BEHAVIOUR DIFFERENCES BETWEEN RACES OF BANK VOLES
(genus CLETHRIONOMYS TILESIUS)

by

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I. GENERAL INTRODUCTION

Animals are characteristically more vigorous and fecund when living in the range of environments in which they are normally found than they would be if transferred to another. It has been shown, by Fisher, Haldane and Wright, using mathematical models, that this could have come about in response to natural selection. The simplicity of their theory of how evolution, as visualised by Darwin, occurs was dependent on assumptions about the structure of populations. The usefulness of these ideas has been demonstrated in a number of practical studies (reviewed by Dobzhansky 1951), but very little is yet known about the evolutionary effect of interactions between members of a species or group of species.

A pre-requisite for continued adaptive modification in the face of a changing environment is that genetical variability should be maintained within the population subject to it. Outbreeding tends to conserve heterozygocity. On the other hand, once a group of animals have made a genetical advance beyond their fellows in their own niche, it will be of advantage for the individuals in this group not to mate with others from outside it. Introgressive hybridization between a variant population and its ancestral stock resists the establishment of beneficial gene combinations. Natural selection between populations is a relatively inefficient process. Therefore in this conflict between the advantage which a population gets from being genetically plastic, and the increased fitness conferred on individuals whose offspring resemble them in their relationship with their common environment, the latter can be expected to prevail.

The movement of animals between localities, their activities in their home range, and, especially, the relative readiness with which they will mate with a particular individual or category of individuals from among those available, determine the freedom with which genes flow within and between populations. This is most obvious in the origin of new species. As behaviour patterns influence the adaptability of populations through their control of the mating system, they are important characters for students of speciation despite the technical difficulties which they present. The evolution of the nervous system has greatly extended the possibilities of interaction between individuals. It is likely that the matings among mammals or birds are less nearly random than those among most invertebrates or sexually reproducing micro-organisms.

Dowdeswell and Ford (1953) working on butterflies, Cain and Sheppard (1950) and Sheppard (1952) working on snails, and Dice and Blossom (1937) and Voipio (1950) working on mammals, have all found marked adaptation to local conditions coinciding with relative isolation. Blair (1951, 1953) finds that <u>Peromyscus</u> move surprisingly little during their lifetime, and Howard (1949) gives evidence that full-sib and parent-offspring matings are not rare in the wild. Weber (1950) and Corbet (personal communication) have both found marked differences in the frequency of skeletal characters, which are probably inherited in a simple Mendelian way, between local populations of, respectively, <u>Mus</u> and <u>Clethrionomys</u> separated by no more than a few miles of country inhabited by the rodents on which they worked. This suggests that the population structure of small mammals is such as to allow a considerable degree of local adaptation. In order to investigate the part which behaviour plays in speciation, one requires a group of populations which are characterized by variants that can be described in quantitative terms, and yet are not so distinct as to exclude hybridization in the laboratory.

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The taxonomy of the group of rodents which were used in this study is confused. The genus Clethrionomys, described by Tilesius in 1850, has often been called Evotomys, which the group was independently named by Coues, at a later date. It is found in the north temperate and sub-arctic regions, and, over most of this range, is easily distinguishable from the most closely related genera (Hinton 1926). The less complex cheek teeth, become rooted in the adult, which is unusual for rodents, and the skull is less massive than that of Microtus. The main generic characters can be understood in relation to the less abrasive nature of the diet eaten by Clethrionomys than that of its close relatives. (Miller 1956, Richie 1951). Four of the species groups, proposed by Hinton to include the numerous forms that have been described (Ellerman (1941) names seventy-two), are present in Europe (fig. 1). On the mainland of Great Britain there are small brightly coloured bank voles with a reddish area on the back; it is generally agreed to call these Clethrionomys glareolus britannicus Miller 1900 (plate 1), and that they can be regarded as sub-specifically distinct from the type subspecies found on the continent of Europe. On islands off the

West Coast of Britain are three distinct forms (fig. 1), each of which was first described as a new species. On Raasay is found a large dark vole with a rather long stout tail, *Clethrionomys erica* Barrett-Hamilton and Hinton 1913, (plate 2); on Mull, another inner Hebridean island, the relatively short tailed form, which is also larger and darker coloured, was termed *Clethrionomys alstoni* Barrett-Hamilton and Hinton 1913, (plate 3); off Wales a large and sandy coloured vole is found on the small island of Skomer, *Clethrionomys skomerensis* Barrett-Hamilton 1903, (plate 4). Hinton considered these taxa to be allied to the *nageri* species group, and to be derived from a population of *C. nageri* which has since been replaced on the mainland by *C. glareolus*. *Clethrionomys nageri*, a large dark bank vole, inhabits high land on the continent of Europe, but was unfortunately not available for the present study. On the basis of larger samples than those available to Hinton, Steven (1953) came to the conclusion that the island forms are subspecifically distinct from *C. g. britannicus*. It is hard to understand on what grounds Morrison-Scott (1952) allied *alstoni* to *glareolus*, but *erica* to *Clethrionomys rufocanus* Sundervall, which is a sub-arctic form distinguishable at a glance from the other bank voles in question by an observer unfamiliar with the group.

Clethrionomys rutilus Pallas, typical of the other arctic species group, is a small vole, in appearance rather similar to *britannicus* but of a pale sandy colour. The identity of the voles called here *norvegicus* is far from clear. They have been considered a subspecies of *C. glareolus* (Miller 1912), of *C. nageri* (Hinton 1926, Ellerman 1941), or as indistinguishable from *C. glareolus glareolus*, (Collett 1911, Steven 1952).

That *rutilus* and *rufocanus* alone, are specifically distinct from the other bank voles mentioned here is concluded by Steven (1955), from the fact that most of the possible crosses between British forms and *norvegicus*, between island forms and *britannicus*, and between the island forms *inter se*, had been made by him. These crosses gave viable and fertile hybrids. It may be noted here that two of the crosses that had not been obtained by Steven have since been found by the writer to produce viable young, namely *britannicus* male x *alstoni* female and *britannicus* male x *skomerensis* female. It is clear that there is no impassable barrier to gene interchange. The question remains open whether a barrier, apart from gross inviability or sterility, or geographical separation, could maintain these polytypic forms distinct from one another. The potential means by which isolation can be affected are numerous (Dobzhansky 1951); an investigation of some of them will be reported later.

The idea common to the numerous biological definitions of a species is that groups of animals, in order to be considered species, must have characteristics which inhibit the free exchange of genes between them. Spatial isolation is excluded as a criterion of specificity, except in so far as it can be shown to be the result of either differential mortality or choice of habitat. As the species concept has become more precise (Cain 1953), especially as used by botanists (Gilmour and Heslop-Harrison 1954) and ornithological taxonomists (Mayr 1942) it has become apparent that the term is used for different purposes. The treatment of allopatric populations shows this most clearly. It is used in classifying specimens in a convenient way, organisms being included in a species if they fall within a definite range of phenotypic variation. It is also used in the natural classification of well studied groups. For this purpose an operational definition is used. The most familiar and successful of these, particularly in classifying angiosperms, is whether viable and fertile offspring result from the cross pollination, in captivity, of members of a pair of putative species. It seems likely, on general grounds, that this sort of definition can be expected to become improved as the techniques of experimental taxonomy progress. It is hoped that this communication will show how provisional any diagnosis of specific status, using this kind of information, must be, at any rate in animals, where differences in behaviour or ecology may function as isolating mechanisms between populations which are not distinguished by incompatible gene complexes. The readily modified behaviour that seems to be characteristic of mammals may lend itself to this sort of process. It has been suggested recently however (Manning 1957) that the behaviour of bees in response to the interspecific releasers of angiosperm flowers may be important in the speciation of the latter. In considering species as stages in evolutionary change it is important to know what factors function as barriers to gene interchange. If differences in behaviour or ecology are sufficient to isolate two natural populations, then the investigation of the absolute sterility relationships between them loses the attraction it had of being a biologically meaningful criterion of specific rank.

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III. POPULATIONS STUDIED AND GENERAL METHODS

The taxonomic status of the animals used in this work is discussed in Sections I and VII, but this is not conclusive. The most appropriate nomenclature seemed, therefore, to be the trivial names of the forms in question. These are used without prejudice as to whether they should properly be regarded as of specific or subspecific rank, or, for that matter, as to what species the subspecies belong. The only named form which has been collected from widely separated localities is britannicus. Where appropriate, the locality is used following the trivial name. In the absence of an indication of this sort, britannicus can be taken to refer to the bank voles from the Edinburgh district. The term race is used here to designate the taxonomic sub-divisions of the genus Clethrionomys. Its use does not imply that none of these taxa is sufficiently distinct to be given a higher rank, but merely that it is not helpful to do so in discussing the work presented here. Similarly qualifications of the term are not used. All the forms, if races, are geographical ones on the customary criteria (Mayr 1942); it is hoped to demonstrate that they are distinct in other ways.

Details of the collections of bank voles which have been used are given in Table 1. These animals were kept in captivity using methods developed by D. M. Steven, and described fully by him in the second edition of the U.F.A.W. handbook (1957). Details of particular methods will be given as they become necessary.

Throughout this investigation, except where the contrary is stated explicitely, both animals that have been caught in the wild and maintained in captivity for varying periods of time, and animals that have been bred in captivity for one or more generations have been used. The latter category has not been avoided, as the hybrids used in a number of studies were of necessity laboratory bred, and an important aspect of the work was the comparison of these with members of the several races of *Clethrionomys*.

