	Sexual condition	Subjective aggression index	Tested aggressive index	MAY Weight (grm.)	Length (cm.)	Sexual condition	Subjective aggression index	Tested aggressive index
APODEMUS										
1.	30.0	10.3	$\frac{1}{2}$F.	2	6	28.5	10.0	$\frac{3}{4}$F.	3	19*
4.	27.5	8.5	$\frac{1}{2}$F.	2	5	28.0	9.0	$\frac{3}{4}$F.	2	8
5.	21.0	8.5	$\frac{1}{4}$F.	1	1	27.0	8.5	$\frac{3}{4}$F.	2	5
9.	30.0	10.7	$\frac{3}{4}$F.	3	9*	31.5	10.5	F.F.	3	20*
22	27.5	10.75	$\frac{3}{4}$F.	2	6	28.5	10.5	$\frac{3}{4}$F.	2	9
CLETHRIONOMYS										
10	22.5	9.75	$\frac{1}{2}$F.	2	5	23.5	10.0	F.F.	2	7
13	19.5	10.0	$\frac{1}{4}$F.	1	2	20.0	10.0	F.F.	2	4
18	22.5	10.0	$\frac{1}{2}$F.	3	7	23.0	10.0	F.F.	3	7
19	22.0	10.0	$\frac{1}{2}$F.	2	2	21.5	10.0	$\frac{3}{4}$F.	2	6
20	22.5	9.5	$\frac{1}{2}$F.	3	8*	24.0	10.0	F.F.	3	9

* indicates dominant animals (revealed by χ^2 test)

At the head of this series was a dominant animal which obtained a consistently high aggressive score in all encounters. Dominance was also apparent by the corresponding defensive and submissive behaviour exhibited by opponents in encounters and by greater confidence and activity.

The programme of encounters between the two batches of animals was repeated in May, with the same provisos in the choice of participants. Higher scores for aggressive display were achieved at this time, but the hierarchical relationships remained stable: members of the graded series retained their positions relative to other animals.

Simple 'Chi-squared' tests were performed to test the null-hypothesis that animals of each series were, in fact, all of homogeneous aggression. The results of these tests are indicated in Table 2. In April one male mouse was dominant (that is significantly different from others of the series, $p < 0.20$). In May two co-dominant mice were revealed ($p < 0.01$ in each case). The series of voles, in April, was dominated by one animal ($p < 0.20$) but dominance was at an insignificant level in May ($p > 0.50$).

Two pairs of animals from each series were subsequently tested each week for a further period of three weeks in May and June. Dominants and subordinates from the series were chosen for these tests, each pair was repeatedly tested. When animals repeatedly encountered the same individual in this way, differences between the two species are apparent. Dominants of both species retained their social superiority but mice seem to stabilise their relationships, whereas voles do not. Repeated encounters between mice result in a decrease in aggression, and fighting between individuals is eliminated. In later encounters dominance-subordinance relationships are recognised, not by initiation of fighting and defeat, but by aggressive grooming by the dominant of a submissive subordinate. No such stabilisation was observed in voles. Repeated encounters still retained initial frequency and intensity of aggression between individuals.

Data supporting this is given in Table 16.

TABLE 16. Repeated Encounters

* - dominant animal.

APODEMUS

	PAIR 1.				PAIR 2.			
	*1		4		*9		5	
May, Week 2	18	6T 6A 4F 1W 1C	7	4T 3A	20	8T 6A 5F 1C	6	3T 2A 1F
Week 3	12	4T 2A 2F 1C 3AG	2	2T	18	8T 4A 4F 2C	6	4T 1A 1F
Week 4	6	2T 4AG	1	1T	12	6T 4A 2AG	4	4T
June Week 1	4	4AG	0		6	6AG	1	1T

CLETHRIONOMYS

	PAIR 1.				PAIR 2			
	*20		13		18		10	
May, Week 2	10	6T 2A 2F	4	2T	9	4T 2A 2F 1C	5	2T 2A 1F
Week 3	9	5T 2A 2F	3	2T 1A	10	4T 3A 3F	3	2T 1A
Week 4	10	5T 2A 2F 1C	5	2T 2A 1F	6	3T 3A	4	2T 2A

TABLE 16 (contd.)

June, Week 1	8	4T 3A 1C	4	2T 2A	9	4T 2A 3F	5	2T 2A 1F

SEX OF THE AGGRESSOR.

1. Male and Female Encounters.

Fighting never resulted from male-female encounters in mice. Aggressive elements which were shown were always of low intensity (eg. Threat and Aggressive Groom) and ceased after the tension of strangeness had been relieved by initial contact. Both animals then moved freely around the cage making frequent subsequent contact.

Aggression frequently occured between the sexes in voles. Males readily fought females - maintaining a dominant status towards the more defensive and submissive females. Overall intensity of aggression in these encounters was judged to be somewhat lower than that occuring in all-male encounters. Dominance in voles was not accompanied, as in mice, by greater activity and confidence. Females were generally more active than males, and they frequently approached males - the reverse rarely occurring.

General behavioural differences between the species were again apparent in these encounters. Mice displayed more exploratory and Non-Social behaviour than voles, being generally more active. Voles accompanied aggressive behaviour often with vicious squealing - in a degree seemingly correlated with the intensity of aggression. The males were more vociferous than the sometimes mute females. (See Table 3)

2. Female Encounters.

During encounters between females a similar pattern to that occurring in the inter-sex encounters is seen.

Mice are again more active and exploratory. No aggression is shown at any time, though there is frequent contact between the animals.

Voles are again aggressive. Though no actual fighting takes place, any approaching animal is always threatened and attacked - the latter usually retreating. A few individuals are quite aggressive and a dominance-subordinance relationship is established similar to that seen between males.

It seems that in mice aggressive behaviour is the virtual prerogative of male individuals; whereas, in voles, both sexes show agonistic behaviour in varying degrees. (See Table 4).

DEFENCE OF HOME CAGE

In these encounters, resident animals were mostly sedentary, most of the activity being due to the exploratory behaviour of the intruder. Intruding animals therefore initiated contacts and the ensuing conflict situations.

1. Males and Home Cage Males (See Table 5)

Resident mice seem more aggressive during these encounters - displaying proportionally more agonistic behaviour than intruders. However, a confident statement about this apparent enhancement of aggressiveness is impossible to make from the evidence of so few encounters.

The apparent bias in aggressive display in favour of home cage animals is more marked in voles. Again it is difficult to decide what significance to attach to the results of so limited a number of observations.

Animals showing dominance on neutral territory again asserted this dominance in encounters in home cages, whether these animals were intruders or residents. Subordinate voles often adopted submissive postures and were intimidated into inactivity without any contact with the dominant. Dominants achieved this by threatening and squealing at every move made by the other animal.

2. Males and Females. (See Table 6.)

No distinction could be made between these encounters and those previously described on neutral territory for mice. The familiar pattern of an exploratory intruder was again seen. Mutual investigation was commonplace, and aggression was shown only by males aggressively grooming females. Both participants often remained stationary together for some minutes in one corner of the cage, after contactual behaviour had taken place.

On home territory, both sexes of vole exhibited the bias described for the all-male encounters. Samples were again small, however. Aggression is of a lower intensity compared with that of all-male contests.

Resident vole females with young exhibited a dramatically high level of aggression against the intruder. Young were protectively sheltered in one corner, from which the female made repeated sorties to attack and fight the male. The female was particularly persistent in her attacks and vicious fights and prolonged chases were observed. The males were very defensive and unobtrusive in their behaviour - their only activity being retreat before the attacks of the female.

It is interesting that the attacking females, in the above encounters, never once squealed, whereas the males accompanied their defensive postures with almost continual squealing. This phenomenon was noted in other all-male combats. The initiater of high intensity aggression (e.g. Fight) rarely squealed, whereas the defensive animal receiving such attacks was always vociferous. There seems to be some correlation between dominance and subordination here - or, at least, between attack and defence.

3. Females and Females (See Table 7)

The familiar pattern of exploratory intruder and relatively static resident was again observed.

Female mice, as expected, displayed no aggressive behaviour. Intruders were confident and initiated frequent contact with the resident.

Vole encounters generally contained little activity. Exploratory sorties by the intruder met the familiar brief display of aggression from the relatively static resident.

Resident female voles with young were again highly aggressive. The intruder was repeatedly attacked and chased, gaining respite only when the mother broke off the conflict in order to tend her young. Intruders displayed submissive postures frequently (unlike intruding males) but this in no way lessened the intensity or frequency of the residents' aggression.

COLONIAL ACTIVITY AND JUVENILE BEHAVIOUR.

1. Colonies (See Table 8)

Strange animals were introduced into the home cage of a resident pair. The pair, one male and one female, had been in residence since July. When the intruding male mouse was a dominant animal the subordinate resident male sometimes displayed aggression that ordinarily would not be expected when stable social relationships have become established. Brief fighting took place but the dominant quickly asserted his superior social status. After a while normal relationships returned: the dominant frequently aggressively groomed the submissive subordinate.

In the above encounters the resident female was inactive. However, in encounters where subordinate male mice were introduced into a colony containing the dominant male, it was the resident female that showed an unusual level of aggression. The intruder was repeatedly approached and groomed in an aggressive manner. At one time one female was on top of the intruding male - the latter adopting a submissive posture.

Female intruders into mice colonies seemed to have a less disruptive effect on the normal behaviour of residents. The intruder seemed to be accepted, after initial investigation by the residents. Shortly, all three animals could often be seen occupying the nest, or one particular corner.

Male vole residents were not abnormally aggressive towards the exploratory intruder: towards subordinates no more than in normal encounters, towards dominants perhaps even less so. There was, on the whole, little activity or aggressive behaviour.

Resident female voles appeared somewhat more aggressive than normal. They were more active and exploratory and persistently approached the intruder, whether the latter was male or female.

A prominent feature of the introduction of a strange male vole into a resident colony was the apparent disruption of previous social harmony between the residents. Both male and female residents readily threatened and attacked if approached by the other - there being no apparent distinction between the intensity of this aggression and that directed by both towards the intruder.

Female vole intruders did not have the same effect upon the colony. Agonistic display between the resident pair was never observed on these occasions.

2. Juvenile Clethrionomys. (See Table 9.)

The colony of three juveniles (two males, one female) was set up in the first week in August. (Juveniles were, for the purposes of this study, animals under 15.0 g. and not yet of adult pelage.) Several days of aggression and unrest within the colony was observed before animals finally settled down. (This prolonged unrest was also noted when the adult colonies were established.) After a week no further disturbance was heard.

After a fortnight the animals in the colony were reweighed. One male was then far advanced, developmentally, above the other two animals. This particular male was then as big and heavy as a normal adult male (22.5 g.), and had the full dark pelage of a mature animal. The other residents only showed an increase in weight of the order of 2.5 g. This 'increase' could result from the daily fluctuations of weight and might not be a real increase. Their size had not changed and they still retained their juvenile pelage.

It seemed that a social hierarchy had been established in the colony. Certainly the large 'dominant' was confident and active compared with the other members of the colony. Aggression and hierarchical considerations might account for increased growth in the 'dominant', with consequent adverse effects on the growth in the other two animals. Equally well, aggression and increased growth might be genetically linked, and not be cause and effect.

The introduction of a strange, adult male into the colony had a similar effect to that observed in adult colonies, except that colonial harmony was not disrupted in this case. The large young male and the intruder were the only active participants in the encounter. Aggression of low intensity was shown by both these animals at the approach of the other.

The strange male was left in the colony for a subsequent ten day period. During this time all four animals could be seen huddled together in the nest. No strife was noted after a few days.

After ten days there were no significant changes in weight in any of the animals (See Table 15, Appendix 2).

Two similar colonies were also set up at this time between adult males and a juvenile male in one case, and a juvenile female in the other. No changes in weight were recorded after ten days. All animals had settled down together - often occupying the same nest in apparent harmony.

Encounters organized between juveniles of both sexes and adults of both sexes showed similar patterns of behaviour to those seen in all-adult encounters. Juveniles seemed to be as aggressive as adults, and adults were not abnormally aggressive in any way. One particular juvenile male seemed to be more active and confident than its adult male counterparts.

On one occasion this juvenile elicited submission from the adult. Juveniles are very active and quick-moving in general.

Very few encounters of this nature were staged therefore the above impressions must remain speculative.

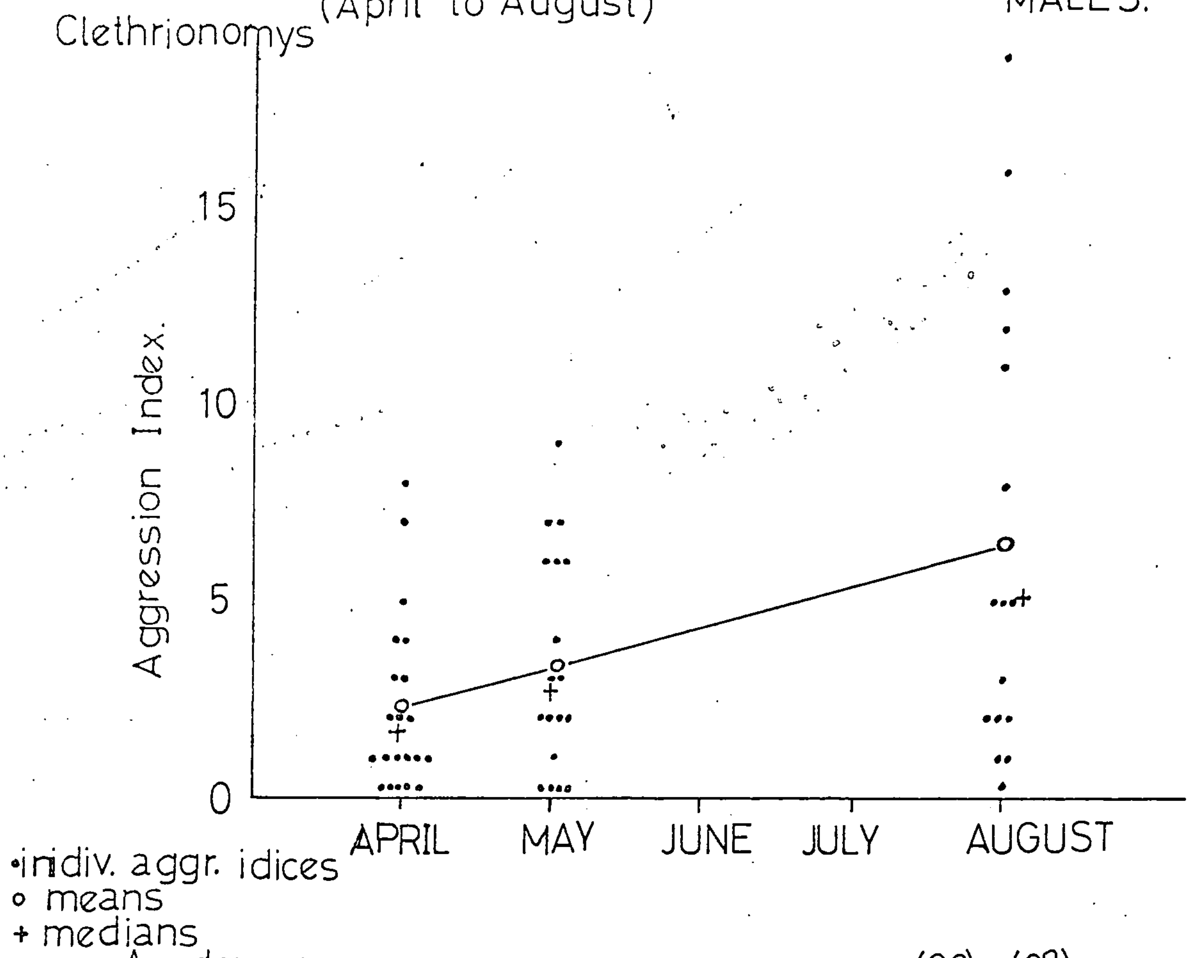
THE CYCLE IN AGGRESSIVENESS.

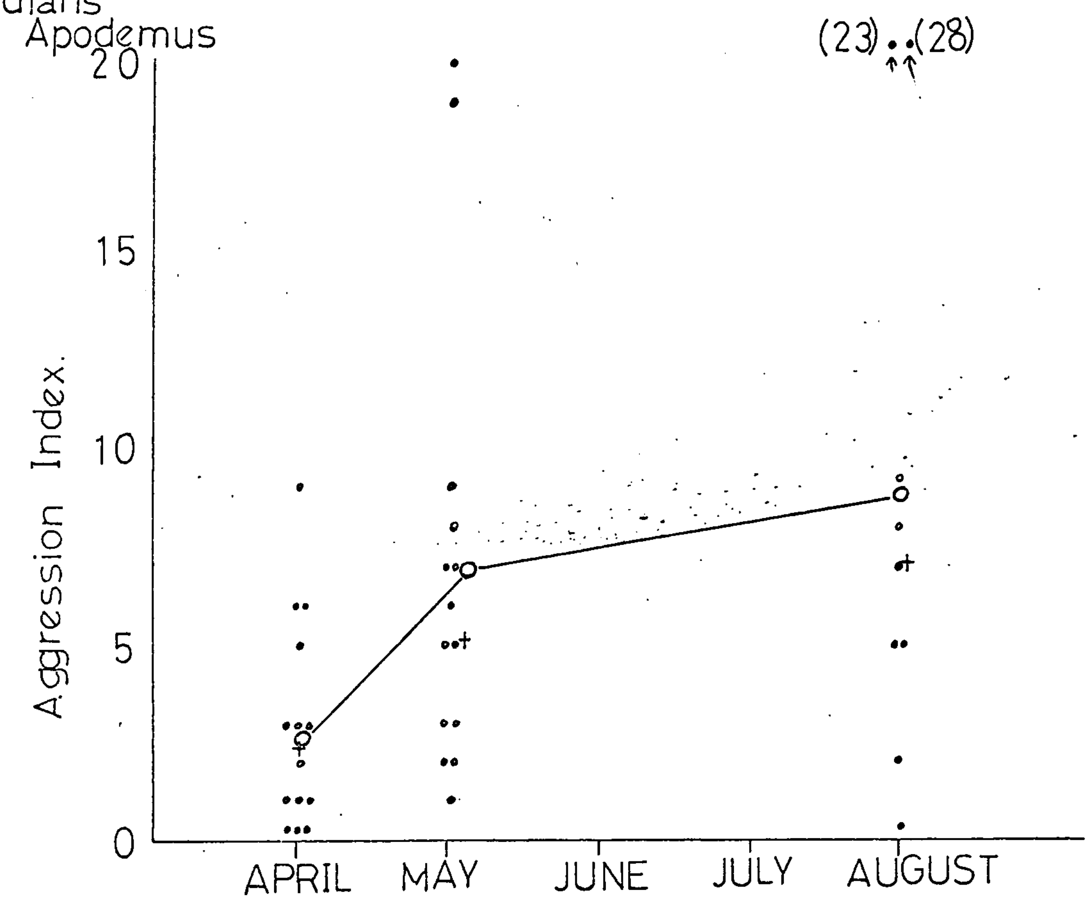
Results for April and May encounters between males of both species, on neutral territory, have been described previously.