IV. INDIVIDUAL BEHAVIOUR

1. TAMENESS

The first impression of variation in behaviour characters between an island race and that from the mainland is that they differ in temperament. As Pitt (1925) puts it "moreover they (britannicus and skomerensis) differ in disposition. Skomer is placid and docile. Any one of the six will let me pick them up and put them on my arm, when they do not seem frightened or even perturbed. A britannicus would have jumped to Jericho".

For convenience, the differences which are responsible for this reaction in the observer are considered as defining the distinction between tameness and wildness. Several examples of this category of behaviour will now be examined.

A. handling

The behaviour of an animal most calculated to produce a subjective impression of tameness to an experimenter is that which makes the animal easy to handle. The most noticeable differences in behaviour characters between an island race and that from the mainland are of this sort.

The speed and the frequency of movements during routine maintenance are greater in voles from the mainland than in the island forms. On these criteria the most active of the island voles are Raasay animals. The experiment to be described was an attempt to put these impressions on a quantitative basis. The general level of spontaneous activity, as measured by the amount of time spent out of its nest by a vole, will be discussed later. To assess tameness it is more important to see if the vole will run when the experimenter is present, and if so in what direction. The rating system used for classifying the ease with which a vole could be handled on a particular occasion, in five steps of decreasing tractability, was as follows:

(1) No rapid running, no freezing (see below), and no persistent movement away from the experimenter.

(2) Freezing; a characteristic hunched attitude which a bank vole may assume on disturbance and maintain despite being pushed, picked up or otherwise stimulated, and despite being left undisturbed, subsequent to this, during a five minute period of observation from a distance of five feet.

(3) Movement away from the handler, but not enough to make handling difficult.

(4) Movement, especially running in circles and jumping, so rapid as to make capture difficult, but not apparently orientated with relation to the handler.

(5) Rapid running or jumping away from the potential handler. Biting.

Five adult makes from each of eight sorts of Clethrionomys were placed in separate cages, and scored on these criteria for ten consecutive days. The results in Figure 2 do not suggest that the rating scale measured a single factor which is continuously variable, but rather a number of partly independent tendencies each of which has an effect on tractability. In the absence of a more detailed study, suggesting what statistical model could generate such results, a statistical analysis of the data as a whole was not considered appropriate. However, the types of bank vole do seem to be characterised by a high frequency of a particular rating. In only the Kintyre specimens of britannicus and the two hybrid groups do less than half the observations fall in the most frequently occuring category.

The differences between the observed records of a particular grade that seems to characterise a type of bank vole, and the expectation on the basis of the frequency with which this grade occurred in the results of the other voles, were tested by the chi squared method.

This analysis is presented in Table 2. *britannicus* from Edinburgh, and *erica* are both difficult to handle, but are characterised by the rating numbers 5 and 4 respectively. *skomerensis* and *alstoni* are both easy to handle. Apart from the differences between the races it is noteworthy that the *britannicus* from Kintyre are different from the Edinburgh sample, and rather similar to some of the island forms; that the new collection of *skomerensis* animals was markedly easier to handle (this was so from the time of capture) than the old stock, which had been in captivity for a number of generations (about four). The two types of hybrid were not markedly different from each other, but resembled neither of their parent races. They were the only animals other than *erica* to be classified as 4 at all frequently. They gave the impression of being wild in a disorganized way.

B. upward flight reaction

If a resident vole is visible outside its nest when the cage is opened, his response to the opening may be any of three broad categories of behaviour, providing that there is no other disturbing factor. These are:

1. rapid upward movement by jumping, climbing or running; termed an upward flight reaction if the vole leaves its cage within about five seconds (estimated),
2. burrowing or running to cover; termed a downward flight reaction if the vole has disappeared from view within five seconds, but has remained within its cage,
3. the vole still visible within its cage; classified as no flight reaction, but probably including weak escape reactions, and some poorly coordinated ones. Some individuals run rapidly in circles when disturbed, and for lack of an unambiguous criterion this has been included in the 'no flight' category.

The results are presented in Tables 3 and Figure 3. There was marked individual variation, especially in *erica*, but it will be seen that in these samples *alstoni* and skomerensis had less tendency to flee than did britannicus and erica, and also that the flight of britannicus was characteristically in a downward, and of erica in an upward, direction. These conclusions are supported by experience of larger number of observations, which were not designed to test escape reactions.

The stimulus operative for these responses may well be the rapid increase in intensity of illumination within the cage on opening its lid of perforated zinc mounted in a wooden frame. This interpretation is supported by the fact that the reactions are found if the lid is opened by the use of a string when the observer is some feet away, but are not found if only the frame of the lid is opened in the normal way, leaving the perforated zinc resting on the walls of the cage. In the previous section on handling, other factors are certainly involved, and, in some cases, the vole makes movements apparently orientated in relation to the observer.

C. strange object reaction

When a vole is confronted by an object with which it is not familiar, in its home cage, it usually backs away from it, and avoids that part of its cage for a while. This is a familiar phenomenon to workers on small mammals. Lorenz (1952), for instance, described how the behaviour of Neomys fodiens changes, when it comes across an unfamiliar object in its home grounds, from rapid and stereotyped movement to what is apparently exploration, with rather slow progress towards its presumptive goal. The avoidance, by Microtus, of traps because they are new objects has been considered the cause of the increase in catching performance that is usually found between the first to the second night that a group of traps have been set (Chitty and Kempson 1949, and a discussion by Linn 1954).

The likelihood of a vole not being caught in a Longworth trap was taken as a measure of the strength of the strange object reaction.

Male Clethrionomys, each of which had been living in the experimental cage, with abundant peat moss and hay so that runs and tunnels could be established as cover, for at least a week, were used. A Longworth live trap (plate 5, and Chitty and Kempson 1949), containing food and bedding, was placed in the cage at the far end from the nest used by the vole, and left there overnight. In the morning it was recorded whether the vole had entered the trap. This vole was not used for further trials. Only animals bred in captivity were used in these experiments, in order to exclude the effects of trap experience. The number of races involved was limited to those available in relatively large quantity.

Applying a chi squared test to the results shown in Table 4 it becomes clear that britannicus individuals enter the strange object less readily than do skomerensis, or hybrids between either britannicus and skomerensis, or britannicus and alstoni (in each case P is less than .001). There is no evidence that the two sorts of hybrid behave differently from one another, or that either is different from the skomerensis animals for this character (in both cases P is greater than .10).

D. open field

The spontaneous behaviour of the same five males of each of eight categories of vole that were tested for tractability (see IV. 1.A) was assessed during ten minute periods of observation in the following circumstances.

The animal was placed at "0" in the centre of the open field apparatus (Fig. 4) under a tin, which was lifted rapidly from the animal after ten minutes. Around "0" was a circular area divided into named sections surrounded by a wall, which had above it four electric lamp bulbs which were the only illumination in the room. The locomotory movements (this term, and the ones following, are explained in footnotes to Figures 5 to 11) were recorded. The total score of each individual for the ten minute period is plotted in Figure 5, and from the standard deviations of the means also shown it can be concluded that the *britannicus* from Edinburgh move more than those from Kintyre in this novel situation, and that they together with the *erica* group moved more than the *alstoni* or either of the two *skomerensis* groups. The two hybrids were intermediate in performance between their respective parental races, but not markedly different from the *britannicus* group.

The number of minutes in which several categories of activity occurred at least once are shown in Figures 6 to 11. The amount of running was, like movement, highest in *britannicus* and lowest in *alstoni* and *skomerensis*. *erica* was the only group exhibiting back flips, and jumped rather more frequently than the rest. Edinburgh *britannicus*, and *erica*, showed a higher tooth grinding frequency than the rest. The island races showed no difference from the Kintyre britannicus in the amount of washing done during exposure to the open field situation, but all these did less washing than britannicus. All the types of vole except erica spent some of most minutes in contact with the wall of the apparatus.

The movement termed backflip, and found in alstoni, is very similar to one frequently performed by Mus musculus spicilegus Petenyi but not by any stock known to the writer of the laboratory M.m. domesticus Rutty.

2. RHYTHMIC BEHAVIOUR

The well known dispersion of many activities of animals into more or less regularly spaced bouts is behaviour which is readily expressed in quantitative terms. This is one reason why these characters have been favoured by physiologists in analysing the proximate causal factors in muscular motor activity. The causation of rhythmic activity has also been studied at the genetical level (and is one of the few behavioural traits to have been so studied) by, for instance, Rundquist (1933), who found that much of the individual variation in the spontaneous activity of rats could be attributed to genetical determinants, and Brody (1942). This work has clearly demonstrated, by the response which has been obtained to selection for increased or decreased activity level, that, within a particular environmental setting, the level of activity observed was not stable to the variability in genetical constitution among the individuals in the population which was studied. Psychologists (Munn 1950, for a general review), who have often used relatively uniform material from the genetical point of view, and ecologists (Calhoun, 1945-6), using members of natural populations, have shown just as clearly that the modification of a number of factors, especially light (Kowalski, 1949, Aschoff and Meyer-Lohmann, 1954, and Hoffmann, 1955) and hormonal balance, has a profound effect on the performance of rhythmic behaviour. It seems clear from this that activity cycles have a complex ontogeny. Far less is known of what factors are important in the ecological adaptiveness of rhythmic patterns in natural populations to their own niches, or range of environments. Two studies on mammals have, however, been made of sympatric, but closely allied, species; and both have lent support to the idea that such species have differences which reduce competition in one or more ecological situations. Crowcroft (1954) has shown that Sorex minutus is less nocturnal than S. araneus, and this limits the heterospecific contacts made in the common hunting grounds. Kalabukhov (1938) has found comparable differences in the diurnal rhythm between Apodemus sylvaticus and Apodemus flavicollis which are correlated both with differences in environmental selection in the laboratory and with habitat preferences in the wild state. Such modification in the periodicity of the things an animal does could have come about, initially, as a result of several possible advantages an individual may get from being out of its home at particular times. For instance, it may avoid exposure to a class of predators, perhaps specializing on the related form, or foodstuffs not utilized by the other species may become available to it without competition. Once a difference has become established it will probably be stabilized by social factors - an idiosyncratic individual may have more difficulty than his fellows in finding a mate. Since speciation probably occurs allopatrically (as will be considered later), any divergence in periodicity between geographical races is likely to be important.