Further results were obtained from the animals brought into the laboratory in August, and tested under a similar laboratory procedure.

The aggression indices of all the laboratory males so tested at these times are plotted in Figure 7. The means of each batch of observations are also plotted. For both species there is an increase in the average level of aggression from April to May, and again from May to August. The increases for *Apodemus* are more dramatic but there are fewer observations. The medians of the distributions are also shown in Figure 7. Assuming linearity their positions might help to explain any insignificance in statistical tests based on comparison of the means, despite an apparently substantial average rise. Uneven distribution of median values would suggest insignificance, though median values do follow changes (increases) in the mean quite closely. This would indicate that the whole batch of experimental animals changes as a whole, and not that only one

Fig. 7. CHANGES IN AGGRESSION IN EXPERIMENTAL MALES. (April to August)





or two individuals change in an erratic manner.

If the scale is non-linear, as suspected, then averaging is not legitimate, but comparisons between medians are. However, it is difficult to statistically compare median values.

A "Student-t" test for small samples was first applied to test increases (Bailey, 1966). However, further examination of data revealed a non-normal distribution and a non-linear scale. Hence, this test is invalid under these circumstances. 'Chi squared' tests were also performed but proved unsatisfactory. Ultimately a non-parametric test was applied to data. The one adopted was the Mann-Whitney U-test for two samples of ranked, non-paired observations. This procedure tests for equality of "location" of two samples. (Sokal & Rohlf, 1969).

The Mann-Whitney U-test reveals no difference between April and August observations for either *Clethrionomys* $(0.01>p>0.005)$ or *Apodemus* $(0.02>p>0.01)$. However, the April to May rise in *Clethrionomys* is significant $(p>0.10)$, whilst the rise for *Apodemus* over the same period is still insignificant $(0.02>p>0.01)$.

Thus presented and analysed the results hardly allow any conclusions to be formulated. Evidence from sexual condition and the correlated subjectively assessed aggression do, however, suggest definite increases in agonistic behaviour over the whole period of observation.

THE EFFECT OF PHOTOPERIOD DIMINUTION ON AGGRESSIVE BEHAVIOUR

Total numbers of aggression indices achieved by laboratory experimental males under a reduced light regime are shown graphically in Figure 8 for the two periods of testing, July and August. April and May mean values for aggression indices taken from Figure 7 are also shown in Figure 8 for comparison.

There is an average increase in vole aggression and a decrease for mice. Numbers of observations are, unfortunately, small.

The Mann-Whitney U-test was again applied to data. For *Apodemus* the apparent decrease in agonistic behaviour is insignificant when taken over the whole period from May to August ($0.02 > p > 0.01$). The decrease from May to July is, however, significant ($0.05 > p > 0.02$). The increase in aggression in the case of *Clethrionomys* over this period is both significant in July ($p > 0.10$) and August ($p = 0.10$).

An overall impression of decreases, both in intensity and frequency of aggression, is gained from the encounters. This was substantiated by a corresponding decrease in aggression assessed subjectively. Sexual regression also occurred during the test period. The laboratory record of five males of each species recorded during July and August, whilst these animals were under the reduced photoperiod, is shown in Table 12. Regression from the May condition in respect of both sexual

Fig. 8. CHANGES IN AGGRESSION IN EXPERIMENTAL Reduced Photoperiod (July to August) MALES.

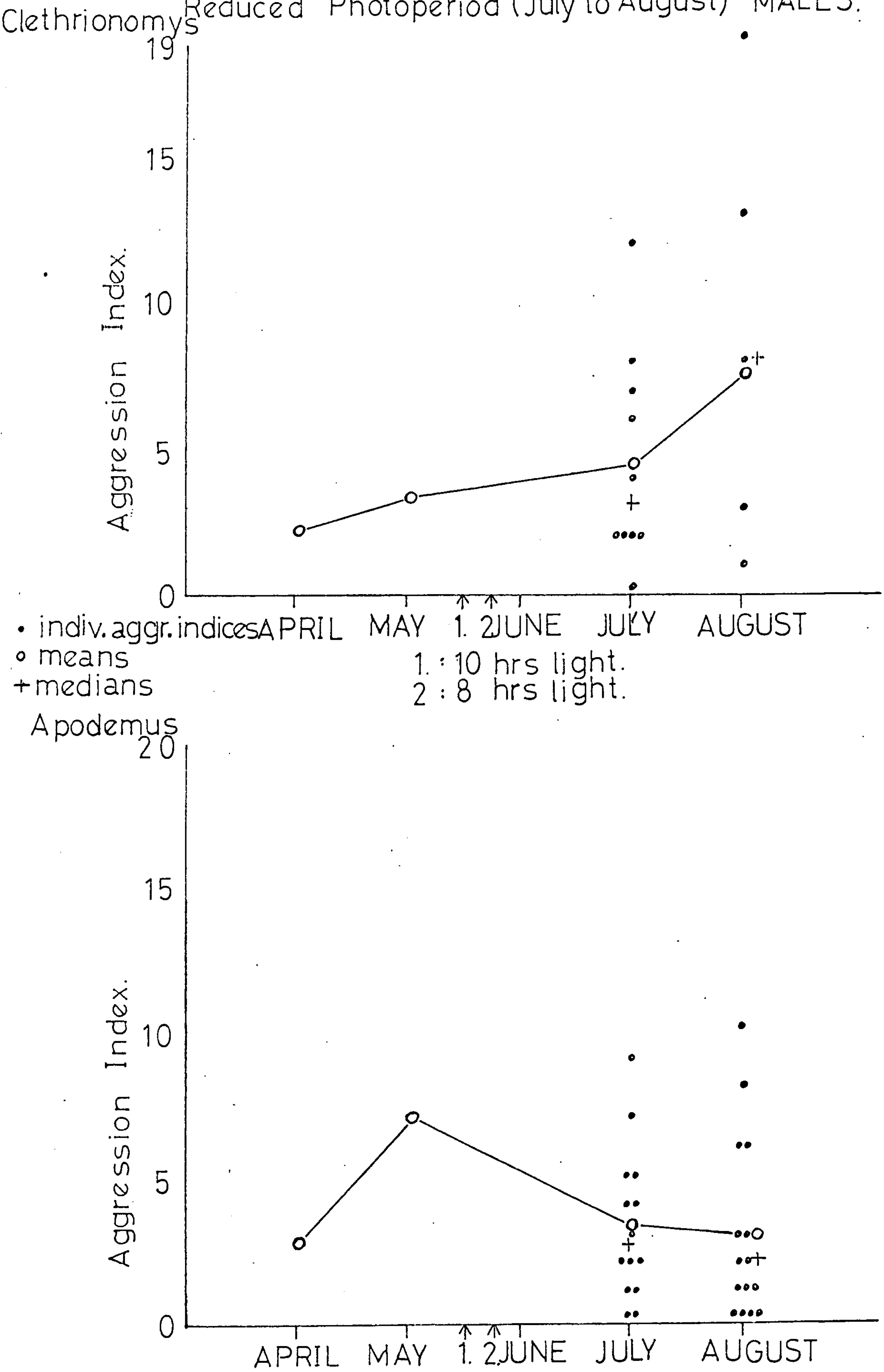


TABLE 12. Laboratory Record of Some Experimental Male Animals (July - August)

APODEMUS	JULY					AUGUST					
Laboratory identification number	Weight (gm.)	Length (cm.)	Sexual condition	subjective aggression index	Aggression index in laboratory	Weight (gm.)	Length (cm.)	Sexual condition	Subjective index	Aggressive index in lab.	Weights of testes (Aug.) (grm)
1	32.5	10.0	F.F.	3	7	31.0	10.0	$\frac{3}{4}$F	3	8	0.48
44	26.0	9.0	F.F.	2	4	27.5	9.0	$\frac{3}{4}$F	2	2	0.56
5	22.5	8.5	F.F.	1	2	22.5	8.5	$\frac{1}{2}$F	1	2	0.60
9	35.5	10.5	F.F.	3	9	33.0	10.0	$\frac{3}{4}$F	3	10	0.81
22	27.5	10.7	F.F.	2	5	24.5	10.0	$\frac{3}{4}$F	2	6	0.75
CLETHRIONOMYS											
10	25.5	10.5	F.F.	2	7	23.0	10.0	$\frac{3}{4}$F	2	8	0.43
13	23.5	10.0	$\frac{3}{4}$F	1	4	21.0	9.5	$\frac{1}{2}$F	1	1	0.57
18	25.0	10.5	F.F.	3	8	25.0	10.0	$\frac{3}{4}$F	2	13	0.24
19	22.0	10.0	F.F.	2	5	21.0	10.0	$\frac{3}{4}$F	2	3	0.50
20	25.0	10.5	F.F.	3	12	23.0	10.0	$\frac{3}{4}$F	3	19	0.38

condition and aggression is shown. (These ten animals are the same individuals whose laboratory record for April and May is shown in Table 2.)

There thus seems good evidence to suggest the somewhat inconclusive decrease in *Apodemus*, and the perhaps anomalous rise in *Clethrionomys* observed in laboratory tests, arises from the small numbers of encounters staged to test hypothetical decreases.

Though there is some statistical evidence for decrease aggression under a reduced photoperiod results cannot be said to be conclusive.

The statistically real rise in aggression for *Clethrionomys* over the observation period might perhaps be anomalous in view of other evidence presented above. The increase may, however, be a real phenomenon. *Clethrionomys* populations are known to sometimes continue breeding during August and early winter. Perhaps the rise is linked with social conditions in the wild population for this particular year. "Aggression build-up" in years preceding a "crash" phase in population is discussed later.

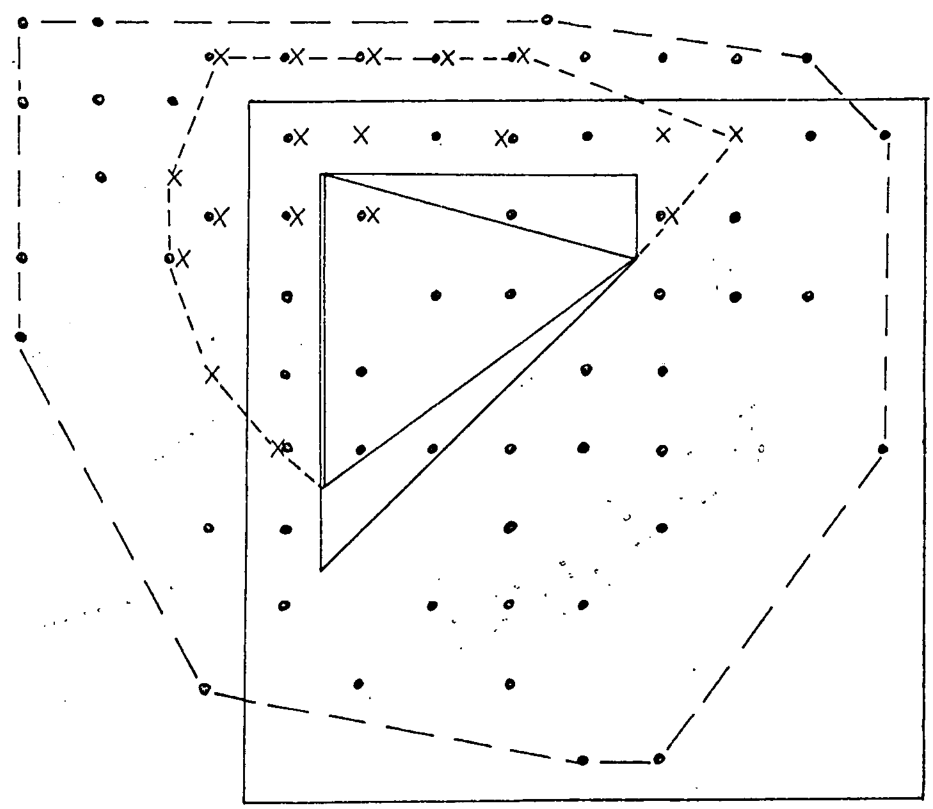
CORRELATION BETWEEN HIERARCHICAL POSITION AND HOME RANGE.

Nine *Clethrionomys* males and two *Apodemus* males, marked in June were recaptured in August. All these animals were tracked in June and July, though some more consistently than others. From combined trapping and tracking data a range for

Fig. 9. TERRITORY SIZE FROM COMBINED TRAPPING & TRACKING DATA (for Apodemus)

INDIV. ANIMAL: LH5 ——— trapping range
— — tracking range
• tracking points visited.

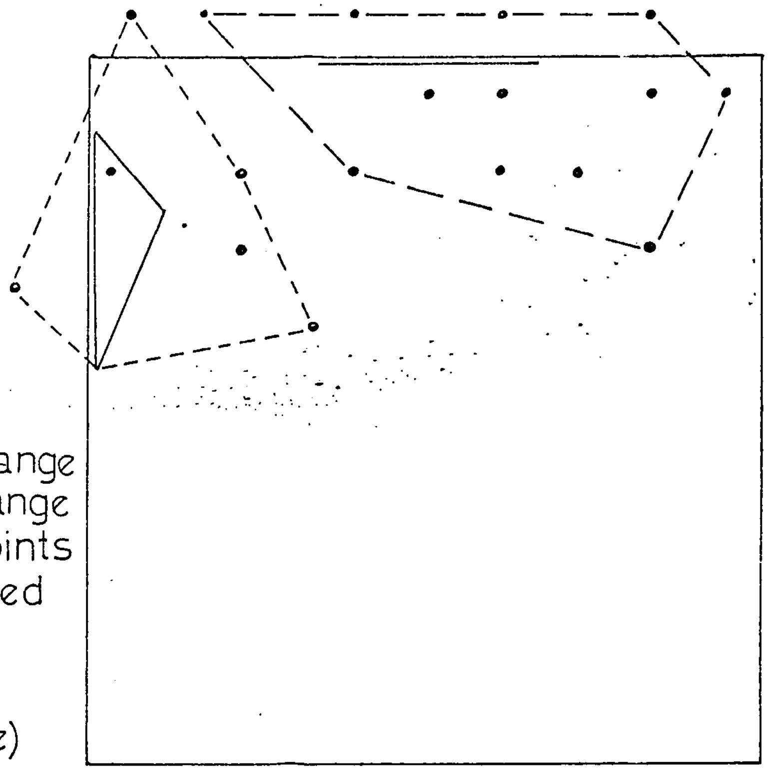
LH4 ——— (as above)
- - - -
x



TOTAL RANGES: LH5 ~ 9000 sq. yd. (1·86 acres)

LH4 ~ 2775 sq. yd. (0·57 acres)

Fig.10. TERRITORY SIZE FROM COMBINED TRAPPING & TRACKING DATA (for Clethrionomys)



Animal: LH 5

——— trapping range

— — — tracking range

• tracking points visited

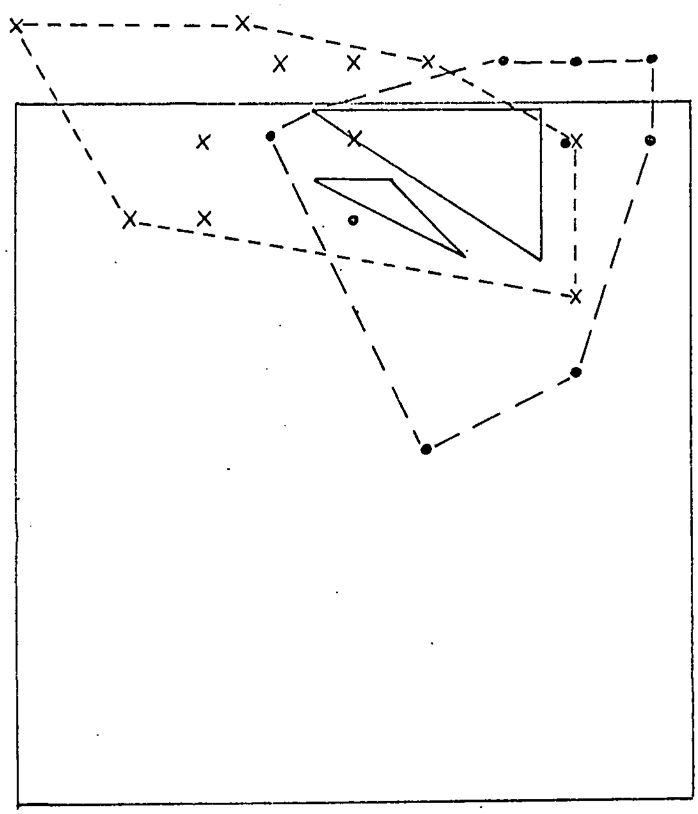
LH 2

———

- - - - - (as above)

•

Total Ranges:		
LH 5	~ 1300 sq. yd.	(0·27 acres)
LH 2	~ 975	(0·2)
LH 3	~ 1700	(0·35)
LF 3	~ 1625	(0·34)



LH 3

———

- - - - - - (as above)

x

LF 3

———

— — — (as above)

•

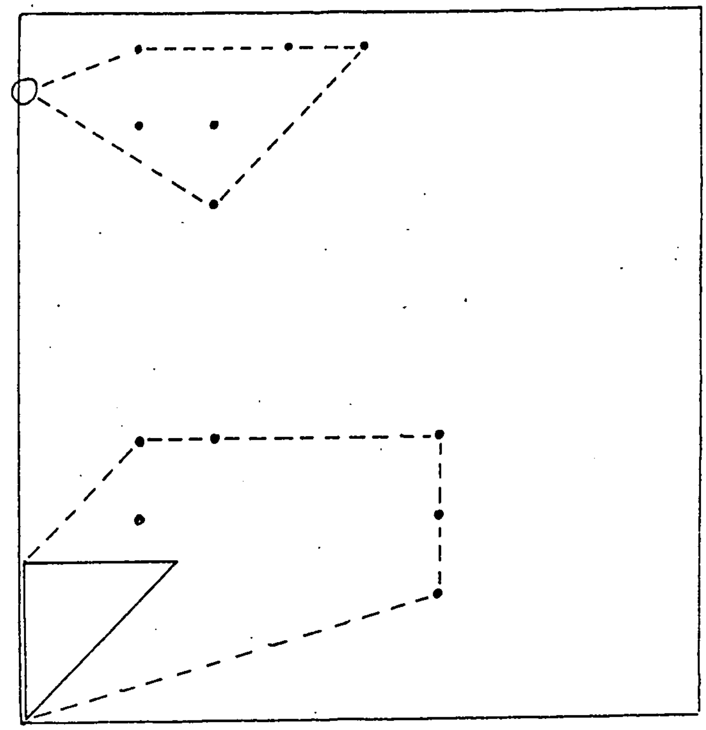
Fig. 11. TERRITORY SIZE (cont.)