From the point of view of speciation, the central problem in the ontogeny of such polytypic characters is whether the crucial difference in the factors affecting development is dependent on a genetical, or on an environmental, distinction between the categories of individuals concerned. On this will depend the stability of a character, acquired by a race in isolation, if the race should subsequently overlap geographically with its parental population. In order to be available to natural selection as an isolating mechanism, between potential species, a phenotypic character must be of this kind.

A. in captivity

The bank voles from the mainland have been shown to move more vigorously when disturbed. This behaviour makes britannicus seem more active than the other races, and led to the starting of the investigation reported here. It should be remembered that a negative result would not have meant that there were no important differences in rhythmicity between the races studied, but that such differences, if they existed, were not stable over the whole range of environments in which these races can live successfully (see section VII, on natural selection, for evidence of the success with which britannicus lives in captivity, in relation to its breeding and survival performance in the wild).

In order to find if there are inter-racial differences in rhythmic behaviour in bank voles, in spite of individual variation within races, it was necessary to make a quantitative estimate of behaviour in time. This was done mechanically because preliminary watching suggested that any rhythms would be long term, and not suitable for direct observation.

(i) methods

Two main factors, apart from simplicity, were considered in designing an apparatus to study rhythmic behaviour:

(a) Which variable was to be recorded as behaviour. The term normally applied to the data obtained as 'activity', whether this is measured by the number of turns of a wheel (Dice and Hoslett, 1950), or excursions of a tambour mounted cage (Kowalski, 1949), or movements of a door subdividing a cage (Crowcroft, 1954), or any of a group of other criteria (for reviews see Kalabukhov 1940, Munn 1950, and Southern 1953). Similar results are not obtained by all these methods, and it is probable that a simple factor is not scored as activity. It was decided to use excursions out of the nest as the measured variable. This seemed more natural than activity wheel performance, for instance.

(b) The sensitivity of various recording systems has been discussed by Crowcroft (1954), and he points out that the limiting factor has often been the length of drum paper available for each time unit of the record. Six minutes has been the smallest unit used. To avoid this difficulty it was decided to use a strip of paper running over a roller, and in this way ten inches of record for an hour, allowing analysis to the nearest minute to be made accurately, was easily obtained (plate 6).

The design of a unit of the apparatus used is shown in Figure 12, and plate 8. The nest box was supplied with hay for bedding; its sides were double, the outer metal walls being removable in order to observe the animal in its nest. This box and the food container, which was supplied with mixed corn, turnip, and water in a removable plastic container, were suspended from opposite walls. Both had steeply sloping lids in order to prevent voles from sitting on them.

When a vole left its nest the floor sank to complete a circuit operating a signal lamp, and (plates 9 and 10) a uno pen filled with barograph ink which wrote on paper coming from a reel such as is used on a Remington adding machine. Four such cages were used to accommodate, separately, one male Clethrionomys from each of four different populations. Replicate observations on races were dispersed between batches of experiments in order to reduce any systematic effect of seasonal variations in temperature, noise, or other uncontrolled environmental factors. The cages were placed so that the inside of each could be seen from the same observation point in a room (plate 7) in which the schedule of lighting periods was as follows:

Darkness for eight hours between 10 p.m. to 6 a.m. (G.M.T.). From 6 to 10 a.m. indirect illumination from four six-watt bulbs diffused through translucent white glass simulated twilight. Day was the eight hours from 10 a.m. to 6 p.m., with indirect light from three sixty-watt bulbs. A second twilight period proceeded darkness.

An experiment was normally run for two or three weeks. Each day the cage was cleaned, and food and water replenished, and the pens inspected. This proceedure lasted approximately two minutes, for each unit. About once a week the reel of paper was replaced. Visual observation was carried out during part of each day period, and often other experiments were in progress in the same room. The amount of time for which observations were made, and other activities performed, was not standardized between experiments however. The voles were apparently less disturbed by the sight of movements than by sounds. During the earlier experiments counts were made of the frequency of sounds produced by the voles in the night periods. In the last two sets of experiments observations were made during the night by means of an infra-red image convertor apparatus (Figure 13 and plates 11 to 13). The infra-red source was an ordinary tungsten filament lamp screened by a filter glass passing infra-red. The principal of the device is that the image of the cage in infra-red is focused by an optical lens onto the semitransparent photocathode consisting of silver caesium oxide which emits electrons with the same distribution as the incident image. The Electrons are accelerated by a large potential difference applied between the anode and cathode. This beam is focused electrostatically on a luminescent screen where the energy of the electrons is converted into visible light, so that a reproduction of the scene used as the object is obtained. During the observations by visible and infra-red illumination, a record was made, each minute, of the occurrence of a group of activities which could be recognized in the converted infra-red image, which usually had poor definition. These were: locomotion, feeding, urination and presence outside the nest box.

(ii) results

For the purpose of comparisons between and within races, the records obtained from all the experiments were examined to determine, for each half hour period, how many minutes the vole spent some of the time outside his nest box. The mean score, for each clock half hour, is plotted in Figure 14 (i) - (vii) for all experiments. It will be seen that most races exhibited a short term periodicity in the distribution of excursions within the twenty four hours.

Although there was considerable individual variation within groups, each was characterised by a particular pattern; the bursts of activity in *britannicus* from Kintyre and Edinburgh were less frequent than in *alstoni*, but more frequent than in *skomerensis*. The number of cycles was obvious only in *skomerensis*, which had five per 24-hour period, and *britannicus* from Kintyre, which had six. Probable figures for the other races are six for the Edinburgh *britannicus*, about eight for *alstoni* and five for *erica*. *norvegicus* seems to have had more numerous cycles than *rutilus*. The *britannicus* from the New Forest apparently lacked this short term rhythmicity. The hybrids did not resemble either parental race; their performance did not show regularity, except that they were more active during the night.

The total amount of time spent out of the nest box, and its distribution between the lighting periods, for the several races, was subjected to an analysis of variance. The groups of animals were first analysed separately. It was found that, (see Table 5, I) (a) New Forest britannicus, skomerensis and the group of hybrids showed differences in total performance within a group significant at the five per cent level. (b) New Forest britannicus (one per cent level of significance) and the hybrids (five per cent level) showed difference between lighting periods in the distribution of excursions. (c) There was no evidence of interaction between animals and periods; that is, no difference in the pattern of distribution of activity between individuals within a group could be demonstrated.

An overall analysis (Table 5, II (i)) shows (a) There was a difference between groups (Table 5, II (ii)). The significance of this difference was caused mainly by the New Forest britannicus, which had a lower performance than most others, and by erica, which was also low. (b) There was a marked rise from day to dusk and night, and a fall from night to dawn. (Table 5, II (iii)). (c) There was no evidence of difference in distribution of excursions between periods for the several groups.

A difference of over 40 would probably have been revealed by the analysis. No consistent difference in the proportion of minutes during light and darkness in which a vole performed some recognizable activity was found by visual observation. During the night, however, the periods of feeding were more protracted. Except when the excursions out of the nest were long, the proportion of an excursion spent performing an activity was roughly constant. During the long spells on the floor more minutes were spent sitting motionless, usually in a corner of the cage.

B. in the wild

In order to determine if there are short term rhythms, of the same sort as have been described in the previous section, in wild *Clethrionomys* the technique described by G. K. Godfrey (1953 and 1954 a and b) for marking *Microtus* with a radioactive ring, and tracing it with a Geiger counter, was used. A monel metal leg ring (Chitty 1937), onto which was soldered a brass tube containing about 100 μc of Cobalt^{60} embedded in plaster of Paris, was used to locate of the marked vole. A portable dry battery operated Geiger-Muller counter was used, the tube of which was attached to a ten foot bamboo pole. It had headphones to allow the label to be located in darkness.

In Figure 15 the observations made with this apparatus are recorded. The term 'nest' is given to the position at which the vole spent long periods without appreciable movement, and where it was present at each of about six previous visits during daylight. Each quarter hour the nest was approached, and the counter probe held over it, the observer being about eight feet away. It will be seen that the visits during which the vole was absent from the nest are associated into four groups in each of the twenty four hour periods of observation. These were evenly spaced during the warm, damp, moonless night, but not so during the moonlit night during which the bank vole also was less frequently away from its nest.

C. rhythmic behaviour in the wild in relation to that found in captivity

On Skomer voles were frequently observed moving about in low vegetation, sometimes in small groups, during the day. Trapping did not suggest that the population density was particularly high. *britannicus* and *alstoni* were comparatively seldom seen active in daylight in although they occur commonly both in individuals living in adjacent areas at Wytham where there is ground cover (Kikkawa, unpublished), and also in individuals trapped near Edinburgh and studied in the laboratory. This suggests that the absence of ground cover in the wild has a similar effect on rhythmic behaviour to that apparently produced by a bright daylight regime in the laboratory. It is possible, therefore, that the lack of observations of activity by mainland animals in daylight is due to these animals being more readily inhibited from foraging outside thick cover by bright illumination than is <u>skomerensis</u>. This hypothesis could be tested by greatly increasing the power of the light sources used, in the recording room, and finding if <u>britannicus</u> is, then, more nocturnal than <u>skomerensis</u>.