Animal: RH1

——— ------ (as before) •

LF4

——— - - - - •



Total Ranges:

RH1 ~ 1375 sq. yds. (0·27 acres)
LF4 ~ 500 (0·12)
RH4 ~ 1375 (0·27)
RH3 ~ 2225 (0·46)

RH4

——— — — — •

RH3

——— - - - - - ×

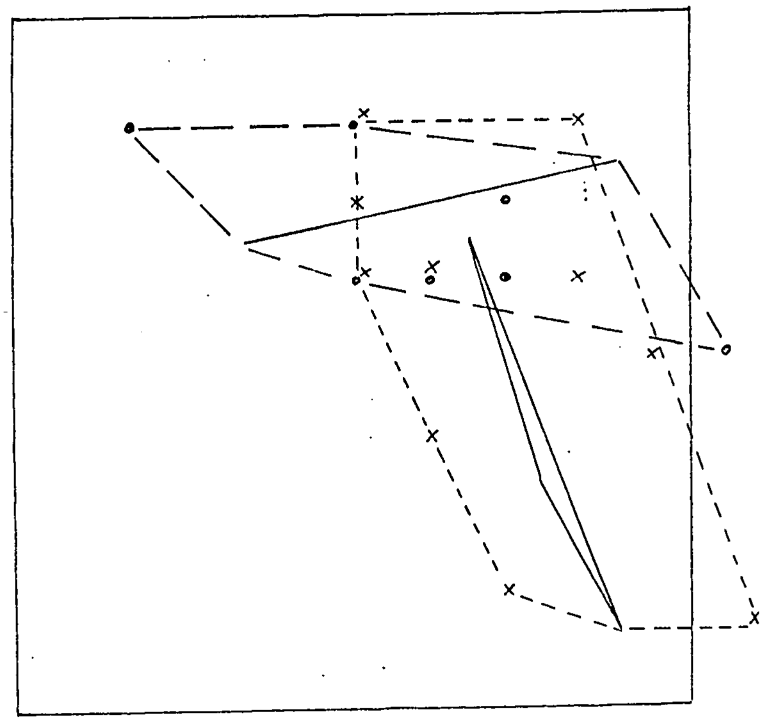
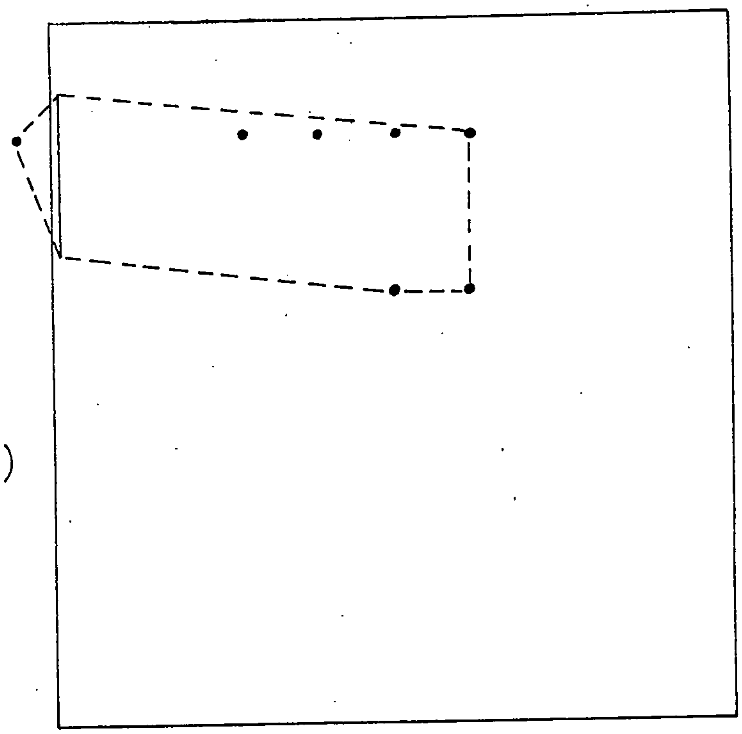


Fig. 12. TERRITORY SIZE (cont.)



Animal: RF2

______ - - - - (as before)
•

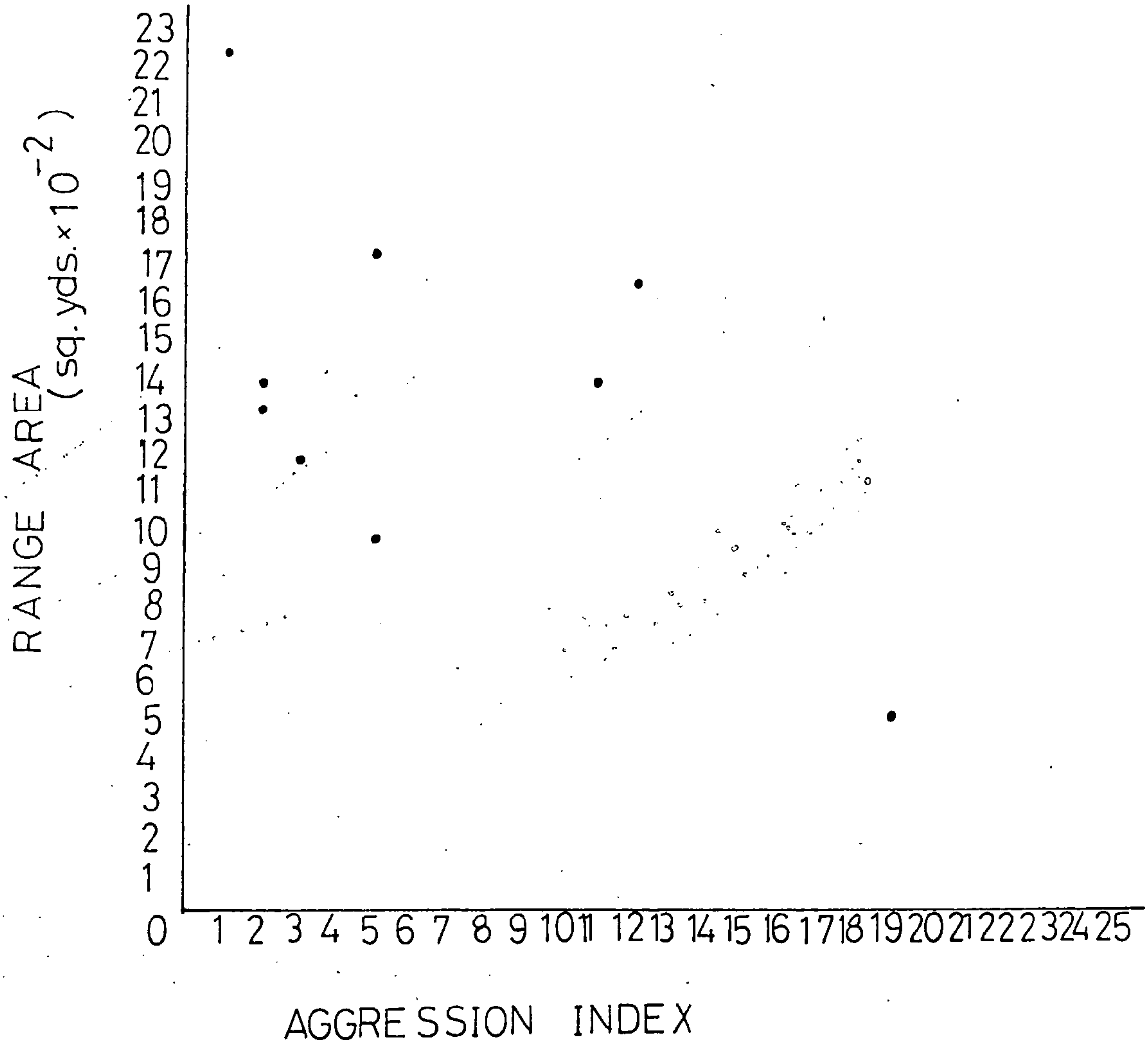
Total Range : RF2 ~ 1175 sq. yd. (0·24 acres) each individual was estimated from Figures 9 to 12. These ranges must only be an estimate of total range since the period of observation was relatively short. No real evidence was gained as to whether Home range remains constant throughout the summer. From trapping results (Table 10) it can be seen that marked animals were recaught in August very near points (or point) of initial capture in June - sometimes in the same trap. Thus, there does not seem to be a substantial shift in ranges, either in area or position, in the intervening time between trapping periods. Trapping ranges are on the whole a poor indication of home range or territory size (Brown, 1966). They are very localized and animals seem to travel great distances to enter certain traps (Jewell, 1966).

Tracking and trapping data for each individual is shown in Tables 10 and 11. Diagrams of combined tracking and trapping ranges are presented in Figures 9 to 12.

In the laboratory encounters between these animals and a batch of control animals were arranged with the same experimental provisions as those applying to all-male encounters described previously. Results of these encounters were also similarly recorded.

The aggressive indices thus obtained for each individual vo vole was plotted against estimated territory size in Figure 13. The scatter diagram thus obtained does not show any relationship between the two parameters. There cannot be a positive

Fig. 13. SCATTER DIAGRAM : Aggressive Index vs. Range Area (for CLETHRIONOMYS)



correlation, though a negative correlation seems more applicable. The small number of observations does not lend itself to any further statistical treatment.

The two mice differed greatly both in territory size and aggression indices. One animal was obviously dominant to the other, and apparently ranged over a much greater area of territory. However, since only two animals were tested, no conclusion can be drawn from such a low sample number.

The results for the two mice are shown: tabulated form below:

Individual Animal	Estimated Territory Size	Aggression Index: In the lab.	Aggression Index: Subjective
LH 5	9000 sq.yds. (1.86 acres)	28	3
LH 4	2775 sq.yds. (0.57 acres)	8	2

DISCUSSION.

Individual variation in Aggression.

The Dominance Hierarchy.

Males of both species showed marked differences in aggressive behaviour. The graded series set up in the laboratory is considered a good index of their differences. A dominance hierarchy is very evident in *Apodemus*. Those at the top of the graded series showed consistently higher scores in encounters with other males. These scores are higher, by a factor of four or five, than those achieved by animals lower down the series. In *Clethrionomys* a hierarchy is present but the range of aggressive indices is not so wide as that seen in *Apodemus*.

It is difficult to extrapolate such laboratory findings to conditions in the field on so little evidence. Brown (1966, 1969) describes social interactions in *Apodemus* where the "more normal evidence of a more dominant animal is that of submissiveness of other mice in his presence. Once hierarchical order is established it is not always challenged." Laboratory evidence of this acceptance of hierarchical position (i.e. without challenge to the dominant animal) was tested by repeated encounters between the same pair of animals. Initial encounters involved fighting initiated by the dominant male against a defensive but not submissive subordinate. Later encounters contained little or no fighting and aggressive behaviour was limited to aggressive grooming of the submissive subordinate by the dominant. Initial tension between the animals was quickly dispelled by mutual investigation and identification. The dominant was always confident and active whilst the subordinate, though not entirely static, would curtail any movement and adopt a submissive posture at the approach of the dominant.

It seems that fighting in mice only occurs in encounters between strange animals and animals of proximate hierarchical position, or if factors of home territory and presence of a female override hierarchical considerations.

Oldfield (1968), though he found no evidence of a hierarchy in Apodemus, suggested that stability in this species was achieved by a specific set of social releasers (nasils).

Sadleir (1965) and Healey (1960) have described a similar social structure for Peromyscus to that postulated in Apodemus by Brown (1966). Aggressive males are at the head of social units. Within these social units mutual antagonism is reduced, though members remain highly antagonistic and are intolerant of any stranger wandering into their home ranges. In both Apodemus and Peromyscus, population structure is purported to be stabilised by agonistic behaviour.

Social structure in Clethrionomys is less clear from the results of these present studies. Though dominance-subordination relationships exist, no such stability as that observed in Apodemus is immediately recognisable from repeated encounters between the same pair of animals. Results obtained from the establishment of colonies show that aggression does not desist for a few days after animals have been brought together. Furthermore the social harmony that is eventually achieved is readily disrupted by the introduction of a strange animal of either sex. Aggression then occurs between residents with the same frequency as it does between residents and intruder.

Population structure in Clethrionomys has not been documented so well as that of Apodemus. Kikkawa (1964) has suggested the existence of a social hierarchy with dominant males. He reported aggressive activity between voles, but did not observe similar activity in mice.

Oldfield (1968) concluded that Clethrionomys was more aggressive than Apodemus. The latter was a more tolerant species in his view and large stable colonies could be formed which never resulted in any deaths of participating animals. The greater frequency of contactual behaviour in mice is cited as perhaps reducing or inhibiting intraspecific fighting. The same worker suggested stability in Clethrionomys colonies was achieved "by the formation of a system of formalised social relationships in which one animal was dominant over subordinate males". This supposed stability was, however, disrupted by deaths (apparently due to social strife) and "only slight disturbance of the social structure" - by the introduction of a strange animal. The latter phenomenon has been described in this present study.

Factors of sex and home territory affecting aggression.

Brown (1966) has suggested female *Apodemus* maintain a home site and defend breeding ranges - "often challenging the movements of the males amongst these ranges". Healey (1966) described female aggression in *Peromyscus* when single females showed a high degree of cage possessiveness towards other females.

This study has shown that generally females are much less aggressive than the males of both species. Aggression seems to be the virtual prerogative of the males in mice. Threat and aggressive grooming were the only aggressive behavioural elements ever observed for female mice. This aggression was limited to encounters between strange males where tension between the animals was high, and to encounters involving the introduction of a strange subordinate male into the home cage of a resident dominant male and resident female. The inter-female aggression described by Healey was never observed.

No information relating to breeding *Apodemus* females was obtained in this study. However, some evidence that female aggression in *Clethrionomys* is heightened during the breeding season, with consequent increased possessiveness of territory, was obtained.

Female *Clethrionomys* readily show aggression towards strange animals of either sex. This disagrees with Oldfield's (1968) generalisation that: "neither males nor females (voles) were aggressive towards members of the opposite sex." Aggression displayed by females was generally of a lower intensity than that exhibited by males. Fighting rarely occured during encounters involving females. Even the most aggressive females, those which educed submission from other females, displayed only aggressive grooming in their agonistic behavioural repertoire. Aggressive grooming is in itself a rare occurrence in Clethrionomys behaviour.

When female Clethrionomys have young and an intruder is introduced into their home cages, the normally less offensive females become aggressors. The level of aggression, persistence of attacks and viciousness of the prolonged fights that occur during these encounters, have no counterpart in any other type of encounter organised in this study. Clarke (1952) and Eisenburg (1962) recorded similar high intensity aggression for breeding females in respectively: Microtus agrestis and Peromyscus. Perhaps there is a summation of the effects of motivation from the two factors in defence of home cage and defence of young.

Fighting in several rodent species is associated with territorial defence. Barnett (1958) has described the situation in the wild rat where fighting depends on being in familiar territory and encountering a strange animal. Eisenburg (1962), similarly, has described a territorial motivation for fighting in Peromyscus.

The present study provides little evidence that aggression is exacerbated by a home territory factor. Results do show an apparent bias (of amount of aggression displayed) in favour of the resident, in all types of encounter except those involving female mice. This bias applies also to the generally less offensive female voles in encounters with a male intruder. However, all these encounters do not significantly differ from encounters between strange animals on neutral territory in intensity and amount of aggression displayed. The apparent bias might be explained by differences in behaviour between resident and intruder. The resident is normally static and the intruder exploratory; the former being aggressive towards an exploratory approach of the latter.

Dominance, where it exists, seems to override any possible presence of enhanced aggression due to residence in home territory. Thus, a very aggressive intruder would not be intimidated in the presence of the home territory of a subordinate, and submission would be elicited in a similar way to that seen in neutral territory.

Oldfield (1968) also found little evidence for the existence of a home cage factor in either species. The enhancement of male aggression by presence of females has been described in rat colonies by Barnett (1958). Oldfield (1968), similarly, seemed able to make a confident statement to this effect.

In this present study, only in encounters between colonial mice was this effect noticeable. In one case, a resident subordinate showed some unexpected aggression towards an intruding dominant. There was a brief fight, but dominance was soon asserted. In normal circumstances (on neutral territory, without a mate) the subordinate would be expected to show submission in the presence of the dominant, and no fighting would take place.

Colonist voles did not show this effect in any instance. Rather, males resident with females seemed less than normally active and aggressive. In the same week these animals were highly aggressive in the neutral arena, against other male voles.

Conclusions cannot be drawn from so few observations.

Male Aggression and Territory Size.

Brown (1966, 1969) has shown that dominant *Apodemus* males, at the head of a social hierarchy, have a much greater territorial range than their subordinates. The whole colony uses the area (4 - 6 acres) which the dominant marks out; but individual subordinates have small overlapping ranges within this larger area. Kikkawa (1964) suggests that male *Clethrionomys* are wide-ranging relative to the more resident females, but does not suggest any correlation between his purported male dominance hierarchy and range size.

The average size of male *Apodemus* and *Clethrionomys* territories, quoted by various authors, range respectively from 0.45 to 0.77 and 0.38 to 0.55 acres.

The aim of the present study was not to elucidate absolute values for ranges but to obtain an estimate thereof.

Such a relatively short period of trapping and tracking of individually marked animals would not be expected to reveal total ranges of animals, especially since at this time of year there is some evidence for migration and a shift of population, especially in Apodemus (Brown, 1966). Ranges obtained in this study were from 0.12 to 0.46 acres for Clethrionomys, and from 0.57 to 1.86 acres for Apodemus.

Since so few results were obtained it is impossible to make a confident statement about a possible correlation between range size and hierarchical position.

In the case of voles, plotting of hierarchical position against range size does not reveal a relationship. The most aggressive animal has the least range and vice versa. Perhaps the relationship is the exact opposite to that initially sought, but this has not been tested in view of the paucity of observations.

The situation with Apodemus is a little clearer, but there are only two results. The dominant animal of the pair has an aggression index far in excess of the subordinate, and also has a range more than three times as large. This range is outside the average limits for male Apodemus, being nearly 2.0 acres. This perhaps could be equated with a dominant from Brown's data, taking into consideration the shortcomings of the present study.

However, two results cannot constitute quantitative evidence for Brown's hypothesis.

Seasonal Variation in Aggression.

In a number of previous studies intraspecific strife is the postulated regulatory factor in the population dynamics of several species of small mammals. Clarke, working with experimental populations of *Microtus* recorded differences in social status amongst adult males and further concluded that social factors governed the population cycles in this species.