3. DISCUSSION

The main outcome of the investigations on individual behaviour described here is that the distinctions between the races of *Clethrionomys* are of the same order of magnitude for these characters as for those which have been used by the taxonomists of the group. This is not remarkable. More thorough demonstrations of this point have been made by Pilters (1954) on the Tylopoda, Lorenz (1941) on the Anatidae, Hinde (1955) and Mayr, Andrew and Hinde (1956) on the genus *Fringilla*, and Spieth (1957) on the *willistoni* group of *Drosophila*.

Several differences between the races of *Clethrionomys*, in tendencies to behave in particular ways, have been found to substantiate the impression which they give of differences in temperament. *britannicus* animals, for instance, are apparently shy, running away from an observer; they also tend to become hidden rapidly when disturbed, and run about a lot in a strange situation from which they cannot escape, and they avoid a strange object more than do other voles. *erica* gives the impression of being wild, tending to jump upwards a good deal when escaping, and not remaining in contact with the wall when in a strange situation. *alstoni* and skomerensis are similar to one another in appearing tame, and having their normal activities little changed by alterations in their environment which evoke reactions in other voles.

Geographical differences in rhythmic behaviour have been described, both in the distribution of activity between day and night, and in the number of short term cycles during the twenty four hour period. A comparison of the published reports on Clethrionomys confirms that the genus is polytypic for activity pattern, although the differences in technique employed in the studies makes this conclusion less reliable. Miller (1955), who made records of the transit of bank voles between a cage and annexe to it, which contained food, states that his specimens, from Wytham Wood, near Oxford, fall into two distinct categories; one having a marked short term feeding rhythm rather evenly expressed over the twenty four hours, and the other showing an Apodemus-like nocturnal preference. Possible these animals have rhythms of the sort found in britannicus from Edinburgh, and from the New Forest, respectively. Brown (1956), also working on britannicus in the South of England, failed to trap animals during the night. She suggests that activity is stimulated by a decrease in illumination, and that Miller (1955) found activity during darkness because his regime included only bright light and darkness. Miller's result is confirmed by the observations reported here, in which the light and dark periods were separated by four hours of dim illumination, and yet activity was found during complete darkness. Brown found that the catch rate had peaks at dawn and dusk, with a lower one in the afternoon, and claims to have found a two-hourly rhythm, but, as her visits to the traps were also at this interval, it is felt that the short term rhythm, if real, is likely to have been modified by the method used to observe it. In France, Chappellier (1947) found that Clethrionomys glareolus in the wild visited food during the day and the night. Schleidt (1950), observing bank voles in semi-natural conditions in Austria, found six to eight cycles of activity evenly spaced over the twenty-four hours. Ostermann (1956), automatically recording the activity of captive bank voles from Passau, Germany, in natural lighting conditions, provides data which suggest a short-term rhythm of about eight cycles in the spring, but not at other times of the year. He finds that most activity occurs at night during the summer, but by day in winter. Kowalski (1949) working in Poland, found very frequent cycles of activity, between ten and twenty in the twenty-four hours, using a cage mounted on tambours which operated a recording pen. He also found that the diurnal rhythm is easily modified by changing the lighting system, although the rhythm of Apodemus flavicollis flaviocollis persists in the same conditions. Kalabukov (1938) reports a similar difference between A. sylvaticus and A. flavicollis, and, in this case also, the difference in physiological control is associated with a difference in the amount of cover available in the habitats of the species. Differences in the dependence of physiological clocks on environmental factors are well known in other organisms (see, for instance, Pittendrigh 1954 on Drosophila).

The work summarised by Braden (1957) has shown that the occurrence of ovulation and oestrus in the mouse is geared to the light cycle by the mediation of the eyes, central nervous system, and anterior pituitary gland. Braden interprets the difference he finds in the responsiveness of outbred stocks to a change in the lighting regime as being, at least partly, due to the genetical control of a neural mechanism

It is considered probable that the distinctions in behaviour between the races of Clethrionomys which have been described, although probably biased by conscious selection for characters which could be easily scored, are representative of differences which will influence the relative success of the voles living and breeding in the same environment, and, in particular, that they will modify the reactions of voles with related individuals.

A general survey, using ethological methods, of the behaviour of Clethrionomys glareolus has been made by Schleidt (1950), but there has been little other work done on rodents with which to compare it. Eibl-Eibesfeldt (1951) has described numerous behaviour patterns of Meriones persicus persicus, and Thorpe (1956) considers that many of them must be inborn. Zippelius and Goethe (1951) have performed Kaspar Hauser experiments on Muscardinus avellanarius and find that toilet sucking, climbing, concealment and fright postures, nest building and vocalization all develop in the way that they would be expected to have done had other members of their species been present during their growth.

There has been little work reported on the behaviour of related species that will interbreed. Hinde (1955, 1956 a and b) describes a thorough ethological study of several species of Finches, and of the sterile hybrids between them. He concludes that the hybrids exhibit in an unchanged form those behaviour patterns which their parental species have in common, and that the behaviour patterns which differ quantitatively between the species are intermediate in the hybrids. Clark, Aronson and Gordon (1954) report similar findings in the hybrids between Xiphophorus maculatus and X. helleri, together with the absence of behaviour patterns which were found in only one of the parent species being more or less dominant over presence. A tendency to resemble the species used in making a backcross, and to show segregation in the F_2 suggests that the genes influencing the behaviour are numerous. The behaviour of bank vole hybrids is only partly in line with this work. Several of the characters studied were intermediate between the parental races, for instance, the amount of movement, and the frequency of tooth grinding, washing and wall contact in the open field situation, and the frequency of bed shredding (Section VII, 2.C). Hybrids are more variable, both between individuals and at different times in the same animal, than are members of a particular race; but they are more similar to one another than are individuals belonging to different races. The hybrids did not resemble either parental race in crosses between britannicus and alstoni, or britannicus and skomerensis, in their rating for ease of handling. They were similar to erica animals in being wild, but were not so successful in escaping.

Inbred strains of mice have been compared for a number of behavioural characters, chiefly connected with activity and aggressiveness. It has been demonstrated that differences in expression of these traits are partly determined by differences in hereditary factors (Rundquist 1931, 1933, Dawson 1932, Scott 1942, Calhoun 1956). It is not known how important traditional distinctions may be (King and Gurney 1954, King 1956). More illuminating work has been done with breeds of dogs which differ in behaviour, and several breed characters have been found to be simply inherited, some probably being due to a single Mendelian factor. (Whitney 1932, Stockard 1941, Thorne 1944). Some physiological, rather than behavioural characters have given similar results (Fuller 1951, Scott 1954).

V. SOCIAL BEHAVIOUR

1. INTRODUCTION - AGGRESSION AND SUBMISSION

In groups of animals that have highly developed social behaviour, differences in the form that this takes could result in reproductive isolation even if the specifically sexual releasers were similar.

In the previous section it was shown that races of Clethrionomys differ in their behaviour to man Comparable variation between the races in some of their social behaviour will be reported in this section. It should be emphasised that the characters to be described are probably not entirely representative of the activities carried out by these voles. They were selected for the ease with which they could be recognised. Obvious factors involved in this selection were; the type of movement - slow, repeated or gross movements being more easily recognised, and whether the movement could be interpreted in the light of work done on other animals. The aggressive behaviour of Clethrionomys seems to be similar in general to that reported by Clarke (1956) for Microtus.

Dominance relationships (Allee 1942, 1950) are easily recognised in Clethrionomys. A bank vole which has been resident in a cage for a day or more will almost always retain the use of its nest, and freedom of movement about the cage, compared with a vole of the same race, that is strange to the cage. This is taken to mean that, where a clear dominance relationship is apparent, the resident vole is usually dominant over the visitor.

This regularity in behaviour was used in standardizing the conditions for observing the social behaviour of male voles. A male was put in a large (approx. 90 x 50 cm.) glass walled cage with sawdust (about 1 cm. deep) on the floor, containing corn, turnip and a small nest box. The following day another male, of the same race, was added, and the cage observed for the subsequent hour. The results summarised in Table 6 show that some behaviour patterns are characteristic of resident animals, some of visitors, and that the races differ in the occurrence or frequency of these categories of behaviour.

Scuffling (plate 21) is a slow forward movement, with the body carried low, in which the front paws move backwards much more in relation to the body than the body moves forward in relation to the ground. Sawdust is flung backwards by this. The movement is a prelude (Haldane and Spurway 1954) to attack, and may be a displacement activity due to the simultaneous tendency to attack and to flee. It is characteristic of resident britannicus and erica. Boxing (plates 17 and 20) is frequent in encounters between males where neither is clearly dominant, and is often followed by brawling (plate 18). It is usually preceded by the resident male assuming the pre-lunge position (plates 16 and 17); the visitor then raising its head and forelimbs. The alternative sequel is a lunge (plate 23) by, usually, the resident vole, and flight by the visitor. At the close of a bout of encounters the visitor often assumes one of two quite distinct postures, which are submissive in the sense that they inhibit further attacks by a dominant animal. Hunched submission (plate 19) has been observed only in erica and alstoni. The vole often holds its tail curved well off the ground. Rigid submission (plate 22), on the other hand, is characteristic of britannicus. Neither of these has ever been observed in skomerensis, nor do these animals show any behaviour which seems to be equivalent.

From the frequency of these behaviour patterns it is concluded that *alstoni* and *skomerensis* are less aggressive than *britannicus* and *erica*. This is confirmed by inter-race encounters between males. *erica* is markedly the most successful, and *skomerensis* least. It is noticeable that *skomerensis* animals are attacked more persistently than the others. It is suggested that this is due to the lack of a submission signal. *alstoni* seems to initiate more fights early in a bout than does *britannicus*, but is less often successful. This may be because *britannicus* weight less than the other races.