Barnett (1964) has reviewed social stress in small mammal populations. Stress, he concludes, arises principally from social strife, which, in turn, usually arises from territorial behaviour. Even where no formal dominance hierarchy exists, as in *Rattus norvegicus*, fighting occurs when an adult male in familiar surroundings meets a strange adult male. A general consequence of territorial behaviour is that species' numbers rarely become so great that there is an excessive consumption of food or use of other resources. Hence, intraspecific conflict constitutes a negative feedback regulating density, and is an example of a density-dependent factor governing population growth.

Ashby (1967) found evidence of a four-year cycle in natural populations of *Clethrionomys*. Aggression, acting in the context of a negative-feedback mechanism, as described above, is cited as a possible cause for the crash phase in these cycles.

Results for the present study indicate a significant rise in adult male aggression, in Clethrionomys, during the spring. However, both sexes and young animals exhibit agonistic behaviour towards any other strange animal in varying degrees. Though work has not proceeded far enough to make a confident statement, my impression is that social structure is not so formal and clear-cut as in Apodemus. Voles display aggression in a more random manner. This may contribute to differences in population dynamics between the two species. Thus, as Brown (1966) suggests, the stable population structure in Apodemus leads to annual fluctuations and avoid population explosions and subsequent 'crashes' that are seen in Clethrionomys. The less stringent and formal social interactions in Clethrionomys lead to a more gradual build-up of aggression, and consequently a higher population density is achieved before aggressive factors affect a dramatic drop in numbers.

The rigid population structure with accompanying formalised social relationships has been described in Peromyscus by Healey (1966). Male aggression was found to change seasonally: there being a spring increase, a summer high and an autumn decrease to a winter low. Juvenile mortality and recruitment closely followed this annual cycle. Low summer numbers in the population as a whole were attributed to high male aggression, and only in autumn when the latter subsided did numbers increase

As mentioned in the Introduction to this thesis, Brown (1966) believes a similar pattern to occur in Apodemus populations. Male aggression is postulated as the main causee of low summer numbers. Juveniles are dispersed during the breeding season and are not recruited into the population till autumn.

Ashby (1967) also found a spring drop in numbers of Apodemus, low summer recruitment, and an autumn rise in numbers. His observations suggested a correlation between the spring drop in numbers (and low summer recruitment) and a spring rise in adult aggression. Watts (1969), in a recent paper describing the regulation of Apodemus numbers, also records a spring drop in population, a stationary density in the summer breeding season, and a rapid increase in numbers in autumn. Both changes at the beginning and end of the breeding season were found to be density-dependent and were related to changes in recruitment of juveniles. Poor summer survival of juveniles may have been due to antagonistic behaviour of established adults.

The present study has not provided results of statistical validity in regard to the increase in aggression in Apodemus. However, both field and laboratory observations give a real impression of such a change, initiated as animals develop breeding condition.

Attempts to simulate the onset of autumn, by a diminution of photoperiod, also failed to achieve significant results.

After more than two months in a reduced light regime, experimental male voles displayed an overall increase in aggression. Mice displayed a decrease which approached significance. Numbers of observations were, however, small, especially in the rise of vole encounters. Again, despite statistical insignificance, observations provide an overall impression of decreased aggression. This impression was substantiated by decreased fecundity in experimental males.

The social implications, in particular the effect on juveniles, of the putative cycle in aggression were not examined in a formal laboratory procedure in this study. The few encounters staged between adult and juvenile voles revealed a capacity in the latter for aggression of equal intensity to that displayed by some adults. Observations suggested dominance-subordination relationships exist amongst juveniles. There is a capacity for rapid growth and assertion of adult characteristics in the more aggressive juveniles.

SUMMARY

Wild populations of Apodemus and Clethrionomys were trapped during spring. The parameters sexual condition and aggressive behaviour when handled were investigated and monitored throughout this period. A correlation between these parameters was sought. It seems the development towards breeding condition is accompanied by increased aggression and activity in male animals.

In March male animals were brought into the laboratory and aggression was tested in a formal laboratory procedure involving intraspecific encounters between two animals. Dominance is apparent in certain very aggressive animals. From repeated encounters between the same animals a social hierarchy with formalized dominance-subordination relationships is apparent in Apodemus, but not in Clethrionomys.

Similar testing in May and August revealed an average increase in aggression, from the condition in April. Statistical tests applied to these increases revealed significance in the case of voles (April - May) but not in mice. Overall impressions were of a definite rise in aggression in both species. Paucity in observations is the suggested cause of their inconclusive nature.

When animals were subjected to a decreased photoperiod from May to August, testing at the end of this period revealed a rise in aggression in voles and a decrease in mice.

The social implications of male aggressiveness is discussed.

In May, adults of both sexes contributed to encounters arranged to test the possibilities of female aggression, and enhancement of aggression by a "home cage factor".

Female mice were generally not found to be aggressive. Female voles were aggressive towards strangers of both sexes, but less so than male animals. Female voles with young were most aggressive. Intruders of either sex were repeatedly attacked and fought.

Conclusive evidence of the existence of a "home cage factor" was not found, though results did indicate a bias of aggressive behaviour in favour of resident animals (in both sexes in voles, in males only in mice). Differences in behaviour between resident and intruder could explain this apparent bias in home cage encounters. Previously demonstrated dominance always prevailed against any possible exacerbation, of aggression due to residence in a home cage.

Colonies of males and female animals of both species were established in July. The social background of these animals seemed to explain abnormal differences in behaviour exhibited when strange animals of both sexes were introduced into the colony. Resident female mice became aggressive toward the intruder and resident subordinate male mice briefly challenged an intruding dominant. No consistent pattern could be seen in voles in such encounters. Social relationships in voles were considered less stable than in mice. The relevance of this to the population dynamics of both species is discussed.

An estimate of home range of males of both species was obtained. Males were individually marked, tracked and later recaptured. Recaptured, marked animals were brought into the laboratory and their aggressive behaviour tested in a procedure similar to that previously used for other males. A correlation between range size and aggression was sought. No correlation could be seen in voles, though the number of observations was small. A direct correlation, corroborated by previous subjective assessment of hierarchical position, was obtained in mice. The obviously dominant animal ranged over a much greater area than the subordinate. However, only two marked mice were recaptured and no conclusion can be made.

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TABLE 3 ENCOUNTERS BETWEEN MALES AND FEMALES

(Neutral Territory)

A.G. = aggressive groom   F. = Fight
T. = threat   C. = Chase   *Dominant individuals
A. = Attack

MICE Encounters	Introductory Elements ♂	Introductory Elements ♀	Aggressive Elements ♂	Aggressive Elements ♀	Defence Elements ♂	Defence Elements ♀	Withdrawal Elements ♂	Withdrawal Elements ♀	Submission Elements ♂	Submission Elements ♀	Contactual Elements ♂	Contactual Elements ♀	Ambivalent Elements ♂	Ambivalent Elements ♀	Non-Social Elements ♂	Non-Social Elements ♀
8	8	4	3 (2AG) (7T)	0	0	0	0	0	0	3	13	5	0	0	7	14
	1	8	2 (1AG) (7T)	0	0	0	0	1	0	1	1	6	0	0	3	12
	0	6	0	0	0	0	0	2	0	0	8	9	0	0	3	22
	6	0	1 (1AG)	0	0	0	1	0	0	1	11	2	0	0	12	3
	10	0	3 (3AG)	0	0	0	0	3	0	3	12	0	0	0	13	9
	4	0	3 (3AG)	0	0	0	0	1	0	3	3	2	0	0	11	6
	10	8	1 (1AG)	0	0	0	0	0	0	1	8	3	0	0	7	9
	10	3	0	0	0	0	0	3	1	0	9	2	0	0	11	3
TOTALS	49	11	13 (10AG) (3T)	0	0	0	0	10	1	12	65	27	0	0	67	78

VOLES	Introductory Elements		Aggressive Elements		Defence Elements		Withdrawal Elements		Submission Elements		Contactual Elements		Ambivalent Elements		Non-Social Elements	
Encounters	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
13	1	1	2 (2T)	4 (2T2A)	0	0	1	2	0	0	0	0	0	0	1	2
	0	0	1 (1T)	0	0	0	0	0	0	0	0	0	0	0	2	4
	0	3	6 (3T) (3A)	0	0	0	0	1	0	0	0	0	0	0	0	0
	0	1	2 (1T) (1A)	0	0	0	0	1	0	0	0	0	0	0	0	3
	0	* 2	17 (67,SF SA 1C)	5 (3T, 2A)	0	0	0	4	0	0	0	0	0	0	0	1
	0	1	5 (4T, 1A)	4 (4T)	0	6	0	1	0	0	0	0	0	0	1	2
	2	1	2 (1T, 1A)	0	0	0	0	3	0	0	0	0	0	0	1	4
	3	1	4 (3T, 1A)	3 (2T, 1A)	0	0	2	1	0	3	0	0	0	0	2	1
	0	8	14 (8T) (6A)	7 (7T)	0	0	0	8	0	0	0	0	0	0	0	9
	0	5	8 (5T, 3A)	4 (4T)	0	0	0	5	0	0	0	0	0	0	0	5

VOLES	Introductory Elements		Aggressive Elements		Defence Elements		Withdrawal Elements		Submission Elements		Contactual Elements		Ambivalent Elements		Non-Social Elements	
Encounters 13	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
	3	0	6 (4T) (1A,1 AG)	7 (4T) (3A)	0	0	0	2	0	0	0	0	0	0	10	3
	0	4	0	1 (1C)	0	0	2	0	0	0	0	0	0	0	0	2
TOTAL	9	33	82 (44T) (29A) (1AG) (1C) (5F)	39 (30T) (8A) (1C)	0	6	7	28	0	3	0	0	0	0	20	54

TABLE 4

ENCOUNTERS BETWEEN FEMALES (NEUTRAL TERRITORY)

MICE Encounters	Introductory Elements ♀	Introductory Elements ♀	Aggressive Elements ♀	Aggressive Elements ♀	Defence Elements ♀	Defence Elements ♀	Withdrawal Elements ♀	Withdrawal Elements ♀	Submissive Elements ♀	Submissive Elements ♀	Contactual Elements ♀	Contactual Elements ♀	Ambivaent Elements ♀	Ambivaent Elements ♀	Non-Social Elements ♀	Non-Social Elements ♀
6	5	3	0	0	0	0	0	0	0	0	3	3	0	0	9	6
	1	0	0	0	0	0	1	1	0	0	4	4	0	0	6	3
	7	2	0	0	0	0	0	0	0	0	10	5	0	0	8	16
	0	3	0	0	0	0	0	0	0	0	3	4	0	0	9	10
	2	9	0	0	0	0	1	0	0	0	5	6	0	0	6	9
	8	3	0	0	0	0	2	1	0	0	5	6	0	0	8	7
TOTALS	23	20	0	0	0	0	4	2	0	0	30	28	0	0	46	51
VOLES																
7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0
	0	1	2 (1T) (1A)	0	0	0	0	1	0	0	0	0	0	0	4	4
	0	2	0	0	0	0	0	2	4	3	0	1	0	0	11	1
	1	0	0	2 (1T) (1A)	0	0	1	0	1	0	0	0	0	0	2	2

VOLES	Introductory Elements		Aggressive Elements		Defence Elements		Withdrawal Elements		Submissive Elements		Contactual Elements		Ambivalent Elements		Non-Social Elements	
Encounters	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀	♀
7	0	3	5 (3T 2A)	1 (1T)	0	0	0	3	0	0	0	0	0	0	0	4
	* 8	6	12 (3T 9HL)	3 (2T 1AG)	0	0	2	0	0	7	7	4	0	0	8	0
	* 3	12	16 (11T 5A)	10 (8T 2A)	0	0	1	4	0	0	0	0	0	0	7	8
TOTALS	13	24	35 (18T 8A 9AG)	16 (12T) (3A) 1A.G.	0	0	4	10	5	10	7	5	0	0	26	19

* Dominant individuals - very aggressive.

TABLE 5 HOME CAGE ENCOUNTERS I (Males vs. Males)

H.C. = Home Cage

*particularly aggressive individuals (dominants)

	Introductory Elements		Aggressive Elements		Defence Elements		Withdrawal Element		Submission Element		Contact Element		Ambivalent Element		Non-Social Element	
MICE	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂
No. of Encounters 6	0	0	(3A) (6T)	3 (T)	0	0	0	0	0	0	0	0	0	0	0	12
	1	*4	19(7T) (8F) (2C) (2W)	20 (4T) (3C) (8F) (3A) (2W)	0	0	0	0	0	0	0	0	0	0	1	15
	0	0	7(6T) (1A)	2(2T)	0	0	0	0	0	0	0	0	0	0	6	9
	0	0	8(7T) (1AG)	2(2T)	0	0	0	0	0	0	0	0	0	0	5	7
	6	2	6(5T) (1AG)	3(3T)	0	0	0	0	0	0	0	0	0	0	3	9
TOTALS	7	6	56(39T) (2AG) (3A) (2C) (8F) (2W)	31 (15T) (3A) (8F) (3C) (2W)	0	0	0	0	0	0	0	0	0	0	29	77
VOLES No. of Encounters 5	0	4	5(4T) (1A)	4(2T) (2A)	0	0	0	1	0	0	0	0	0	0	0	5
	0	0	1(1T)	0	0	0	0	0	0	0	0	0	0	0	1	2
	0	1	1(1T)	0	0	0	0	1	0	0	0	0	0	0	1	1
	0	4	9(6T) (3A)	4(4T)	0	0	0	1	0	0	0	0	0	0	0	3

	Introductory Elements		Aggressive Elements		Defence Elements		Withdrawal Elements		Submission Elements		Contact Elements		Ambivalent Elements		Non-Social Elements	
VOLES	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂	HC♂	♂
	*0	1	22(15T) (7A)	0	0	0	3	1	0	4	0	0	0	0	1	2
TOTALS	0	10	38(27T) (11A)	8(6T) (2A)	0	0	3	4	0	4	0	0	0	0	3	13

TABLE 6 HOME CAGE ENCOUNTERS

II (Males and Females)

H.C. = Home Cage
* Home cage female and young

MICE	Introductory Elements		Aggressive Elements		Defensive Elements		Withdrawal Elements		Submission Elements		Contactual Elements		Ambivalent Elements		Non-Social Elements	
	HC♂	♀	HC♂	♀	HC♂	♀	H ♂	♀	HC♂	♀	HC♂	♀	HC♂	♀	HC♂	♀
4 Encounters	0	0	3(3T) (2AG)	0	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	2(2T)	2(2T)	0	0	0	0	0	0	0	0	0	0	0	0
	2	6	2(1T) (1AG)	0	0	0	0	0	0	0	0	0	0	0	1	5
	30	18	0	0	0	0	0	0	0	0	0	0	0	0	20	25
TOTALS	32	24	9(6T) (3AG)	2(2T)	0	0	0	0	0	0	0	0	0	0	21	30
	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀
2 Encounters	4	3	2(2AG)	0	0	0	0	1	0	2	4	1	0	0	11	1
	10	7	1(1AG)	0	0	0	0	0	0	1	7	2	0	0	12	5
TOTALS	14	10	3(3AG)	0	0	0	0	0	1	0	3	11	3	0	23	6
VOLES	HC♂	♀	HC♂	♀	HC♂	♀	HC♂	♀	HC♂	♀	HC♂	♀	HC♂	♀	HC♂	♀
1 Encounter	1	0	2(1T) (1A)	2(1T) (1A)	0	0	1	0	0	0	0	0	0	0	0	4
TOTALS	1	0	2(1T) (1A)	2(1T) (1A)	0	0	1	0	0	0	0	0	0	0	0	4

VOLES	Introductory Elements HC♀	♂	Aggressive Elements HC♀	♂	Defensive Elements HC♀	♂	Withdrawal Elements HC♀	♂	Submission Elements HC♀	♂	Contactual Elements HC♀	♂	Ambivalent Elements HC♀	♂	Non-Social Elements HC♀	♂
2 Encounters	0	1	2(1T) (1A)	0	0	0	0	1	0	0	0	0	0	0	2	2
	0	0	1(1T)	2(1T)	0	0	1	0	0	0	0	0	0	0	1	1
TOTALS	0	1	3(2T) (1A)	2(1T) (1A)	0	0	1	1	0	0	0	0	0	0	3	3
	*HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂	HC♀	♂
2 Encounters	6	1	25(7T) (7A) (3W) (8F)	7(7T)	6	7	0	0	0	0	0	0	0	0	2	2
	4	1	15(4T) (4H) (6F) (1C)	0	4	1	0	0	0	0	0	0	0	0	2	2
TOTALS	10	2	40(11T) (11A) (14F) (3W) (1C)	7(7T)	10	8	0	0	0	0	0	0	0	0	4	4

TABLE 7.

HOME CAGE ENCOUNTERS 3 ; Females vs. Females.

HC. = Home Cage.
* = Home Cage Female+young.

	INTROD.	AGGR.	DEF.	WITHDR.	SUBM.	CONT.	AMBI.	NON-SOCIAL.
	H.C.♀ ♀	H.C.♀ ♀	H.C.♀ ♀	H.C.♀ ♀	H.C.♀ ♀	H.C.♀ ♀	H.C.♀ ♀	H.C.♀ ♀
Mice 5 encounters	2 0	0 0	0 0	0 0	0 0	9 0	0 0	7 5
	1 0	0 0	0 0	0 0	0 0	0 0	0 0	15 4
	3 5	0 0	0 0	0 0½	0 0	0 0	0 0	7 8
	5 8	0 0	0 0	0 0	2 0	8 8	0 0	7½ 13
	1 3	0 0	0 0	0 0	0 0	8 3	0 0	7 9
TOTALS.	12 16	0 0	0 0	0 0	2 0	25 11	0 0	41 49
Voles 4 encounters	0 0	0 0	0 0	0 0	0 0	0 0	0 0	1 5
	0 3	3 0 2T. 1A.	0 0	0 0	0 0½	0 0	0 0	0 4
	1 1	2 0 1T. 1A.	0 0	0 1	0 0	0 0	0 0	0 1
	0 1	1 0 1T.	0 0	0 1	0 0	0 0	0 0	0 0
TOTALS.	1 5	6 4	0 0	0 2	0 0	0 0	0 0	1 10
* 2 encounters	4 2	14 3 7T. 3T. 5A. 2C.	0 0	4 10	0 5	0 0	0 0	1 5

Cont.:-

*3 5	14 5 4T. 3T. 5A. 2A. 2W. 2F.	0 0	0 0	0 0	0 0	0 0	0 0
TOTALS.							
7 7	28 8 11T. 6T. 10A. 2A. 2W. 2F, 2C.	0 0	4 10	0 5	0 0	0 0	1 5

TABLE 8.

COLONIES.

I.: Intruder.
R.: Resident
* : Dominant.

	INTROD.	AGGR.	DEF.	WITHDR.	SUBM.	CONT.	ALBI.	NON-SOCIAL
MICE	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.	♂I. ♂R. ♀R.
2 encounters								
	*+ 6 1 0	6 3 0	0 0 0	0000	0 1 0	2 1 0	0 000	13 8 5
		1T. 1T. 3F. 2F. 2AG.						
	0 2 6	1 1 7	0 0 0	0 1 1	3 0 0	1 2 3	1 0 1	21 11 8
		1AG. 1AG.	7AG.					
TOTALS	6 7 6	7 4 7	0 0 0	0 1 1	3 1 0	3 3 3	1 0 1	34 19 13
		1T. 1T. 3F. 2F. 3AG. 1AG.	7AG.					
VOLES								
	1 0 2	2 3 2	0 0 0	1 0 1	0 0 0	0 0 0	0 0 0	4 0 0
		2T. 2T. 1A.	1T. 1A.					
	1 1 5	6 9 0	0 0 0	1 0 "2	0 0 0	0 0 0	0 0 0	0 1 4
		3T. 5T. 3A. 4A.						
	3 0 1	1 11 9	0 0 0	2 0 0	3 0 0	0 0 0	0 0 0	8 0 1
		1T. 7T. 5T. 4A. 4A.						
TOTALS	5 1 8	9 23 11	0 0 0	4 0 3	3 0 0	0 0 0	0 0 0	12 1 5
		6T. 14T. 6T. 3A. 9A. 5A.						

	INTROD.	AGGR.	DEF.	WITHDR.	SUBM.	CONT.	ALBI.	NON-SOCIAL
	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.	♀I. ♂R. ♀R.
MICE	* 5 0 0	0 0 1	0 0 0	1 0 0	0 0 0	5 3 3	0 0 0	7 10 2
		1T.						
	5 3 1	0 2 1	0 0 0	0 0 0	2 0 0	4 4 4	0 0 0	8 6 2
		2AG. 1AG.						
TOTALS	10 3 1	0 2 2	0 0 0	1 0 0	2 0 0	9 7 7	0 0 0	15m 16m4
		2AG. 1T. 1AG.						
VOLES	2 1 0	0 9 0	0 0 0	0 0 0	6 0 0	0 0 0	0 0 0	0 0 1
		6T. 3A.						
	4 2 0	4 0 7	0 0 0	4 2 0	0 0 0	0 0 0	0 0 0	2 1 0
		2T. 4T. 2A. 3A.						

Cont.:-

INTROD.	AGGR.	DEF.	WITHDR.	SUBM.	CONT.	AMBI.	NON-SOCIAL.
1 0 1	2 3 0 1T. 2T. 1A. 1A.	0 0 0	1%1%1	0 0 0	1 0 0	0 0 0	[illegible] 1 1
TOTALS							
7 3 1	6 12 7 3T. 8T. 4T. 3A. 4A. 3A.	0 0 0	5 3 1	6 0 0	1 0 0	0 0 0	3 2 2

TABLE 9.

ENCOUNTERS INVOLVING JUVENILES.

J.= Juvenile.
* =Home Cage Female + Young.

	INTROD.	AGGR.	DEF.	WITHDR.	SUBM.	CONT.	AMBI.	NON-SOCIAL.
	♂J. ♂	♂J. ♂	♂J. ♂	♂J. ♂	♂J. ♂	♂J. ♂	♂J. ♂	♂J. ♂
Voles & ENCOUNTERS.	4 0	4 9 4T. 5T. 4A.	0 3	4 2	0 3	0 0	0 0	5 0
	2 2	11 2 7T. 1T. 4A. 1A.	0 3	1 3	0 0	0 0	0 0	0 0
	0 2	1 3 1T. 2T. 1C.	3 0	3 0	0 0	0 0	0 0	1 0
TOTALS.	6 4	16 14 12T. 8T. 4A. 5A. 1C.	3 6	8 6	0 3	0 0	0 0	6 8
	♀J. ♂	♀J. ♂	♀J. ♂	♀J. ♂	♀J. ♂	♀J. ♂	♀J. ♂	♀J. ♂
	3 0	2 5 2T. 3T. 2A.	0 0	30	0 0	0 0	0 0	5 2
	♀J. ♀	♀J. ♀	♀J. ♀	♀J. ♀	♀J. ♀	♀J. ♀	♀J. ♀	♀J. ♀
	1 1	4 9 3T. 4T, 1F. 3A. 2F.	0 0	2 1	0 0	0 0	0 0	3 2
	2 7*	6 13 3T. 8T. 3A, 5A.	0 0	1 3	0 0	2 0	0 0	4 1
	J.♂ J.♂	J.♂ J.♂	J.♂ J.♂	J.♂ J.♂	J.♂ J.♂	J.♂ J.♂	J.♂ J.♂	J.♂ J.♂
	8 0	13 6 5T. 3T. 3A. 3A. 5C.	0 0	0 12	0 0	0 0	0 0	4 1
Juvenile Colonies.	♂J.♂♀	♂J.♂♀	♂J.♂♀	♂J.♂♀	♂J.♂♀	♂J.♂♀	♂J.♂♀	♂J.♂♀
	3 1 3	3 8 0 2T. 4T. 1A. 4A.	0 0 0	1 1 0	0.0 0	0 0 2	0 0 0	7 0 0

APPENDIX I.

Notes on Tracking Techniques

1. Smoked Paper.

Various difficulties were experienced with this method. Marked papers could not be renewed in the field, but necessitated transportation to and from the laboratory. In order to protect the sensitive tracking surface of freshly smoked paper the tracking cylinders also had to be taken back to the laboratory. Transportation, and the smoking process itself, were lengthy and laborious procedures.

The main difficulties, however, were in the actual tracking process. Satisfactory results were not being achieved with this method. Though the surface was very sensitive it did not, in general, record tracks of animals very distinctly. Such a surface might be more adequate when used in conjunction with larger containers which held papers flat. The containers available (see Methods and Materials) for use in this study were perhaps the main cause of the method's inadequacy. Animals had a very narrow pathway into the cylinder - due to the small diamater of the latter. Animals also had to turn round at the end of most tubes in order to affect an exit. In retracing its steps, the animal confused the tracks it made when entering the cylinder.

Despite this basic shortcoming, quite a degree of success was achieved with tracking of Apodemus. Almost complete lack of success with *Clethrionomys* was attributed to behavioural differences, with the former, when visiting the cylinders. *Apodemus* generally made one journey in and out of the cylinder. *Clethrionomys*, on the other hand, seemed to repeat this progression several times. The tracking surface thus became impossible to interpret, in all but a very few instances. Thus even if all tubes were open at both ends more satisfactory results would not have been achieved. Substantially better results were not achieved with the plastic tubes.

Repeated progression in and out of the cylinder might not be due to one animal alone. Perhaps a number of animals visited the same cylinder. (Only one animal's tracks were ever recorded on a surface marked by *Apodemus*). This might be feasible if there were high densities of voles (as trapping suggests) or if a social relationship allowed different animals to visit the same cylinder. (Dominance of some aggressive male individuals has been cited as the reason why some animals in the population keep away from traps and tracking cylinders. (eg. Kikkawa, 1964 and Brown, 1966).) These possibilities must remain speculative.

In the samples of marked papers provided, evidence of the visiting animal turning round at the end of the tube can be seen. Where animals have slipped on the curved sides of the cylinders can also be seen. Smoked paper only records the pad marks of the foot, and perhaps the claws, and not the whole impression of the foot. This gives rise to the difficulties in interpretation mentioned above.

Another disadvantage of the method was the sensitivity of the surface to moisture. The wet weather during the experimental period destroyed many papers. This is again perhaps due to the inadequacy of the adopted containers. Moisture collected at the bottom of the cylindrical containers and removed the surface from that critical part of the paper.

Another effect of wet weather was the appearance of large numbers of slugs. These were mostly the Large Red Slug (Arion ater rufus (L)). The attraction of these animals to the tubes was largely motivated, it seems, by the provision of food therein. Besides destroying the surface by their numerous tracks and copious excreta, these animals voraciously devoured the paper itself. Many papers were destroyed in this way. Examples of slug damage are shown.

Other slugs were also seen and affected papers in a similar way: some Large Black Slug (Arion ater ater (L)) and a few of the small, common grey slug (not identified). Snails also contributed to the damage (Discus rotundatus and Cepea nemoralis). Radulae marks of both slugs and snails can be seen in the examples provided.

Other inhabitants of the tubes, motivated more from shelter considerations it seems, were spiders, harvestment and on one occasion a toad (Bufo bufo).

Despite all shortcomings quite comprehensive data was accumulated for marked Apodemus males. At all times it was possible to detect which species of animal had visited the cylinder even if further interpretation was impossible. This was sometimes corroborated by the presence of faeces in the cylinder. Defaecation in cylinders seemed the habit of voles only. Urination on papers was normally attributed to Apodemus. (cf. Brown 1966, 1969).

After the first day of tracking about 25% of the papers were marked, roughly in equal proportion by both species. By the end of the week about 75% of all papers were marked in the same rough proportions. The distribution of marked papers and the frequency of visits corresponded roughly to the trapping distribution. Cylinders at the top and bottom of the grid (N. and S.) seemed more popular than those in the centre. As with some traps in the centre of the grid, some cylinders were visited only once or twice or not at all. These cylinders were resited when trapping recommenced in an attempt to overcome their possible location away from regular runways - if indeed this was the cause of their not being visited.

2. Petroleum Jelly and Talcum Powder.

This tracking surface was devised to overcome the main difficulty inherent with the smoked surface. The whole imprint of the foot of animals passing over the surface was recorded in the thick layer of grease. Only the paper at the entrance of the cylinder had the tracking surface spread over it. (See photographs). Spreading of grease all the way along the paper was considered uneconomical since that at the end of the tube would be spoiled in any case by the animal turning round.

Another advantage of this method was that marked surfaces could be renewed in the field, without time-consuming transportation to and from the laboratory.

The only real difficulty that was encountered was that in field conditions direct sunlight caused the grease to melt. Grease then collected in the bottom of the tube and hardened (see photographs). Siting of the cylinders in the shade partly eliminated this disadvantage. (Silicone grease found to be too hard for the purposes of tracking has an advantage in that it is temperature stable.)

The powder was taken up by the grease forming a white compound which contrasted well with the black paper. After a few days the grease (solvent fraction) impregnates the whole of the paper. Besides making the paper less susceptible to moisture (less important here since the actual tracking surface is waterproof) this allows powder to adhere to the paper itself. Thus the whole paper, to a limited extent, serves as a tracking surface.

Occurrence of indecipherable marked surfaces was much less frequent with this method. Some faint tracks thought to be those of juveniles and shrews were sometimes recorded. The main aim - of tracking marked voles - was achieved. Much less difficulty was also experienced with slugs, and snails. Perhaps this can be attributed to the drier weather. A small number of papers were attacked however. Slug movements did not this time destroy the tracking surface, but their appetites still caused trouble. Though paper was still eaten, the grease was now the main source of food. Radulae marks could again be distinguished (see Photographs). Depredations mainly occured at the edge of the grease-film. (Some extensive damage did more rarely occur when the surface film of newly-applied powder was removed and the whole of the grease film was attacked). Snails were still in evidence but again less commonly than in June. They scoured the surface of the grease and did not seem able to eat the grease layer wholesale as did the slugs. (See Photographs).

Damage was caused by the same molluscan species as before. In addition a few Garlic Snails (Oxychelis alliaris) were found.

In the July tracking periods generally, there seemed much less interest in tracking cylinders than in June. Only about 40% of cylinders were visited as opposed to 75% the previous month. Whether animals tire of cylinders, in the same way as they are recorded to tire of traps (Tanton, 1965) can only remain speculative reasoning. If Brown's (1966) observations are generally true, then Apodemus at least, should check objects in their ranges regularly. Presumably, if the cylinders were visited in June there could be no reason why they should not a month later. Perhaps there was a change in behaviour during this period. Disinterest cannot be attributed to lack of animals in the area as the August trapping records show.

Perhaps, on the other hand, the new tracking surface is obnoxious in some way, and this precludes revisits to cylinders - or any visits at all.

Another observation of interest made in this tracking period was that not all animals entering tubes, open at both ends, go right the way through. This might indicate that tubes closed at one end are in no way less attractive because of this. Indeed the frequent tracking records from this latter type of tube prove this. They were visited no less frequently than the former type.

Notes on Trapping.

In August some difficulty was experienced with slugs closing traps. Their bulk and slow movement was capable of setting off most of the traps they entered. Motivation for entry was probably the presence of grain. The main culprit was the Great Grey Slug (*Limax maximus*), and to a lesser extent the Large Red Slug, and Large Black Slug. The smaller, more common slugs (not identified) were not able to trip the trap mechanism.

Predators in the Woodland Study Areas.

1. Area A.

A badger (*Meles meles*) earth was situated in this area. The earth had one entrance. Though no traps were ever disturbed the earth was well used. It was probably the breeding earth of a sow.

Area B.

One single-entrance badger earth was situated in the area. There was frequent disturbance of traps. Fox (Vulpes vulpes) scats were picked up several times in the area, mainly in the N.E. corner. Scats were often quite fresh.

A pair of Tawny Owls (Strix aluco) were regularly seen in the area during June and July. They mainly frequented the Beech trees in the lower quarter of the grid.

A family of stoats (Mustela erminea) was known to inhabit the area in mid-July.

A good view of the stoats was had on 14.7.69. The young animals were making a great deal of noise - crashing about in the undergrowth. Screams, similar to the "spitting rattle" rec recorded by Southern (1964), were heard several times. These screams were being made by the adult animals. The dog, a rich chocolate brown with creamy underparts, was apparently giving an unidentifiable small mammal to the bitch. There seemed to be some dispute between the two animals, - the transfer of the prey was accompanied by screams and hisses. After a while the female retreated up the bank of the dyke where the transfer took place and the dog made his way back up the dyke from whence he appeared to have come. The latter passed within two feet of the observer, making a purring noise. The female seemed to be making its way towards the cubs, three of which were located by noise and fleeting glimpses of the animals themselves. The Badger (or Badgers) inhabiting the set in this area used regular routes when traversing this part of the wood. Though some of these routes were superficially in evidence from well beaten pathways in the undergrowth, others were identified by regular disturbance of traps. Traps were turned over and often carried or pushed up to 10 yards from their original positions.

The frequency of disturbance was much greater in certain traps than others. This difference seemed to indicate differences in the regularity of use of certain routes. Some traps were disturbed every night without fail during trapping periods. Frequency of disturbance was also much greater when trapping was in progress. The smell of small mammals visiting the traps seemed to motivate this increased interest, rather than playfulness. Corroborating this is the fact that only one tracking cylinder was ever disturbed. Perhaps traps are more intrinsically attractive to playful badgers. On the other hand, perhaps the much less frequent visits of small mammals to the containers make them less attractive than the traps.

Most disturbed traps were found closed. This is to be expected - the sensitive mechanisms are easily set off by an impact of any sort. However, some traps were actually opened during the period when all traps were closed for the duration of the tracking periods. Proof of the dexterity of the badgers in opening the self-locking doors of traps was further shown by partial or complete removal of bedding from some opened traps. The opening of traps must require quite subtle manipulation on the part of the badgers, especially when bedding is removed, where presumably doors must be re-opened again and again, if the hay was pulled out piecemeal.

Presumably if badgers can open traps when no animals are inside they can do the same when trapping is in progress and a mouse or vole is inside. As mentioned above some traps, disturbed during trapping periods, were found open. Possible losses of trapped animals to badger depredations cannot be ascertained if they did indeed occur.

However, virtually no animals were ever caught in traps regularly disturbed by badgers.

One definite predatory act was attributed to a badger in view of regular disturbance of the particular trap in question. A half eaten shrew (Sorex araneus) was found in this trap. It is known that shrews and juveniles can sometimes escape from the older type of Longworth trap. This individual had been able to free the forepart of its body but had become stuck by its pelvic girdle, half in half out of the trap. Evidently the predator had found the helpless shrew in this position and had eaten all the body forward of the pelvic girdle, leaving the skin and the skull. (This might indict a mustellid - in the author's experience the powerful jaws of the badger might not leave so much of the prey behind.)

TABLE 13

Trapping results 20-23.6.69 (Plot B)

* marked
⋇ recapture marked

Date	Grid Ref.	Species & Sex	Wt. (gm)	Length (cm)	Sexual Condition	Subjective Aggressive Index	Notes
20/7	A_1	CL♀	32.0	11.5	P	1	
	A_2	CL♀	28.0	11.0	P	1	
	A_4	CL♀	23.0	9.5	P	1	
	A_5	CL♀	27.5	10.0	P/Lact	2	
	A_6	AP♀	25.0	9.0	P	2	
	A_7	*CL♂	27.5	9.5	FF	2	marked:LH5
	A_8	*CL♂	30.0	10.5	FF	2	marked:LH4
	B_1	*CL♂	29.0	9.5	FF	2	marked: LH2
	B_2	*AP♂	31.0	10.2	FF	3	marked:LHS(v.act.& strong)
	B_5	*CL♂	36.5	10.5	FF	3	marked:LH3(v.act., struggling -
	C_1	CL♀	32.5	10.5	P	2	- urinating and seminal fluid)
	C_6	AP♀	20.0	8.5	P	2	
	C_8	*CL♂	30.0	10.0	FF	2	marked:LH1
	D_1	*CL♂	23.0	9.5	FF	2	marked:RHS
	D_4	*CL♂	25.0	9.5	FF	2	marked∂RH4
	E_{10}	CL♀	27.5	11.0	P	2	
	F_2	*AP♂	25.0	9.5	FF	2	marked:LH4
	F_3	AP♀	30.0	9.0	P	1	
	J_1	*CL♂	27.5	9.5	FF	2	marked:RH1
	J_1	CL♀	32.5	9.5	P/Lact	2	
	J_8	AP♀	30.5	9.0	P	2	
	J_9	*CL♂	27.5	10.0	FF	2	marked:LF1
	J_{10}	*CL♂	28.0	10.5	FF	2	marked:LF2
	I_3	*CL♂	25.0	9.5	FF	2	marked:RH2 (+ $\frac{1}{2}$ RH1)
	I_9	*CL♂	30.0	10.5	FF	2	marked:RH3
	I_{10}	CL♀	28.0	11.0	Preg/Part	3	(almost parturated in hand)