2. EXPERIMENTAL COMMUNITIES

A. Method

In the wild, reproductive isolation can be concluded if animals select mates belonging to the same taxon when more than one type of potential mate is present in the area. D. M. Steven (1953, 1955) has shown that members of different races of Clethrionomys will mate in captivity if no alternative partner of the same race is available. This does not exclude the possibility of a potentially effective barrier to hybridization. Ecological variables, particularly specific habitat preferences (Lack 1944, Miller 1942), which have been shown to be sensitive to gene substitution at a number of loci in Drosophila (Waddington, Woolf and Perry 1954), lead to population interspersion (Elton 1949) and are recognised as a means of reproductive isolation (Mayr 1940). Differences between groups of animals in their tendency to associate with one another could, similarly, limit the range of potential mates that is available to a particular animal. The latter possibility was first experimentally investigated by Blair and Howard (1944) and later by Blair (1953), who used forms of mice of the genus Peromyscus. The work now to be mentioned employed a technique similar to that used by these authors.

The frequency with which particular animals were found together in the same nest box was used as a measure of the tendency for these animals to associate. Two animals of each sex, all of which were strangers to one another, were placed in a large cage (plate 24) which had four nest boxes. These were accessible for observation from outside the cage. Abundant food and bedding was available to them at all times. Each member of a community was individually marked by ear punching, and its location recorded each day at about 10 a.m., at which time most animals were in a nest box.

In the first series of experiments all the animals in a group were of the same race. A hundred observations were made with the cage and nest boxes remaining in the same place for each trial; another with the cage and nest boxes randomly rotated 90, 180, 270 or 360 degrees between observations.

In the second series a male and a female <u>britannicus</u> and a male and a female of one of the island races, composed the community. Experiments were run for between ten and thirteen days, unless one of the animals died before this.

It was possible for each animal to occupy a nest box alone, or to be together with one or more others. There were fifteen possible categories of distribution of voles in relation to one another. The number of times a particular grouping was found was compared with that expected by chance. The significance of the differences was tested by the chi-squared method.

B. Results

(i) Single race communities (Table 7 (i))

(a) Gregariousness. The overall frequency with which all the voles were together was greater than would be expected by chance (P less than .001). This is considered to demonstrate gregariousness.

(b) Sex differences. There was no evidence that the gregariousness was due to a tendency for homosexual rather than heterosexual associations (P greater than .2 comparing AB; ab; and AB, ab with Aa; Bb and Aa, Bb in Table 7 (i). The females were found together more often than were the males (P less than .01); the males indeed being found together less frequently than would be expected by chance (P less than .01).

(c) Territoriality. In the series where the orientation of the cage in relation to the room was undisturbed between experiments, the number of occasions on which a vole was found in each nest was recorded (Figure 16). The number of times the favourite nest was occupied is plotted as 100, and the second and third most, and the least, favoured nest shown as percentages of this. The steepness of the slope reflects the decisiveness of the choice. A vole at, or near to, the nest which it most frequently occupied often behaved aggressively to an animal normally resident elsewhere. The nest can, therefore, be considered a territory, using the definition of Hinde (1956a). skomerensis showed a less marked territoriality than the others (P less than .001), which showed no evidence of differing among themselves.

Since it was clear that the animals chose particular boxes, further experiments were made to find out what cues were used in locating the preferred box. After rotating the cage together with the nest boxes at random between observations, the choices were scored by position (i) in relation to the cage, and (ii) in relation to the room, (iii) in the control series the cage was undisturbed between observations. The results plotted in Figure 17 show that the voles orientate mainly according to the room. Faithfulness to room position is greater than to cage position (P less than .01), and the faithfulness to room position is not significantly affected by rotating the cage and nests (P greater than .1).

Rats have been found by psychologists (e.g. Hebb 1949, p.91) to use distant cues, rather than stimuli from the object itself, for orientation to a platform onto which they have previously jumped.

(ii) Bi-racial communities. (Table 7 (ii))

Although animals in communities with a male and a female of each of two races were gregarious (P less than .001) they were less so than in single race groups (P less than .001). As in the group of experiments previously mentioned, females associated with one another more than males did (P less than .02), but there was not a marked difference in incidence of heterosexual and homosexual associations (P less than .20).

Racial Segregation. The most striking result was the degree of isolation between sexes of the island and mainland races. The incidence of pairs of the same race (Aa; Bb and Aa, Bb) was greater than that of mixed racial pairs (Ab; Ba and Ab, Ba) (P less than .0001). The effect was significant at the 5% level for the britannicus/skomerensis communities and at the 0.1% level for the britannicus/erica and britannicus/alstoni communities.

Racial exclusion. *alstoni* and *erica* males were more often found with both the females of their community, to the exclusion of the *britannicus* male, than *vice versa* (*P* less than .05 and .001 respectively). Similarly *erica* females exclude *britannicus*, but *britannicus* exclude *skomerensis* females from threesomes (*P* less than .01 in each case). These results may have been due to differences in aggressive behaviour between the races. Voles that were usually excluded from nest box associations did not often remain at the scene of an encounter at its termination. *britannicus* often initiates fights but, if the resulting encounter lasts for more than a few moments, generally retires rapidly.

3. IMPORTANCE OF OLFACTORY CUES

A. Method

This series of experiments aimed at identifying significant stimuli involved in social contacts which attracted or repelled voles. This knowledge was necessary in order to devise some more sensitive test of racial discrimination than the experimental community method described earlier. For this purpose the behaviour of members of heterosexual pairs of voles was investigated.

The description of the experiments will be made with reference to Figure 18 (the apparatus is illustrated in plates 25 and 26). In each experiment a male and a female vole, which were previously strangers, were introduced to one another in a cage not familiar to either animal, and their behaviour observed subsequently. The two novelties in the situation were important because; (a) Clarke (1953) has shown that *Microtus* behave differently towards individuals known from previous experience, (b) it is well known from work done on dominance relationships (for instance Allee 1950) that the outcome of an encounter tends to differ according to whether an animal is at home at the time. Type A introductions were controls, and also accustomed the observer to the type of interactions between a male and a female that could be expected. Type B were made with the female Clethrionomys enclosed in a transparent plastic sandwich box, in the walls of which many holes had been drilled. Type C introductions were made using an intact box the lid of which had been sealed, using sellotape, after putting in the female. In the last series, D, the male was introduced to what was intended to be merely air that had lately been in contact with the female in question. Auditory stimuli, however, may not have been excluded despite the separation of the participants. One of the categories of controls to the experiments, to be reported in the following section, was more critical on this point. Finally another series of controls were performed where a male was introduced to a well washed, and empty, sandwich box, either with holes or without.

It might be thought, at first sight, that this method itself would be suitable for the investigation of racial discrimination as well as social behaviour among similar animals. It has two disadvantages however, first, that the method of scoring by the observation of behaviour, which is of a continuously variable kind, lacks rigour, and, second, that the racial choices to be compared are sequential, and only by a statistical analysis of extensive data could one exclude the possibility that any differences are due to a change in behaviour associated with experience of these experiments. That is, changes in internal state may alter the likelihood of the performance of particular motor acts in response to the same environmental situation. This would increase the variability of the results, and thus efficiency would be lost.

B. Results

The sexual behaviour of *Clethrionomys glareolus* has been described by Schleidt (1950). Here only the behaviour found when the female was enclosed (type B) that seemed to correspond to that found when both animals of a pair were at liberty (type A) will be mentioned.

The male typically approached the box (plate 27) and sniffed at it, squeaking (plate 28), and often climbed over it (plate 29). It has been suggested by Schleidt (1951), on the basis of experiments done with electrical recordings, that this squeaking (much of which is too high to be audible to man) inhibits the flight reaction of a female. After a few minutes investigating the box, a male often performs actions usually seen in aggressive encounters (see Section V.1.), particularly scuffling. When he did so the female usually moved as far away from the male as possible (Figures 30 to 32).

In the series of observations where the female was in a sealed box (type C) the male less frequently approached the box, spent much less time near it, and did not sniff it, or squeak (Figures 33 and 34). If the female moved about inside the box the male would then approach her, usually in an aggressive attitude.[1]

Where the scent of the female alone was presented (type D) the response of the male was very similar to that found in type B experiments (Figures 35 to 37) during the first two minutes. The male did not then perform aggressive movements, but rather washed or rested in a corner of the cage.[2]

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[1] Male voles enclosed in this way evoked the same behaviour.

[2] The scent of a male Clethrionomys induced scuffling, and short runs in the pre-lunge position (see Section V.1). Indistinguishable reactions were made to the scent of male or female Microtus and Apodemus.

C. Conclusion

Female Clethrionomys produce olfactory stimuli which are sufficient for them to be recognised as such by males. Either olfactory or visual stimuli can induce aggressive responses, and probably (Schleidt 1950) auditory stimuli can also. Clarke (1953) found evidence that Microtus males can recognise a strange vole by scent alone. There is no evidence that such recognition in species specific, as is the recognition of females.

4. DISCUSSION

One reason why the progress towards understanding the social behaviour of mammals has been slower than that of birds is the difficulty of making models of the olfactory social signals which are so important in the majority of mammals (Schloeth 1956). This difference in mode of communication between man and most other mammals has probably resulted, also, in the classification of the order being less advanced than that of the birds, species of which, as Spurway (1955b) has pointed out, are often recognized taxonomically by characteristics which have probably evolved as signals to other birds.