TABLE 13

Date	grid ref.	Species & Sex	Wt. (gm)	Length (cm)	Sexual Condition	Subjective Aggressive Index	Notes
21/7	A_2	CL♂	35.0	11.5	FF	3	Very active and strong
	A_4	CL♀	32.5	11.0	P/Preg	3	
	A_{10}	CL♀	20.5	9.0	P		
	B_1	*CL♂	26.0	9.5	FF	2	marked:LF4 ( )
	B_2	*AP♂	26.0	9.0	FF	2	marked:LH4
	B_5	*CL♂	32.5	11.5	FF	3	marked:LH3(v.act.)
	B_6	AP♀	17.5	8.5	P	1	juvenile pelage
	C_1	*CL♂	22.5	10.0	FF	3	marked RF1
	C_6	*AP♂	27.5	9.5	FF	3	marked:LHS
	C_8	*CL♂	25.0	Lo.5	FF	3	marked:LF3 (+LH1) (v.act.)
	D_1	*CL♂	26.5	10.0	FF	2	marked:RF2 (set.inact.)
	D_4	CL♀	27.5	11.5	P	1	
	D_7	AP♀	25.0	9.5	IMP	1	
	E_1	*CL♂	22.5	10.0	FF	2	marked:RHS(fairly active)
	E_2	CL♀	21.0	9.5	P	1	
	F_2	AP♀	28.0	9.5	P	2	
	F_9	CL♀	25.0	10.5	P	1	
	H_1	CL♀	26.0	10.0	P	2	
	H_8	AP♀	26.0	9.5	IMP	1	
	I_3	CL♀	22.0	10.0	P	1	
	J_8	*CL♂	27.0	10.0	FF	2	marked:lf2
	J_9	CL♀	22.0	10.0	P	1	
	J_{10}	*CL♂	20.0	9.5	FF	2	marked:RF3
22/7	A_1	*CL♂	40.0	11.0	FF	3	marked:RF4 (v.active)
	A_4	CL♀			Preg/Lact	2	
	A_6	CL♀			P	1	
	A_9	CL♀	P		P	2	Swollen vulva, oeostrous?
	A_{10}	CL♀			P	1	" " "
	B_2	*AP♂	27.5	9.0	FF	2	marked:LH3
	B_5	CL♂J	17.5	8.0	1/4 F	1	juvenile pelage

TABLE 13

Date	Grid. Ref.	Species & Sex	Wt. (gm)	Length (cm)	Sexual Condition	Subjective Aggressive Index	Notes
22/7	B_6	*AP♂			FF	2	marked:LH4
	C_2	CL♀			P	1	
	C_6	AP♀			P	1	
	D_1	CL♀			P	3	very active, struggling
	D_4	*CL♂			FF	2	marked:RHS
	D_9	CL♂			FF	2	
	E_1	*CL♂			FF	2	marked:LH2
	E_8	*CL♂			FF	2	marked:RH2
	F_1	AP♀			P		
	F_2	*AP♂	28.0	9.75	FF	2	marked:LH2 (F. act.)
	G_2	*AP♂			FF	3	marked:LHS
	H_1	CL♂			FF	2	
	I_9	*CL♂			F^{F}	2	marked:LF2
	J_8	CL♀			P	3	(very active and big♂
	J_9	*CL♂			FF	2	marked:LF1
23/7	A_4	*CL♂			FF	2	marked:LFS
	A_8	*CL♂			FF	2	marked:LH1,LF3
	A_9	CL♀			P:(sv)	1	(swollen vulva)
	B_5	AP♀			P	1	
	B_6	*CL♂			FF	3	marked LH3 (v.active)
	C_6	*AP♂			FF	2	marked:LH4
	C_9	*CL♂			FF	3	marked:LH4 (v.active)
	D_2	CL♀			P	3	(very active)
	D_7	*CL♂			FF	3	marked:RF4 (v.active)
	D_{10}	CL♀			P:(sv)	2	(swollen vulva)
	E_9	CL♀			Preg/part		(v.active)
	E_{10}	CL♀			P	1	
	F_2	AP♀			IMP	1	
	G_2	*AP♂			FF	2	marked:LH3 (fairly active)

TABLE 13

Date	Grid Ref.	Sex & Species	Wt. (gm)	Length (cm)	Sex Condition	Subjective Aggressive Index	Notes
23/7	H_1	*CL♂			FF	2	marked:RH1
	I_3	CL♀			P	1	
	I_9	CL♂			FF	2	
	J_1	CL♂			FF	2	
	J_1	CL♀			P	1	
	J_9	*CL♂			FF	2	marked:RF1

TABLE 11

TRACKING DATE FOR APODEMUS (June and July)

Only marked animals are recorded. (Many unmarked and indistinct tracks are not recorded).

Only the different tracking points visited are recorded here; often one animal repeatedly visits the same point.

*Animals retrapped in August and brought into the laboratory.

Species and Identification	June (week 4) original grid (Smoked Paper)	July (week 2) original grid (Petroleum Jelly and talc)	July (week 4) modified grid (Petroleum Jelly and talc)
AP*LH5	A' 1,2,3,5,7,8	A' 1,2,3,4,5,6,8,9	A' 1,5,6
	B' 1,3,4,5,9	B' 1,3,5,8	4,11,10,12,13,14
	C' 2,5,8	C' 1,2,3,7	16,18,23,20
	D' 1,5,6,7,8	D' 3,4,5	
	E' 2,3,7	F' 2,6,7	
	F' 1,2,4,6,9	G' 1,3,5	
	G' 2,5,7	H' 1,3,4,5	
	H' 3,4	I' 1	
	I' 1,3,5	J' 2,3	
	J' 5,6		
*LH4	A' 1,3,5	A' 1,2,3,4	A' 2,5
	B' 1,2,6	B' 1,4,7	15,20
	C' 1,2,3,7	C' 3	
	E' 1		
	D' 1		
LH3	A' 2,3,4	A' 1,2	
	B' 1,3,5,7	B' 3,4	
	C' 4,5,7	C' 4,5	
	D' 1,3,4	D' 1	
	E' 1,3,5	E' 1,2,3,4,5	
	F' 3	F' 1,3	
	G' 1,4.	H' 2,3,4.	
	H' 2.		
LH2	C' 4,6.	B' 2	
	D 1,3,5.	D 1,2,5.	

CONT. :-

	E'_4	E'_3	
	$F'_{3,4,5}$.	$F'_{1,2,4,7,8}$	
	$G'_{1,2}$.	$G'_{1,3}$.	
	$I'_{2,4}$.		
CL. *LH5.	A'_5.	$A'_{3,5,7,9}$; $B'_{5,8,9}$.	$A_{3,5}$.
	B'_6.	$C'_{5,7,8}$: D'_2	
*LH3		$A'_{5,6,7}$, $B'_{3,4,5,8}$.	5, 8.
		$C'_{3,4}$. D'_2	
*LH2		A'_2 ; $B'_{3,4}$; $C'_{1,3}$	21.
		D'_3 ; E'_4.	
*LF3	$B'_{8,9}$.	$A'_{8,9,10}$; $B'_{4,8}$; C'_6	
		E'_9 ; F'_6	
*RH4		$C'_{3,6}$; D'_7 ; $E'_{6,7,8}$; F'_{10}	
*RH3	F'_9 ; G'_7	$C'_{6,9}$; D'_5 ; $E'_{6,7,9}$; I'_8	41.
*RH1	B'_2 ; G'_4.	$G'_{3,4,7}$; H'_6 ; I'_7	
*LF4	B'_2 ; C_3	$B'_{4,5}$; C'_4 ; D'_3	
*RF2	$C'_{1,4}$;	$C'_{5,6,7}$; $E'_{6,7}$.	
LH4		$A'_{5,6}$; B'_8 ; $C'_{4,5}$; D_6.	A'_4
RH5			
RH2	$F'_{5,6}$.	$G'_{2,3}$; H'_5 ; $I'_{3,4,7}$; J'_8	
LF1		$I'_{7,8,9}$; $J'_{7,9,10}$.	33, 40.
LF2		I'_5 ; J'_{10}	40.
RF1	E'_5.	J'_3	
RF3	$I'_{7,8}$; $J'_{9,10}$.		
RF4	$A'_{3,4}$; D_5; E_4	$A'_{4,5,6}$; $C'_{4,5}$; D'_1.	

TABLE 14

Retrapping results: 30.7.69 - 4.8.69 (Plot 8)

Date	Lab. Identification.	Grid Ref.	Sex & Species	Wt. (gm)	Length (cm)	Sex Condition	Subjective Aggressive Index	Notes
30/7	16	A_1	CL♂	21.0	9.5	FF	3	Young Pelage, v. aggressive
	18	A_4	*CL♂	21.5	10.5	FF	2	marked: LHS
	17	A_8	CC♀J	13.5	8.0	IMP	1	+ tick on leg with v. swollen abdomen
		A_9	CC♀	23.0	10.0	P	1	
31/7	1	A_5	*CL♂	25.0	9.5	FF	2	marked: FL3
	2	A_8	CC♂	20.5	9.5	FF	2	
	3	A_9	CL♂J	14.5	7.0	NF	2	
	15	B_1	*CL♂	22.0	10.0	FF	2	marked:RF2 (quite aggre.)
		B_3	CC♀	26.0	11.0	Imp/Lact	2	
		B_7	CL♂			FF		(v.act. & Aggre.) escaped
		C_1	CC♀	22.0	11.0	P	3	(v.act.)
		C_2	CL♀J	15.0	8.0	IMP	1	Juvenile pelage, grey.
		C_4	CL♂	15.5	9.0	FF	-	dead
	11	C_5	CCJ♂	13.5	8.5	NF	1	
	13	C_6	CL♂	23.0	10.0	FF	2	
	14	C_7	*CL♂	31.0	11.0	FF	3	marked:LH3 (v.agg. testes down)
	11	C_8	CLJ♂	12.5	8.0	NF	1	Juvenile pelage
	19	C_9	*CL	22.5	9.5	FF	2	Marked:RH4
		C_{10}	CL♀	22.0	9.5	Imp/Lact	2	
	11	D_2	CLJ♀	11.0	6.7	IMP	1	Juvenile pelage
	12	D_3	*AP♂	28.0	9.5	FF	2	(2nd yr.pelage)v.act. & marked:LH5
	5	D_4	CL♀	18.0	9.7	P	1	1st yr.pelage
	4	D_8	CL♂	20.5	10.0	FF	2	
		D_7	*CL♂	23.0	10.0	FF	-	(dead) marked:RF1
		D_{10}	CL♀	20.5	9.5	P	1	swollen vulva; oestrous?
		E_1	CL♀	18.0	10.0	IMP	1	young pelage
		E_5	CL♀	18.0	9.5	IMP	1	young pelage (dead)
	1o	E_9	CLJ♂	11.0	7.5	NF	1	juvenile pelage
		E_{10}	CL♀	30.0	10.5	IMP	2	
		F_8	CL♀	25.5	10.0	Imp/Lact	2	

TABLE 14 (Contd.)

Date	Lab. Identification.	Grid Ref.	Sex & Species	Wt. (gm)	Length (cm)	Sex Condition	Subjective Aggressive Index	Notes
31/7		F_9	CL♂	26.0	10.0	FF	-	dead
		G_2	AP♀	33.0	9.5	P/Lact	2	
		G_3	CL♂	17.5	9.0	3/4 F	2	young pelage
	7	G_5	CL♂	18.5	9.0	FF	1	young pelage
		G_8	*CL♂			FF	2	marked:RH3(+tick) escap.
	9	H_5	AP♀	17.0	7.8	IMP	1	young pelage
		J_8	CL♂J	14.5	8.5	NF	-	juvenile pelage (dead)
	8	J_{10}	CL♂	17.0	9.0	3/4 F	2	young pelage
1/8	27	A_5	CL♀	33.0	11.0	Preg/Lact	3	young later born in lab.
		A_6	CLJ♂	15.0	8.5	NF	2	juvenile pelage
		A_7	CLJ♂	16.0	8.0	NF	1	juvenile pelage
		A_8	CL♂	17.5	7.5	1/4 F	1	juvenile pelage
	26	A_9	CL♀	24.0	10.5	Lact/Preg	3	v.act & strong
	24	A_{10}	CL♀	25.5	10.0	IMP	2	(later gave birth in lab.)
	25	B_5	CL♀	22.5	10.0	IMP	1	young pelage
		B_6	CLJ♀	13.5	8.0	IMP	1	
		B_7	CL♀	16.0	8.5	IMP	1	young pelage
2/8		A_2	CLJ♂	14.0	7.5	NF	1	juvenile pelage
		A_6	CL♀	27.5	10.5	PREG	2	
		A_7	CLJ♂	15.5	8.0	NF	1	
		A_8	CL♂	25.5	10.0	FF	2	
		A_9	CLJ♂	15.5	8.0	NF	1	
		A_{10}	CL♀	25.0	10.0	P/Lact	2	
		B_1	CL♀	25.0	11.0	P	1	
		B_7	CL♀	17.0	8.0	IMP	1	young pelage
		C_1	CL♀	27.0	10.5	Lact/Part	2	(about to perturate)
		C_9	CL♀	21.0	9.5	P	1	
		D_1	*CL♂	20.0	9.5	FF	-	marked:RHS (died)
		D_2						
	21	D_5	AP♂	17.5	8.5	FF	2	young pelage
	20	D_9	CL♂	25.5	10.5	FF	2	
		D_{10}	CL♀	25.0	10.0	P	3	v. active indeed

TABLE 14 (Contd.)

Date	Lab. Identification.	Grid Ref.	Sex & Species	Wt. (gm)	Length (cm)	Sex condition	Subjective Agressive Index	Notes
2/8	22	E_1	AP♀	26.5	10.0	P	2	
		E_6	CL♀	15.5	8.5	P	1	young pelage
		E_8	CLJ♂	15.0	8.0	NF	2	
		E_9	CL♀	22.5	9.25	LACT	2	about to perturate
		E_{10}	CL♂	20.0	10.0	FF	2	
		F_9	CL♀	20.5	10.0	P	1	
		G_3	CL♂	26.0	10.5	FF	3	v.act.; 1st yr.pelage
		G_8						
	23	H_3	*CL♂	28.0	10.0	FF	2	marked:RH1
		I_4	CL♂	18.0	9.5	FF	2	
		I_6	CLJ	11.0	7.0	-	-	dead
		J_9	CLJ♂	15.0	8.5	NF	1	
		J_{10}	CL♀	21.5	9.5	IMP	1	
4/8		A_2	CL♀	25.0		P/Preg	2	
		A_4	CL♀	20.0		Imp/Lact	1	
		A_5	CL♀	15 20		IMP	1	young pelage
		A_8	CL♀	15 20		IMP	1	young pelage
		A_9	CL♀J	15		IMP	1	young pelage
		A_{10}	CL♀	25		P/Lact	2	
	28	B_1	*CL♂	25.0	10.0	FF	3	marked:LF4 (v.aggr.)
		B_4	CL♀J/V	15		P	1	
	32	b_5	APJ♂	14.0	7.0	½F	1	(escaped later)young pel.
		B_7	CL♂	25.0		FF	2	
		B_8						
		B_9	CLJ♀	15.0		P	1	
		C_1	CL♀	25.0		Preg/P	2	
	29	C_2	*CL♂	25.5	10.5	FF	2	marked:LH2
	31	D_1	*AP♂	20.0	8.5	FF	2	marked:LF4
		D_2	CL♀	30.0+		Preg	2	
	30	D_7	*CL♂	27.5	10.5	FF	1	marked:RH3

TABLE 14 (Contd.)

Date	Lab. Identification.	Grid ref.	Sex & Species	Wt. (gm)	Length (cm)	Sex condition	Subjective Agressive Index	Notes
4/8		D_9	CL♀	20.0		p		
		D_{10}	CL♂	25g		FF	2	
		E_4	CL♂J/V	15.0				
		E_7	CL♀	20 25		P		
		E_8	CL♂	20.0		1/4 F	1	young pelage
		F_5	CL♀	25		P	3	very active
		F_6						
	33	F_8	AP♂	18.0	8.0	FF	2	
		F_9	CL♀	25.0		Preg		
		G_1	CL♂	25.0		FF	3	v.act. struggling & squeaking
		G_4	CL♀	25.0		P/Lact	1	
		G_7						
		H_1	CL♂	25.0		FF	3	1st yr.pelage. v.act., struggling, urinating
		H_2	CL♀	25.0		P/Lact	2	
		H_4	CL♂	25.0		FF	3	very active
		I_1						
		I_3	CL♂	20-25.0		FF	2	quite active
		I_5	CL♀J/V	15.0		P	1	
	6	I_6	CL♂	17.5	8.5	½F	1	young pelage + 2 ticks on back leg
		I_9	CL♂	15-20.0		1/4 F	1	young pelage
		J_1	CL♂	25.0+		FF	1	not very aggressive
		J_9	CLJ	15.0		NF	1	

TABLE 10

TRAPPING: MARKING AND RECAPTURE (JULY AND AUGUST)

Species and Mark	Marked (Grid ref.)	1st re-capture (Grid ref.)	2nd re-capture (Grid ref.)	3rd re-capture (Grid ref.)	First recapture (August) (Grid ref.)
APOD*LH5	B_2	C_6	G_2		D_3
*LH4	F_2	B_2	B_6	C_6	D_1
LH3	B_2	G_2			
LH2	F_2				
CLETH*LH5	A_7	A_4			A_4
LH4	A_8	C_9			
*LH3	B_5	B_5	B_6		C_9
*LH2	B_1	E_1			C_2
*(+LF3) LH1	C_8	C_8	A_8		A_5
RH5	D_1	E_1	D_4		⌿ (D_1)
*RH4	D_4				C_9
*RH3	I_9				ǂ (G_8) D_7
(+RH1) RH2	I_3	E_8			
*RH1	J_1	H_1			H_3
LF1	J_9	J_9			
LF2	J_{10}	J_8	I_9		
RF1	C_1	J_9			⌿ (D_7)
*LF4	B_1				B_1
*RF2	D_1				B_1
RF3	J_{10}				
RF4	A_1	D_7			

* Recaptured and brought into the laboratory.

⌿ Died in trap.

ǂ Escaped when first caught.

TABLE 15

RECORDS OF JUVENILES IN LABORATORY

*R.M. = Marking
L.M.

Weights when colony formed (1st week of August)	: ♀ 11.09g. *(R.M.) ♂ 13.59 (L.M.) ♂ 12.59
On 16th August, 1969	: ♀ 16.09g. (1MP) ♂ (R.M.) 27.5 g. (¾F) ♂ (L.M.) 16.09g. (¼F)

On 16th August, 1969 strange male (29') added to colony (25.5g)

On 25th August, 1969	: ♀ (J.) 14.9g ♂ (J.) (R.M.) 22.0g ♂ (J.) (L.M.) 13.9g ♂ (29') 23.3g

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Formation of colonies by adding strange mate to juveniles

16th August, 1969	: (3') J. ♂ (18.0g) (½F) (20') ♂ (23.5g) (17') J. ♀ (16.0g) (1MP) (30') ♂ (22.0g)
25th August, 1969	: (J. ♂) 3' 15.9g. (♂) 20' 21.8g. 17(♀J.) = 14.6 g. 30(♂) = 21.3 g.

APPENDIX II

Trapping Results for Area A.

From the irregular but continuous trapping in Area A from March to April, there arises some interesting problems.

Some of the animals were marked individually by fur-clipping when first trapped. Very few of these were caught again and these were mainly *Apodemus* - which were brought into the laboratory. Most marked voles seemed to have disappeared or were perhaps avoiding the traps, as a result of becoming trap-shy (Tanton, 1965).