The differentiation of the forms of Clethrionomys in movements associated with social behaviour is not as clear cut as the species differences reported by Lorenz (1941) in the Anatidae, or by Antonius (1937, 1939) in the genus Equus, or by Pilters (1954) in the tylopoda. However the social dominance of one race, in mixed groups, is comparable to that of one inbred strain of mice over another (Ginsburg and Allee 1942), or of the brook trout over the rainbow trout (Newman 1956). These fish form a common hierarchical system. Hale (1956) has found that members of one breed of domestic fowl recognised birds of another breed not as individuals but as members of a class. One defeat by a foreign bird led to the subordination of the vanquished bird to all others of the victor's breed. Neither of these studies showed what effect the species discrimination which was demonstrated had in reproductive situations; on the other hand striking differences between closely related sympatric species (Tinbergen et al. 1942), which inhibit mating between the species, are important in nature (Mayr 1942). It is very probable that natural selection favours the development of such differences (Dobzhansky 1951).

The behaviour patterns which give rise to the decrease in gregariousness of bank voles which are members of mixed communities, and to the segregation of the races, and to the dominance of the individuals of one race over the individuals of the other, are factors that would decrease the likelihood of introgressive hybridization, if the races should meet in the wild. However, if the races are derived from a common ancestral population, it is highly unlikely that these differences have arisen due to the disadvantage, to an individual, of mating with a member of another race (see Section VII. 3), because natural encounters between members of the races, if they occur at all, must be rare occurrences.

VI. INTER-RACE BEHAVIOUR

1. RACE DISCRIMINATION

A. Method

Although the absence of consummatory acts in appropriate circumstances provides unequivocal evidence for sexual isolation, it is not the most economical method for investigating mating barriers in mammals. One copulation is liable to result in a long lasting change in the behaviour of a female. It was decided to use the approach of a male to one female, rather than another, as a measure of the relative adequacy of the stimuli provided by the former. It may well be that females are more discriminating than males in their choice of mate (see Seitz 1948 for the ciclids _Tilapia heurdeloti_ and _T. natalensis_; Bateman 1949 for _Drosophila_; Merrell 1954 for _D. persimilis_ and _D. pseudoobscura_; and Knight, Robertson and Waddington 1956 for mutants strains of _D. melanogaster_), but males move about more when reproductively motivated, and their choice is therefore easier to score.

Figure 19 and plate 38 illustrate the design of an apparatus which allows the simultaneous presentation to a male of the odours of two female bank voles. The females were at no time visible to the male making the choice, and the animals did not come together. Entry of the ante-chamber to one of the female's box was scored as a choice.

A male was placed in a box at C. A female was placed in box A and another in box B. These females were chosen from those available on the following grounds: (i) that they were not familiar with the male, (ii) that they were both in oestrus. All available females were examined each day while these experiments were in progress in order to select ones at the same stage of the oestrous cycle, (iii) that they were of appropriate races. The male was released from C, and was confronted with air being sucked, by a fan, from A and B, down the left and right arms respectively, of a Y-tube. If the male had not entered one of the ante-chambers within ninety minutes the animals were removed and the experiment continued the following day. After a choice had been made, the ante-chamber containing the male was exchanged with the box at C. This method of replacing the male in the starting position avoided direct handling, which would probably have influenced the subsequent behaviour of the males of some races (see Section IV, 1). Which arm of the Y-tube, together with the ante-chamber associated with it, occupied the right, and which the left, position for the subsequent trial was decided at random (Fisher and Yeates 1953 Table 33). Similarly, but independently, the position of boxes A and B were randomised between trials. The first randomisation was to avoid the possibility that a male might go habitually to the left or right due to a trail of its own scent (Paclt 1952). The second avoided the systematic choice of a female on the basis either of her constant position, or of her alternating position. In T-maze experiments spontaneous alternation between trials in the entry of one, rather than the other, of alternative passages is often found (Montgomery 1952), apparently due to an exploratory tendency.

Between successive experiments, each of which consisted of twenty five trials, the apparatus was thoroughly washed. The experiments were of six kinds (Details of the animals used are given in the tables mentioned):

(i) In the main series a male was given the choice between a female of his own kind and one that was different (series A, F and G).

(ii) A single experiment was similar to (i) except that the females had been removed from the apparatus before the trials were commenced. This was done to test the possibility that the deciding factor was a difference in the sounds made by the females (series B).

(iii) A series of controls for factors not specific to the females chosen. The females were removed, and the boxes A and B were washed before the trials were begun (series C).

(iv) A control series to test whether differences that were significant to a male existed between females of his own race (series D).

(v) A control series to test whether the difference between two foreign races of females was significant to a male (series E).

(vi) A single experiment where a hybrid bank vole was given the choice between a female of the maternal, and a female of the paternal, race (series H).

B. Results

Tables 8 to 15 show which of a pair of females was approached by the male, and the time he took to decide. The marked positive assorting which was found is clear evidence that a male vole recognised which of a pair of strange females belonged to the same race as himself, and chose that one. This preference was significant in most of the experiments taken individually (see Table 16). Voles from Kintyre and Edinburgh differed sufficiently for discrimination of this kind to have been made.

A male chose a female of his own race rather than a hybrid female between a member of his own race and some other. A male hybrid did not choose a female hybrid rather than a female of one of the parental races. Nor did a hybrid discriminate between a female of the maternal, and one of the paternal, race. Evidence for discrimination between the boxes recently vacated by females was found, but not if the boxes had been washed before the trials were begun.

During experiments where a choice of a similar female and a different female was presented, there was an increase in the mean frequency with which the similar female was chosen (Figure 20). It was noticed that after a male had made ten or twenty runs he usually paused at the Y-junction, moving his head from side to side, before proceeding to one or other of the ante-chambers (plates 39 to 42). The time spent at the choice point was recorded during each trial of the last five experiments (Figure 21). The total time for the first half of the experiments was 10.25 mins, and for the second half 80.25 mins. This increase is significant at the .0001 level, although the total time taken before the choice was made decreased (Figure 22). During these experiments the increase in success was significant at the .05 level.

In none of the experiments was there a tendency to alternate from left to right, or vice versa, between trials, except in series D and E, where the male was given two females between which he showed no evidence of discriminating; here there was a marked alternation (P less than .005).

Discussion - VTE

The increase in the delay at the choice point in these Y-tube experiments, which is correlated with an increase in success of males in discriminating between females of two races, is very similar to a phenomenon familiar to rat psychologists (Tolman 1938, Tolman and Ritchie 1943). Meunzinger (1938) originated the term vicarious trial and error (VTE) for the looking, or running, back and forth that occurs at a choice point in visual discrimination experiments. It has been found to be negatively correlated with errors, and positively correlated with speed of learning, at any rate for some sorts of discrimination (Jackson 1943).

2. DIFFERENTIAL INSEMINATION

A. Method

After successfully copulating, a female vole has an unmistakable vaginal plug, which remains for a day or two (Brambell and Rowlands 1936). In order to determine if a barrier to racial cross-insemination exists, the ideal experiment would be to determine the origin of the vaginal plugs of females in a mixed community, but, in the absence of a marking technique for semen, it was decided to investigate if the insemination rate by a single male was higher for females of the same race. It is known, from breeding experiments where no choice of mate is given, that if such a barrier exists it is not absolute; therefore, in order to detect a preference (by whichever sex this might be exerted), it was necessary to provide each male with more females than he could cover.

Living in a strange cage decreases the chance of a vole being successful in an aggressive encounter. Males die more frequently than females during the period following the establishment of a new mating. Each male, because rather a large number of females would join him, was placed in a large cage, supplied with peat moss and hay, on the day prior to the commencement of an experiment in order to allow him to become familiar with the surroundings. Five females of his own race, and five of another race, having been individually marked by ear clipping, were placed with him in the morning and left there for seventy two hours, when they were examined for plugs, and isolated. The experiment was intended to be continued in order to get information on the success of the inseminations in producing young, and the viability of these offspring, but unfortunately most of the females died, from a cause not associated with the experiment.

Females for use in the experiments were selected on the basis of there being five or more available; if there were more than this number, five were selected at random from them. (using Fisher & Yeate's tables, each female having been given a random number).

B. Results

Male Clethrionomys inseminated females of their own race more readily than those of other types (P less than .03). The data are too few to discuss the relative isolation of the races (see Table 17). It should be noted that where more than one of the females of the other race were plugged, all the females of the same race had been. This is consistent with the hypothesis that the results would have been more clear cut if a larger ratio of females to males had been employed.

3. DISCUSSION

Male bank voles recognise whether strange females belong to the same race as they do themselves. They approach the scent of females who originated from the same locality in preference to others. There is no evidence, however, that hybrid males discriminate between potential mates. Although free cross breeding occurs where no choice of partner is available, male voles inseminate females of the same race more frequently than alternative mates. It has been suggested that a biologically important limitation to the fecundity of males was a prerequisite for the demonstration of differential insemination by the method used. It may also have been necessary for the phylogenetic development, by males, of the ability to discriminate between classes of female voles. The existence of social hierarchy, together with territoriality, (part V, 1 and 2) probably enables dominant male bank voles to mate with a disproportionate number of females in the w ild, as seems to happen with wild house mice in semi-natural conditions (Crowcroft 1955). If the supply of gametes in these favoured males is a limiting factor in their production of offspring, there will be a selective advantage conferred on such of them as use the available supply for inseminating those females most likely to raise vigorous progeny. In the next section the relative fitness of hybrids will be considered.

As has been pointed out by Haldane (1953a), if sexual releasers, and preferences, are partly determined genetically, as seems to be the case in bank voles, differences may arise between isolated populations due to the disadvantage of having a rare genotype for these characters, which would reduce the chance of finding a sympathetic mate. Such a process would allow more rapid divergence of island forms than could be expected by the action of the Sewall Wright effect. It is not necessary to Wright's theory of genetical drift that rare types should be at a selective disadvantage, except in so far as they are likely to disappear from random causes.