Later in the trapping period (May) very few *Apodemus* were caught, whilst many 'new' voles were entering traps, Perhaps this indicates an influx of voles into the area. Ashby (pers. comm.) has found no indication of the usual spring drop in vole densities, in other parts of Houghall Wood, for this year. He thinks that there is, possible, an influx of voles into the area.

No indications to the causes of why such movements were taking place could be found..(No formal procedure was adopted to test movements or numbers of 'new' animals.) The habitat changed seasonally in the usual way (a dense cover of bracken and willow herb had grown up by late spring) but this is, of course, normal in open woodland habitats. (See photographs of area, taken in July). This seasonal alteration would not seem to effect either species differentially. Though

Clethrionomys seems to prefer a more dense ground layer (perhaps linked with the fact that it is diurnal) (Kikkawa, 1964; Ashby, 1967 and others) Apodemus thrives in both open and dense vegetation (perhaps linked with mainly nocturnal activity). Of interest here, perhaps, is the fact that no animals of either species were caught in the steep bramble-covered bank (see Map) for the whole of the investigation period.

The proximity of the study area to the wood-edge might have some relevance here, in relation to movements of animals, at this time. Seasonal movements to and from arable land and wood-sides, in relation to food resources, have been documented by Brown (1966) and Kikkawa (1964).

TABLE I APPENDIX II

Trapping Results for Area A. * (March - May)

*(Unless otherwise indicated)

Date	Species and Sex	Weight (gm.)	Length (cm.)	Sexual Condition	Subjective Aggression Index	Notes
March	AP♂	24.5	8.6	½F	1	
Wk.2	AP♂	19.2	7.9	F	1	
*	AP♀	15.0	8.0	1MP	1	3 months old
	CL♂	13.0	8.7	N.F.	0	
	CL♂	14.0	8.4	N.F.	0	Very docile
	CL♂	12.0	8.8	N.F.	0	Moribund
	CL♀	13.0	8.6	1MP	0	
	CL♂	11.5	8.0	N.F.	0	
	CL♀	12.0	9.3	1MP	0	Moribund
	CL♀	10.0	8.6	1MP		Dead
	AP♂	15.5	7.8	½F	1	
	AP♂	22.5	8.9	F	2	Quite aggressive
	AP♂	16.5	8.5	N.F.	1	
	AP♂	17.5	8.3	F	2	Fairly aggressive
	AP♀	18.5	8.4	1MP	1	
	CL♂	14.5	9.1	½F	2	Aggressive
	CL♂	12.0	8.1	N.F.	1	
	CL♀	10.5	7.8	1MP	0	
	CL♀	12.8	8.2	1MP	0	
	CL♀	12.5	10.0	1MP	0	
	CL♀	12.0	7.9	1MP	1	
March	AP♀			1MP	1	
wk.3	AP♂			NF- F	1	
	CL♂			N.F.	1	
	CL♂			N.F.	1	
	CL♀			1MP	0	
April	AP♀			1MP	1	
wk.1	AP♂			½F	1	
	CL♀			1MP	1	
	CL♂			N.F.	1	
	CL♂			F	1	
	CL♀			1MP	1	
	CL♂			N.F.	1	
	AP♂			F	2	Very aggresive and active
	CL♂			F	1	
	CL♂			F	1	
	AP♂			F	1	

Date	Species and Sex	Weight (gm.)	Length (cm.)	Sexual Condition	Subjective Aggression Index	Notes
April wk.2	CL♀	25.0	9.5	1MP	1	
	AP♀	21.5	8.2	1MP	1	
	AP♂	27.5	8.5	F	2	
	AP♂	21.0	8.5	F	2	
	AP♀	20.0	8.0	1MP	1	
	AP♂	30.0	10.3		3	Very big, active and aggressive
April wk.4	CL♀	20.0	10.2	1MP	1	
	CL♂	22.5	9.75	F	2	
	CL♂	22.5	9.75	½F	2	
	AP♂	30.0	10.75	F	2	Very aggressive
	CL♀	18.5	9.0	1MP	1	
	AP♀	18.0	9.75	1MP	1	
	CL♂	19.5	10.0	N.F.	1	
	CL♂	22.0	8.75	F	2	
	CL♀	18.0	8.7	1MP	1	
May wk.1	CL♂	11 .0	9.75	F	2	
	CL♀	22.5	9.5	1MP	1	
	CL♂	22.5	10.0	F	2	
	CL♀	18.0	9.5	1MP	1	
	CL♂	22.5	9.5	½F	2	
	AP♀	24.0	8.5	1MP	1	
	CL♀			1MP	1	
	CL♀			1MP	1	
	AP♀			P.	2	
	CL♂			F	2	
	CL♀			1MP	1	
	CL♂	22.0	10.0	F	1	
	AP♂	27.5	10.7	F	2	
wk.2	CL♂	25.0	9.8	F	2	
	CL♂			F	2	
	CL♂			F.F.	3	
	CL♂	22.5	9.8	F.F.	2	
wk.3	CL♀			1MP	1	
	CL♀			P.	2	
	CL♀			P.	2	
	CL♂			F.F.	2	
	AP♂			F.F.	3	

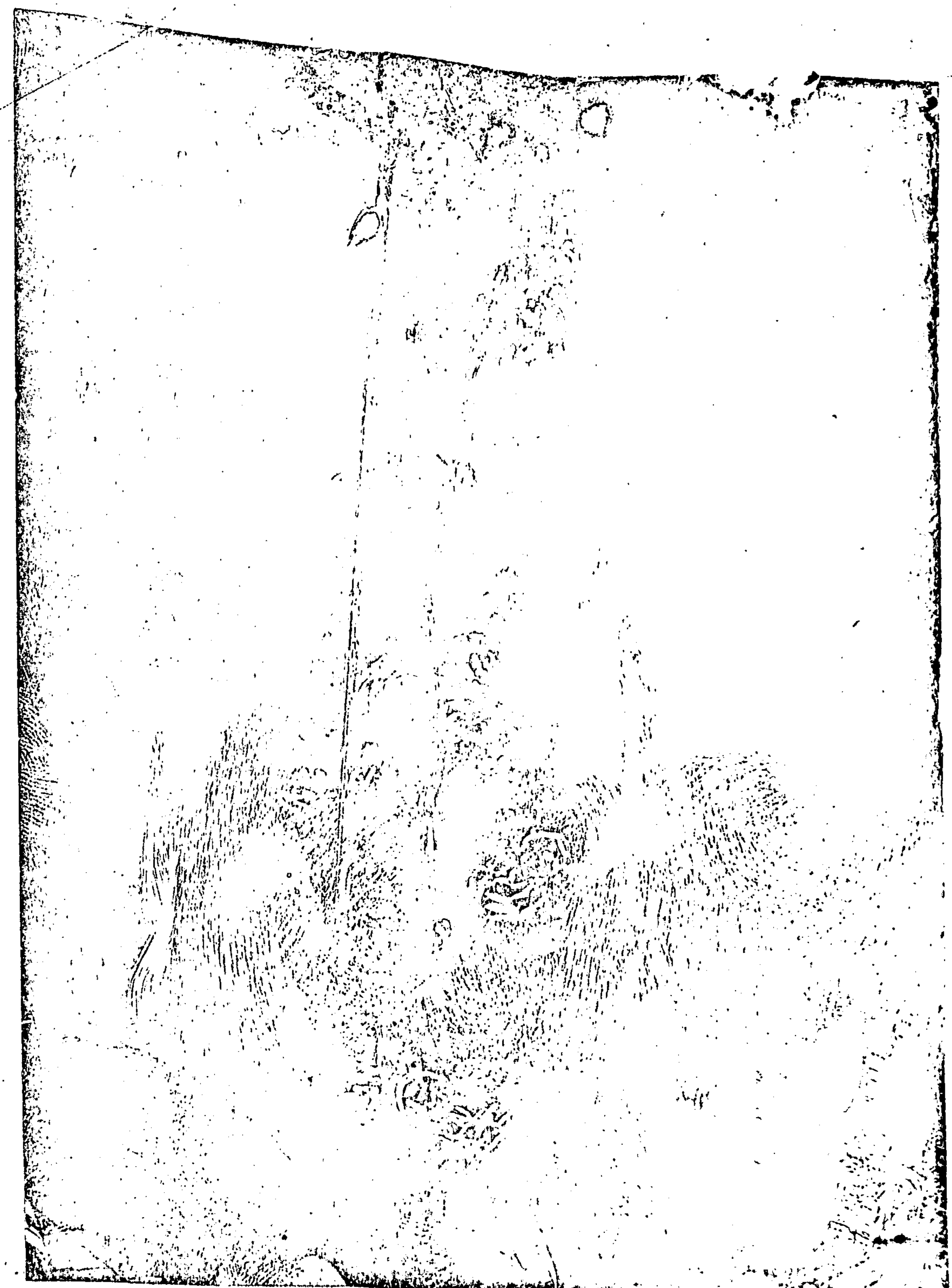
1. Sample of smoked paper showing slug damage at the top and _Clethrionomys_ tracks and marks from the fur and tail.

2. As before - showing small nodules at top centre and right.

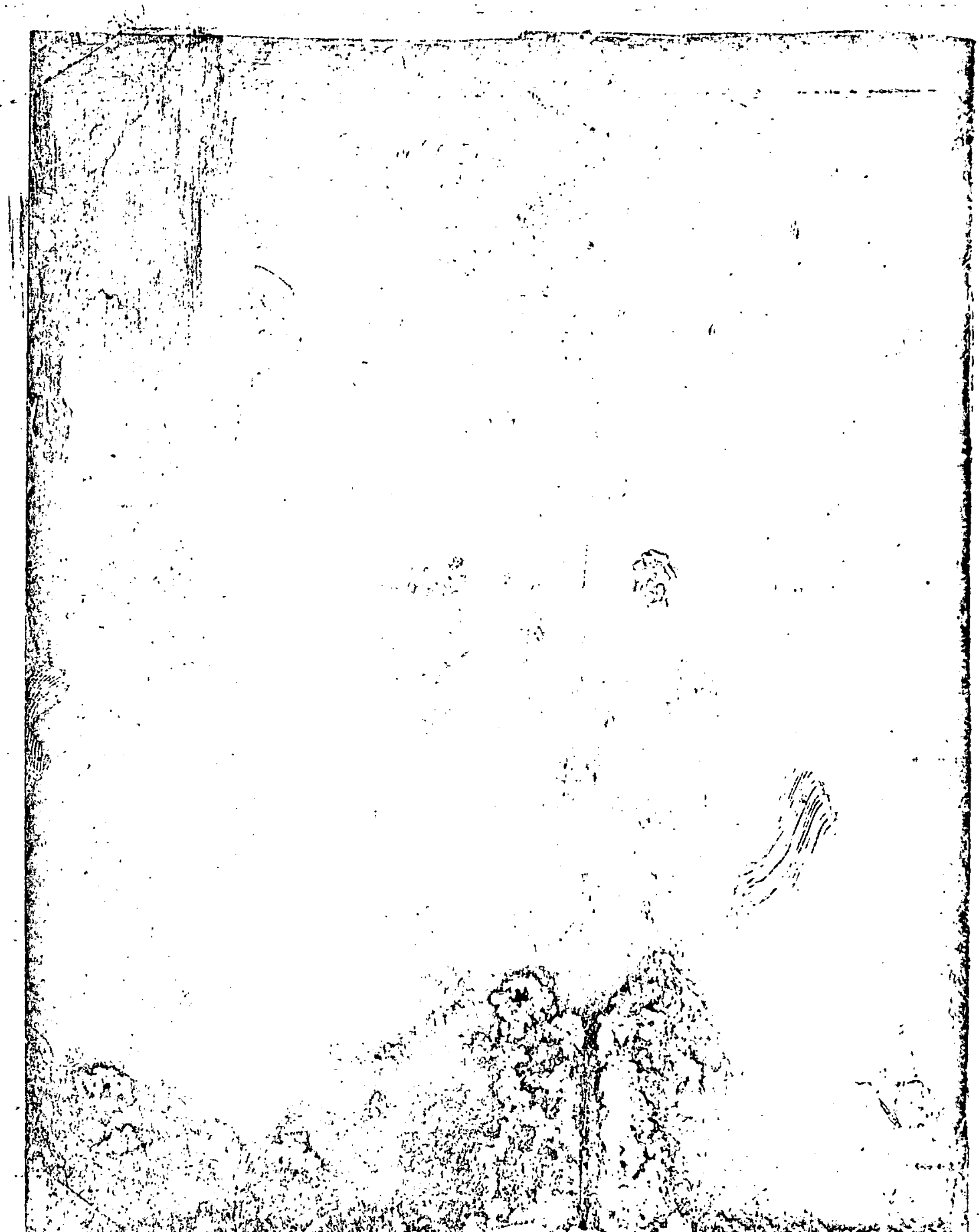
3. As before -- *Clethrionomys*.

4. Sample showing slug and snail tracks and radulae.

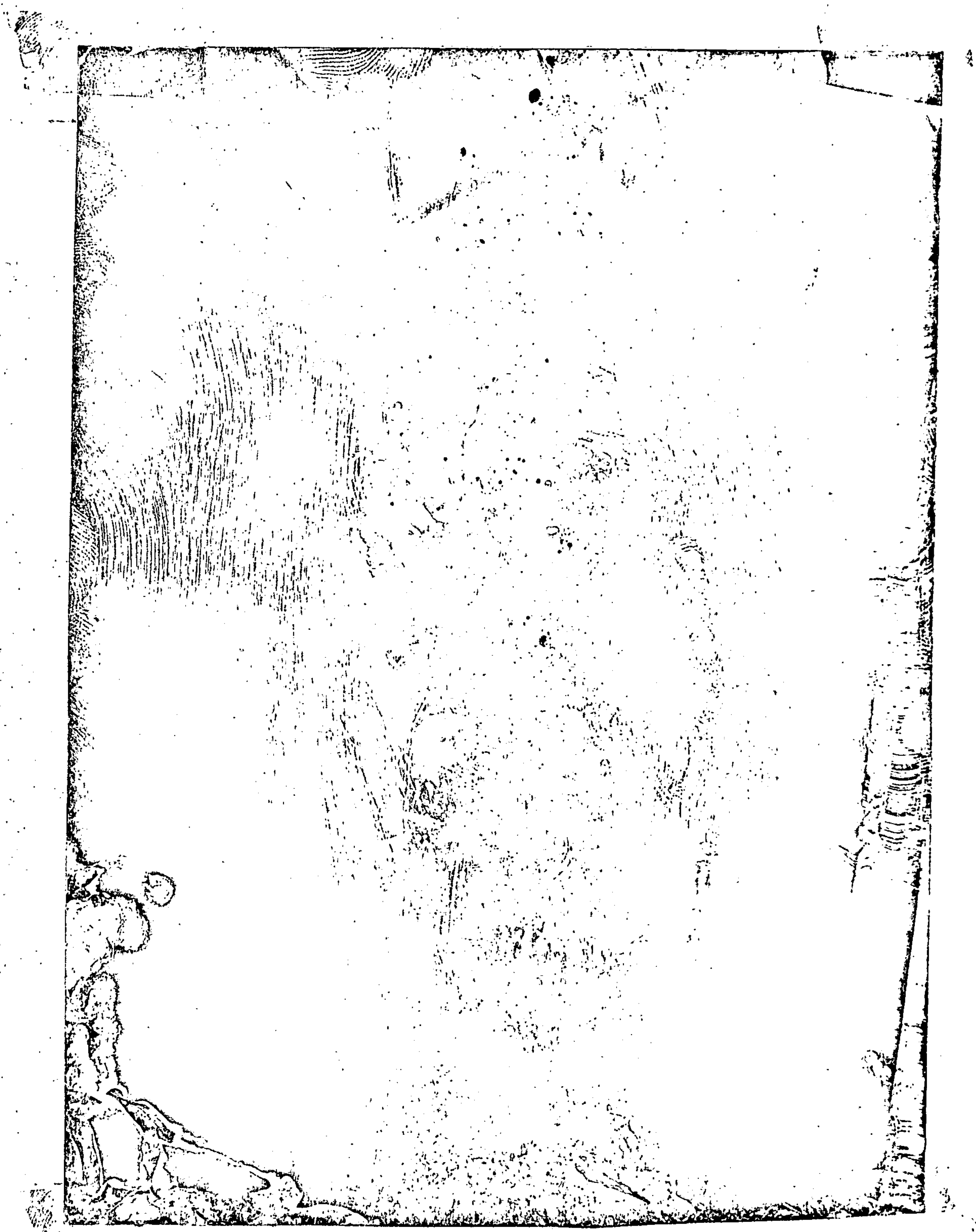
5. As before. Some slug and snail damage.



6. Sample showing extensive damage in the lower part of the [illegible].



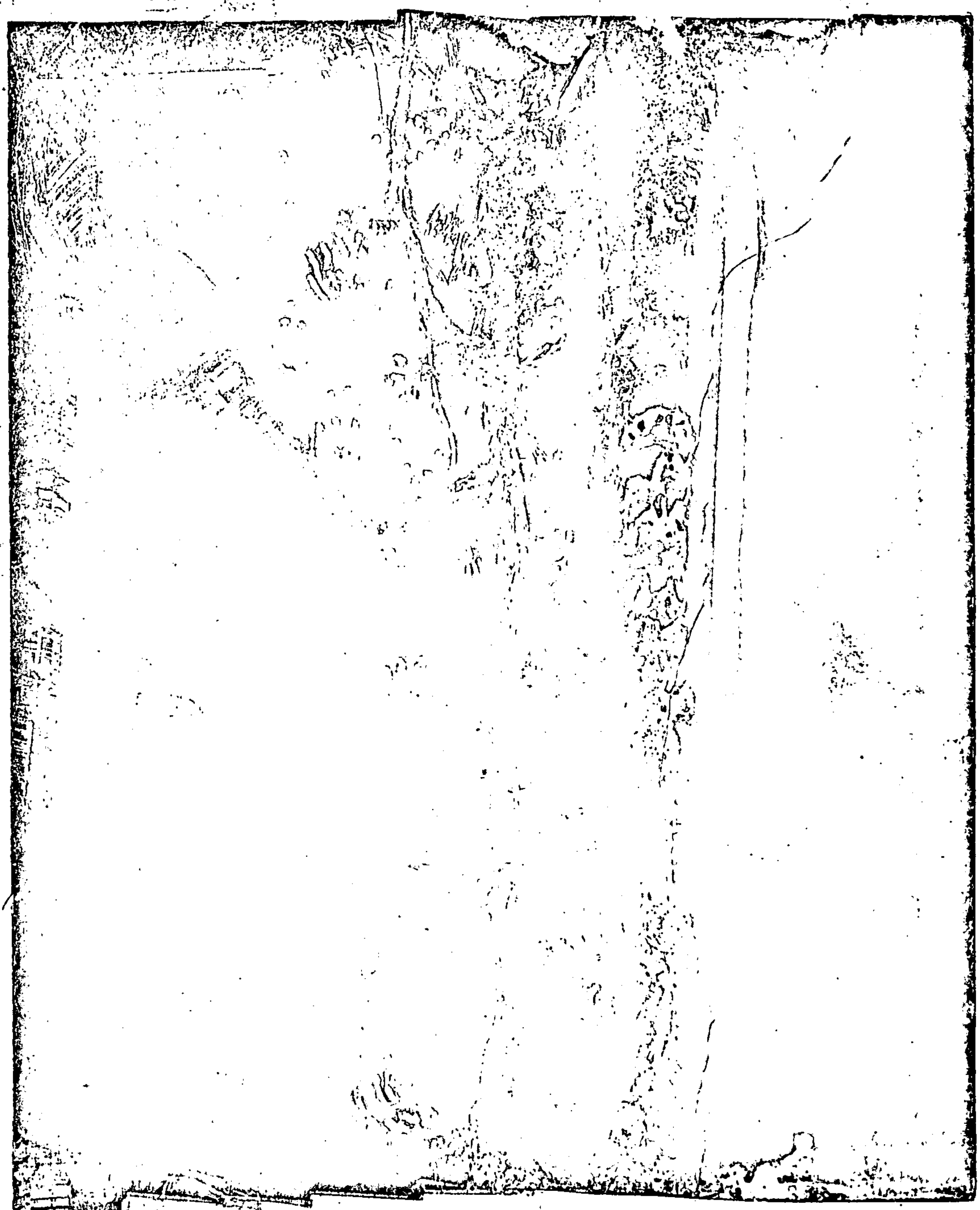
7. As before – [illegible].