Bastock (1956) has shown that a single gene difference can result in an abnormal courtship pattern by *Drosophila melanogaster* males. Randel (1945) and Knight, Roberton and Waddington (1956) have shown that females in *Drosophila* populations are genetically diverse in their willingness to mate with males of this abnormal type. (Some degree of sexual isolation within a species has also been demonstrated in fish (Minamori 1952), in frogs (Moore 1950); in newts (Spurway 1953) and in another species of *Drosophila* (Patterson and Dobzhanski 1945)).

If the development of specific, or sub-specific, recognition in bank voles were due to tradition, then one would expect hybrids to select females of the maternal type in race discrimination experiments. They do not, but this could be due to an inability to learn to select a particular scent as a result of their peculiar genetical constitution. This point could only be settled by cross littering (or inovulation) experiments.

VII. NATURAL SELECTION

In order to determine with certainty if the differentiation of the races of Clethrionomys is of adaptive value to the members of the genus, it would be necessary to make a field study of reproduction and longevity on sample populations, both in their respective native habitats, and when reciprocally exchanged between them. Less direct information on the evolutionary significance of the races can be derived from the correlation of the polytypic characters with environmental variables (Blair 1947, and Dice 1947), and the effect of hybridization on fitness.

1. GEOGRAPHICAL VARIATION IN BRITANNICUS

If the establishment of the differences which are now found between the mainland and island forms of Clethrionomys has been the result of natural selection, the voles from the mainland would be expected to be variable for the distinguishing features. The climate, vegetation and, in general, the fauna of the West Coast of Scotland is similar to that of the Inner Hebridean Islands, on which erica and alstoni are endemic. If the voles in these localities are similar to specimens from the islands, it would support the theory that the latter have evolved from the ancestors of the former (Steven 1953), rather than the theory that progenitors of the *nageri* stock were cut off when Mull and Skomer were isolated (Hinton 1926, Zimmermann 1950) and have remained there as relatively unchanged relicts. A pre-requisite for genetical adaptation to local conditions is the restriction of gene interchange with any large population not subject to the same selective forces. On the West coast are a number of peninsulas where bank voles live, which, from the distribution of sea and unsuitable mountainous country, seemed to be more or less isolated from other bank vole populations. Trapping in Kintail, in the neighbourhood of Raasay, did not procure any *Clethrionomys* (author's observation, 1954), nor did trapping in Storr, further North (Edinburgh University Biological Expedition 1955).

In 1955 *Clethrionomys* was found to be common in Kintyre, the longest and most constricted of the West Coast Peninsulas (Figure 1). The character which the island races certainly share, and which distinguishes them most clearly from the collections of *britannicus* about which information is published, is their relatively large body size (Steven 1953). Weight was chosen to determine body size because its measurement is less liable to variation due to the idiosyncrasy of the observer than is body length, which is subject to errors in the degree of stretching, particularly if some specimens are alive and some dead. Weight is probably more sensitive to seasonal fluctuations in environmental conditions than are linear dimensions, and therefore the sample of the mainland population used for comparison was one collected at the same time of year (September-October), although this was small (Table 18). The Kintyre collection had a greater mean weight than that from the Edinburgh district (P less than .001, using a t-test). It was also more variable (P less than .05). The significance of the difference in size should be regarded with caution as the t-test used in estimating it is not strictly valid for populations of different variability.

In order to confirm this finding, the sample of britannicus from the published data (Table 18) which had the largest mean weight (that from Reigate) was chosen to compare with the Kintyre collection. The published report did not state which estimate of spread was used, but if we assume that it was the standard deviation of the mean, which would be least favourable for establishing a difference between the means, the difference was significant at the 1% level.

The island race closest to Kintyre, geographically (both are in Argyllshire) as well as in body size, is alstoni. The difference in their mean weights (Table 18) is not significant (P greater than .1).

Kintyre britannicus resemble the Hebridean races in colour as well as size. They are darker than those from most of the mainland, and do not have the characteristic patch of brighter red on the back. Geographical variation in the colour of bank voles has been reported by Matheson (1936).

Discussion

It is not clear why the britannicus from Kintyre were found to be more variable in size than those from Edinburgh. The two most likely explanations are: (i) That the samples differed in age distribution. Most individuals alive in the autumn are under a year old (Section VII, 3,B). If the bank voles start breeding earlier in the year in Kintyre, there is likely to be a greater variance in age in the autumn there. This is not supported by a study of the breeding seasons of

Clethrionomys in captivity, which did not however include animals from Kintyre (Steven 1957). (ii) That the difference in variability is the result of a difference in genetical diversity for factors influencing size, or to a genetically determined difference in sensitivity to environmental variation. This distinction is comparable to that between the greater variability of an F_2 than of its parental inbred lines, and the greater variability of one inbred line rather than another, for some character (Gruneberg 1954, Michie and McClaren 1954, 1956, Yoon 1955). Tantawy (1956) has found that intensive selection of an outbred population for a metrical character is accompanied by a fall in fertility, with recovery when the selection is relaxed. The difference between these sorts of genetical determination would be difficult to establish experimentally, and is not important for the present purpose. If either were involved it would suggest that selection for size is less rigorous in Kintyre. Falconer (1953) found that large size and high reproductive rate are correlated in mice. If this is applicable to voles, then relaxation of selection for small size is likely to be followed by an increase in size. Small size is probably an advantage in escaping some predators. Small voles, and small laboratory mice, are more successful in escaping from man, and may well be from smaller mammals.

A common feature of the environmental pressures exerted on the island races, and on the britannicus living in the Kintyre peninsula, may therefore account for the large size of all of them. Schmalhausen (1949) and others (Simpson 1949, Lerner 1954) have distinguished between directive selection, and stabilizing selection. Directive selection for a character will tend to accumulate genes which favour the development of individuals differing phenotypically in the appropriate direction from the population mean. It is possible that it will also increase the frequency of genes which render the animals carrying them more sensitive to those environmental factors which modify the expression of the character under selection (Haldane 1931, Robertson 1956). This effect has not been found by Falconer and Robertson (1956) in their study of variability in the body size of mice, although the stabilizing selection exerted on their controls made some progress. Karn and Penrose (1951) have demonstrated the elimination of extreme individuals from a population. Haldane (1954), in discussing the measurement of natural selection, says "In all the cases considered selection reduced the variance, that is to say it was of the type described as stabilizing or normalizing. Probably almost all natural selection for a quantitative character is of this type" It follows that the variance of a character is likely to increase if the action of selection on it is relaxed.

2. ECOLOGY

A. Predators, competitors and ecological specialization

Cover is a major factor determining the population density of bank voles (Sviridenko 1945), possibly acting through predators. Owls eat most mice early in the year when the ground is least covered (Southern 1954). The selection pressures exerted by different categories of predator will favour different phenotypes in the prey species. The tameness of the voles from Skomer may be associated with the absence of mammalian predators from the island; it is possible that an attempt to escape by a vole, when it becomes aware of a predator, has survival value if the predator is a mammal, but not if it is a bird approaching at a much greater speed.

In the course of trapping Clethrionomys, for study in the laboratory, some information has been gained on the distribution of bank voles between habitats, and on the other small mammals found in them. As will be seen from Table 19 and 20 britannicus is most commonly found in mixed country. Plates 43 and 44 show the area where the highest catch rate of britannicus was obtained. Microtus was most frequently found in open grassland. Apodemus was the commonest animal in woods.

On Skomer Microtus is not found, nor are there any trees. Apodemus sylvaticus and skomerensis are ecologically separated: the former occupies the higher ground without cover where Microtus would probably live if present on the island, and also the bracken areas; the latter is the dominant species in the lower lying central areas, where the vegetation is more luxuriant. (Figure 23, plates 45 and 46, and Table 21, and Phillips 1950). Kalabukhov (1938) reports that Apodemus sylvaticus, but not A. flavicollis, can be found in habitats without tree or bush cover, and considers this to be associated with the strictly nocturnal habits which the former alone has. He finds, in the laboratory, that mice of these species select habitats designed to mimic those in which they occur naturally. A similar demonstration of a difference in choice between habitats has been demonstrated by Harris (1952) for prairie and forest races of Peromyscus maniculatus, although in these mice the stimuli which are most important in the discrimination of habitats are tactile rather than visual. It has been argued by, for instance, Miller (1942), and Waddington, Woolf and Perry (1954), that such reactions to the environment are important in evolution.

The geographical differences in the amount of diurnal activity found in Clethrionomys may be due to gene substitution (Bastock 1956, Waddington, Woolf and Perry 1954), or to traditional differences (Cushing 1941). They cannot be a direct response to an environmental switch, because they persisted during prolonged captivity. This does not mean that response by an individual to seasonal change may not be important in a given locality. It would be necessary to rear bank voles, from different localities, bred in captivity by litter exchange, in order to find out what is the developmental cause of the difference. Miller (1955, and personal communication) found that the britannicus from Wytham Wood, near Oxford fall into two categories for activity rhythm, one Microtus-like, and one Apodemus-like; this suggests a genetical switch.

B. Feeding and Drinking

(i) Food preferences

In view of the different environments in which the races of Clethrionomys live, both in terms of plant communities and of competitors, it seemed quite possible that differences between them in food preference might be found. Ritchie (1951) was able to define some differences in food habits between Clethrionomys and Microtus in the laboratory. Microtus co-exists with britannicus and alstoni but not with erica or skomerensis. It seemed possible that the latter races might be less distinct from Microtus, in these respects, than the former. Microtus feeds mainly on grass.

The mean consumption of several foods by the British forms of Clethrionomys, when fresh grass was available ad lib., is shown in Figure 24. No marked difference between the races was found. In a subsequent experiment, in which the fresh grass was not given, the result was similar.