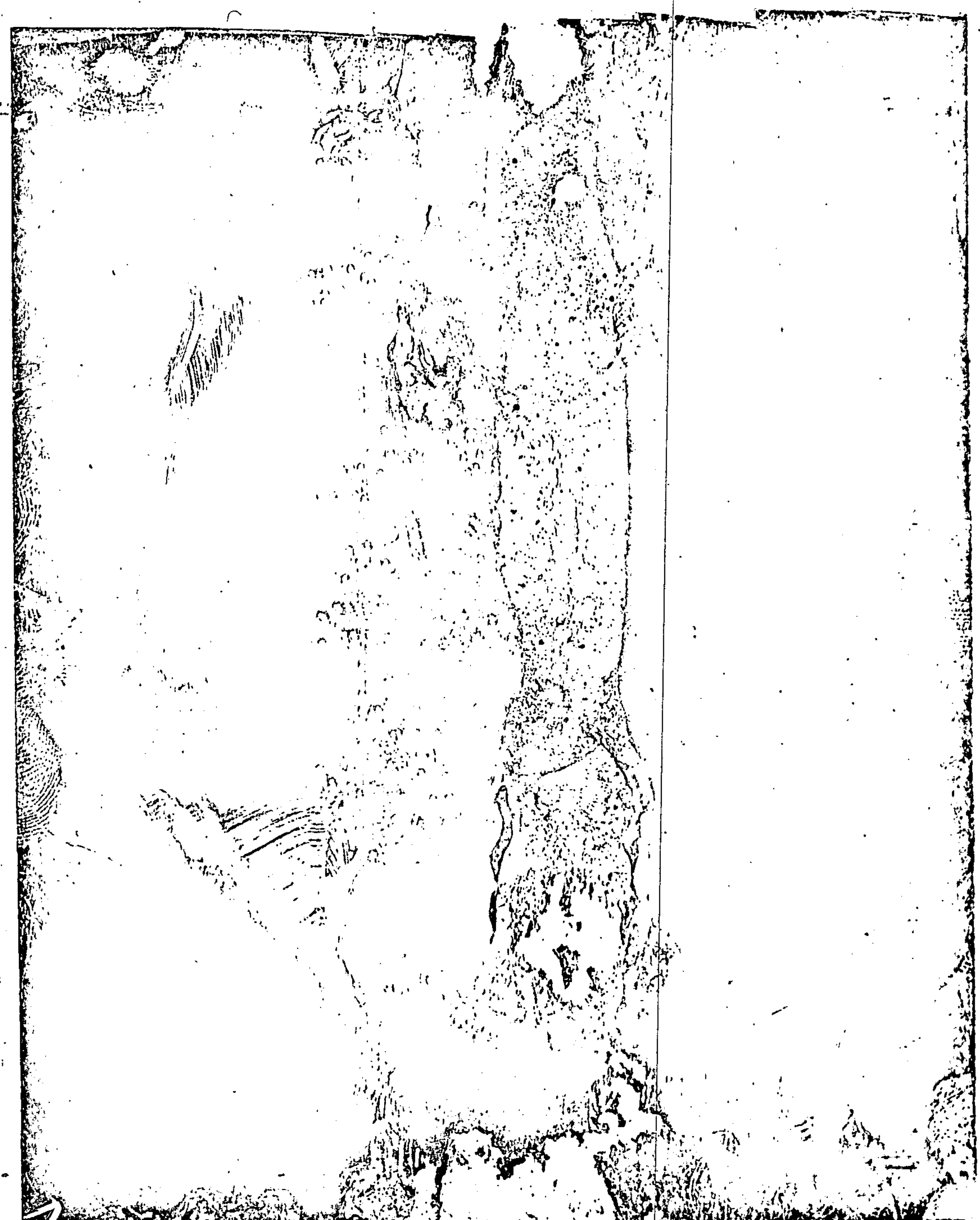
8. [illegible]

9. Sample showing some slight damage and extensive marking of the paper by the fur and tail of the animal. Also shows where animal slipped at the side of the tube.

10. [illegible]



11. [illegible] and some [illegible] damage from [illegible] and eating of the paper.

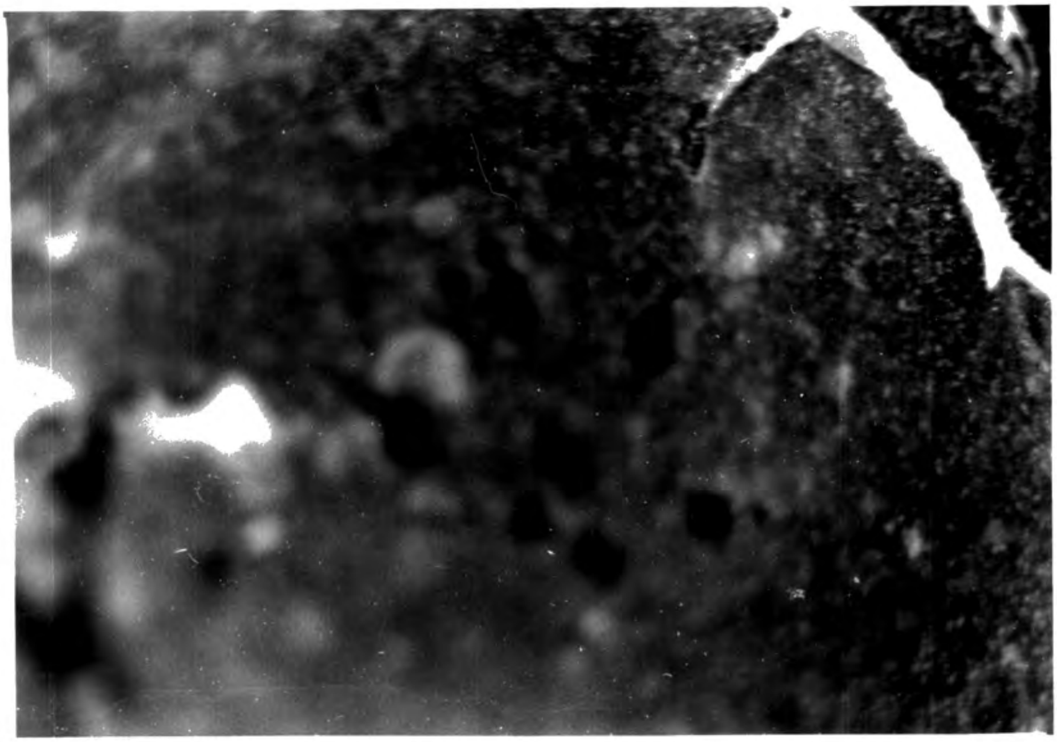


3.

Clethrionomys right forefoot.

4.

Clethrionomys hind feet



PHOTOGRAPHS OF SAMPLE TRACKING PAPERS USING PETROLEUM JELLY AND TALCUM POWDER

1.

Apodemus right forefoot.

2.

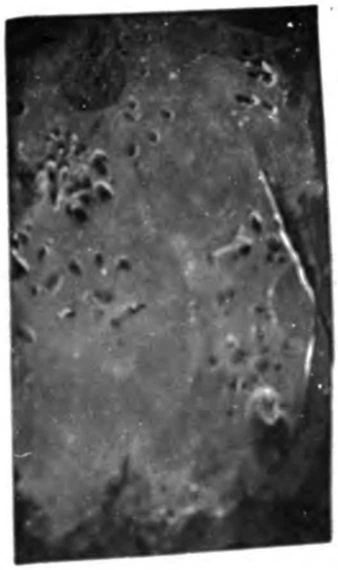
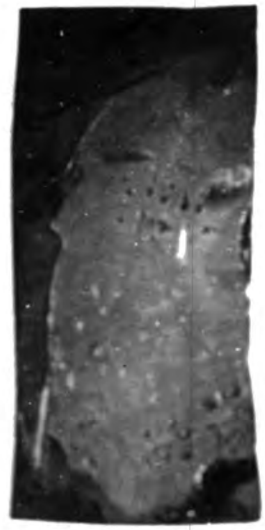
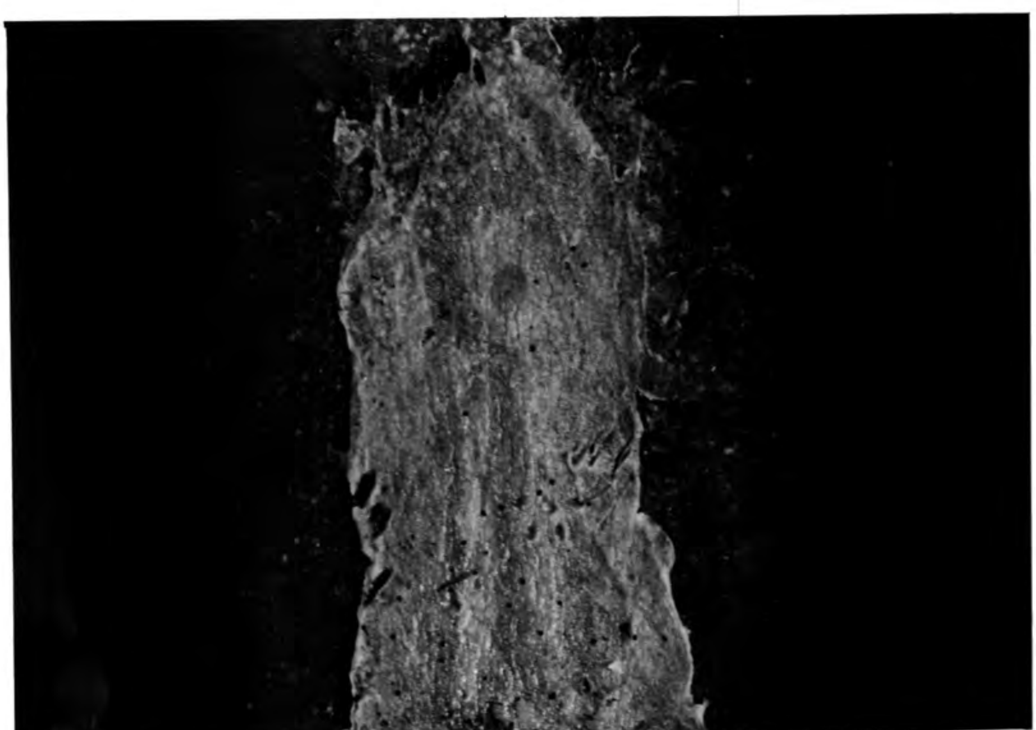
Apodemus right hindfoot.

5.

Sample traces of unmarked animals. *Apodemus* on the left, *Clethrionomys* on the right.

6.

Sample tracking paper, *Apodemus*. Some slug damage at top of photograph.

7.

Sample tracking papers of marked animals, <u>Clethrionomys</u>.

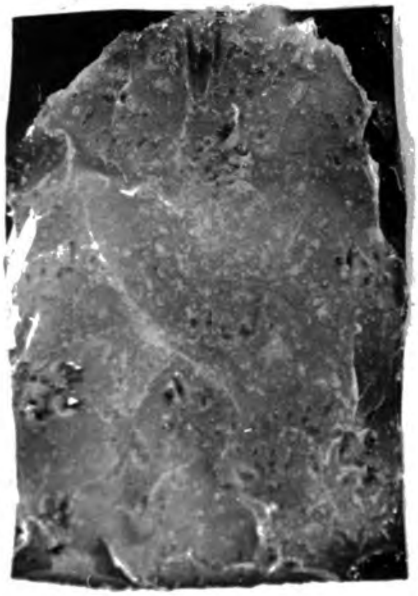
Left.: LF3

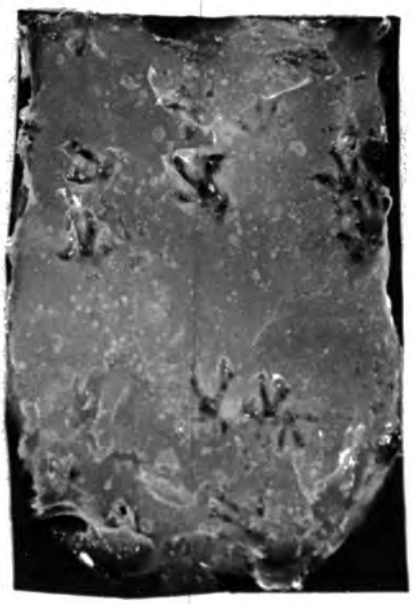
Right: LH3

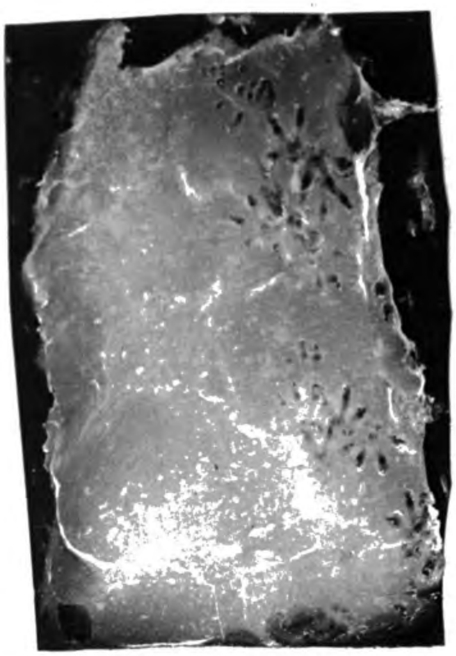
8.

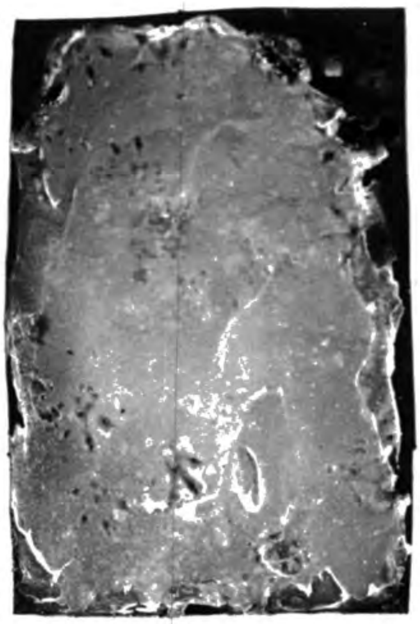
Sample tracking papers of marked animals, <u>Apodemus</u>.

Both : LH5







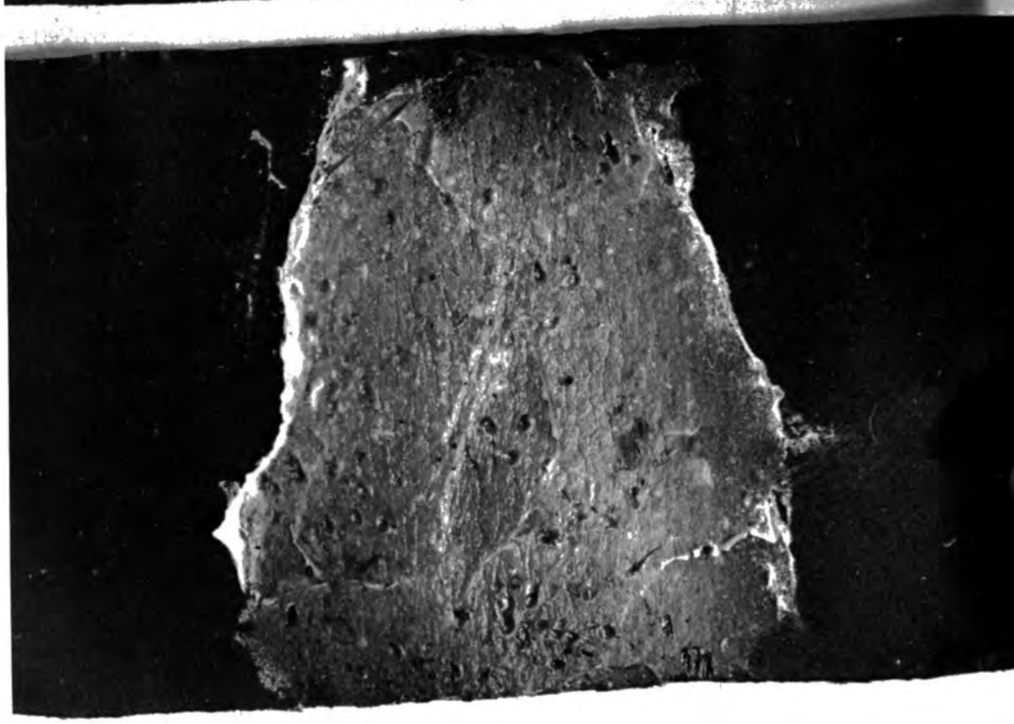


9.

Example of marked tracking paper. Unmarked *Apodemus*.

10.

Example of marked tracking paper. Unmarked *Clethrionomys*.



11.

Tracking paper showing snail damage.

12.

Tracking paper showing slug damage.

13.

Photograph of a whole tracking paper showing application of the grease only at the front. Shows extensive slug damage to grease and paper. Also some slug faeces. Hardened grease melted in the sun can be seen at the bottom of the photograph.