Miller (1954) found only slight differences, using more refined methods than the one employed here, between britannicus and Apodemus sylvaticus living in the same wood. In Russia the local representatives of these animals are apparently more distinct (Sviridenko, 1940), although the Slovakian Clethrionomys (Turček 1953) has similar food habits to the British form. In birds differences of a subtle kind between related species can be ecologically significant (Lack 1944, 1947). It is not concluded, therefore, that differences in feeding habits between the races of Clethrionomys would not be found by another method. A field study would be necessary to settle this point.

(ii) Quantity consumed

The data presented in Table 22 do not suggest that there is a quantitative difference in food intake between the races. This is confirmed by records kept of food consumption during other experiments. As britannicus has about two thirds the body weight of the other races (Table 18) this may mean that the island races have a lower metabolic rate.

The hybrids apparently have a greater food consumption than the parent races. This is not certain, however, as they scatter uneaten, or partly eaten, food about to a greater extent, which makes it more difficult to isolate the remains in order to determine how much has been eaten. In particular the turnip is often bitten into chips which must lose weight more rapidly, by evaporation, than would a lump.

(iii)Food storage

Voles carry food, particularly corn, to a habitual part of the cage. As has been mentioned by Schleidt (1950), there is a sexual dimorphism in this behaviour - females normally carrying food to their nest, but males making several stores in other parts of their cage. There was considerable individual variation in this habit, but in britannicus it is rather more pronounced than in the island races, and in rutilus and norvegicus decidedly more so. In other rodents environmental factors are known to elicit the storing of food (Miller and Viek 1944, Bindra 1947). It is probable that temporary deprivation, as would occur in the wild, would increase the tendency of bank voles to store food. Possibly the difference between the races which has been noted is due to a variation in the sensitivity to transient deprivation, although in the same environment large differences between inbred lines can be observed (Stamm 1954).

C. Nest building

Clethrionomys which it was hoped would breed were kept in cages out of doors (plate 47) with only a sheet of glass immediately over them for shelter from the rain. Within the cages were peat moss, about two inches deep, and hay, which was used in the construction of the nest. Also available for this purpose was grass and the outer layers of turnip, both of which were added regularly as food. The cages were left undisturbed for about three months, except for routine inspection for litters, and occasional capture of voles for examination. Over a period of time cages became riddled with runs and tunnels on and within the litter. Nests were constructed of shredded hay and grass in the form of a hollow ball.

All the British forms of Clethrionomys normally made such nests at the bottom of the cage. If the peat moss litter was at all deep, the nest was below ground level. The nests of rutilus and rufocanus had thicker walls, the outer layers of which were of coarse, unshredded hay stalks. As the level rose, due to accumulation over a period of weeks or months of chewed bedding, faeces, corn husks, uneaten turnip, and corn, which sprouted if part of the cage were damp, the nest was kept at the surface. The nest was usually built on a substrate of dried turnip rind, and was often rather above the general level of the litter, and covered, if at all, by loose hay only.

(i) Bed shredding. There is a sequence of actions very regularly performed by a vole in the manufacture of its nest. It will be described as it occurs in the cages used for measuring rhythmic behaviour, as it is most readily observed when it occurs there. The animal leaves the nest box and stands across the entrance to it, often with the fore paws inside the box, and then, turning its head into the nest box, seizes a piece of bedding material, usually a stalk of hay, with its teeth and fore paws. The head is turned and lifted rapidly away from the paws, so shredding the stalk longitudinally.

The piece of bedding is dropped in front of the vole. This sequence of actions is repeated several times very rapidly. The vole then enters the nest box with the shredded material, deposits it on the inside of the nest under construction, and, typically, leaves, to repeat the series of actions. Such a performance makes a characteristic pattern on the record of excursions from the nest (see Section IV, 2A). This action pattern is probably that termed "Abstreifen" by Schleidt (1950).

The results are shown in Figure 25, which also mentions the criteria used for scoring bed shredding performance. It should be noted that the method of scoring would tend to make a low estimate for animals performing the activity in short or irregular bursts. It was found that bed shredding performances was very irregularly distributed between the races of *Clethrionomys*. Unfortunately the number of individuals of the Norwegian forms is small, but it seems clear that they perform bed shredding more frequently than do the British bank voles, and much more frequently than any but the *britannicus* from Edinburgh. Only one individual of a cross between a Norwegian and a British vole was studied, a *norvegicus* x *alstoni* hybrid. This animal showed a shredding rate similar to that of the *norvegicus* parent.

(ii) Discussion

It is suggested that the differences between the British and the Norwegian, especially the high arctic *rutilus* and *rufocanus*, forms of *Clethrionomys* in nest construction, and in the frequency of the bed shredding sequence of actions, which have been described, can be understood as adaptations to the conditions in which these animals normally live. The colder climate is probably the major determinant, but it cannot account for the building of the nest above the general ground level by *rutilus* and *rufocanus*. It is possible that the habit functions, in the natural tundra habitat, in avoiding the danger of the nest being flooded. When the tundra thaws, during the brief summer breeding season, the land, which is flat and peaty, becomes waterlogged. The higher score for bed shredding found in *britannicus* from Edinburgh than in voles studied from other parts of the British Isles may be associated with the colder winters found in their place of origin. If these factors are the ones ultimately responsible for the differentiation, within the genus, of nest construction behaviour, it is clear that they are not necessarily involved also in the ontogeny of it. *norvegicus* individuals behave similarly whether or not they have themselves lived in Norway. Litter exchange would be necessary to determine whether or not the crucial factor is inherited genetically. Ross, Denenberg, Sawin and Meyer (1956) report that variation in nest construction between different breeds of rabbit are greater than the changes resulting from experience of building.

Although litter exchange experiments could distinguish between these possibilities if one, or the other, were the case, it is not necessary that a clear cut answer would be found. It may be that there is a genetically determined difference in receptivity to parental influence. That is to say, the lack of appearance of a character on fostering, in an animal which would normally develop it, need not necessarily be expected to be accompanied by the appearance of the character as a result of the reciprocal fostering.

3. THE EFFECT OF RACE CROSSING ON FITNESS

The breeding performance of the races of Clethrionomys in captivity can not be expected to yield useful information about the adaptation of these races to their native environments. In the first place, the relative fitness of the races would almost certainly differ according to the methods used for breeding and maintaining them (Haldane 1946, Falconer 1952). In the second place, evidence will be presented that the force of mortality differs greatly between a particular wild, and a particular captive, environment. The interbreeding that can be induced between members of the races does make it possible to obtain information on the difference in range of genetical constitution between the races. A gene will tend to become common in a group of interbreeding individuals if it is of selective advantage in a high proportion of them. Genes which frequently meet in zygotes can be expected to modify one another's action so as to lead to the development of phenotypes acceptable to natural selection.

One method of keeping groups of genes together which make particularly happy combinations, in a specific range of environments, is that of chromosomal inversion.

This is not likely to be found in mammals (Haldane 1957), although known to be important in Drosophila (Dobzhansky 1947, Dobzhansky and Levine 1951). Linkage is probably of wider importance. Sheppard (1953) notes that genes determining polymorphism are more frequently linked than one would expect by chance. He suggests that natural selection will favour translocations bringing genes with benificient interactions onto the same chromosome. It is suggested that speciation can be considered as another method of facilitating the evolution of co-adaptation: one that does not have the disadvantage of reducing the potentiality for further evolutionary change that results from the adoption of a mechanism which inhibits genetic recombination between members of a Mendelian population (Carson 1955 a and b).

A. Information on breeding and length of life in captivity

(i) Method

Matings were made in an attempt to maintain a stock of each race except britannicus, which could be obtained locally, and to make hybrids of various kinds between them: F_1, F_2, first generation backcross, and a few F_3 hybrids were obtained. The breeding colony was kept, between June 1950 and July 1956, in twenty-four large cages in the open air (plate 47), with abundant food, bedding and peat moss litter (Steven, 1957 a and b). The records, most of which were those of D. M. Steven, were analysed as follows:-

Total length of matings of a particular type - as number of females x number of years. Most matings were between one male and two females.

Birth rate - as young per female per year. The number is a low estimate due to loss before the litter was seen, and subject, therefore, to error due to differences in survival from birth to recording age. Similarly weaning success (number weaned/number born) is overestimated.

Age - all animals born in 1955 or earlier, even if still alive at the final census were included. If no record of the date of death could be found, the last date on which they were known to have been alive was used as an estimate of their day of death. This was an underestimate, but these animals were longer lived than the average, as animals that died young could almost always be traced to their death. Their exclusion from the results would have biased the mean age toward zero.

(ii) Reproduction

Matings between animals of different races produced 1.7 litters per female per year (in 35 female years) which is a little more than matings within a race, which produced 1.4 litters per female per year (in 116 female years). Matings between hybrids had more frequent litters; 2.7 per female per year (in 33 female years).

The mean litter size produced by hybrid matings was larger: 4.1 (60 litters) as opposed to 3.3 (159 litters); but the litters of the F_1 young were smaller - 2.7 (on 89 litters). This low productivity of young may be due to a maternal effect on litter size, as hybrid females backcrossed to pure race males produced a mean of 2.9 young per litter (26 young), although the reciprocal backcross produced 3.6 young per litter (43 young).

The hybrid matings had a greater weaning success: 84% of the 243 young born were weaned, whereas the pure race matings reared 69% of 523. The F_2 matings reared 61% of 238 young. The effect of these differences, measured as the number of juveniles produced per female at weaning age (3 weeks or a little over, depending on the size, and apparent vigour, of the young) was 5.9 for the hybrid matings, 3.1 for the intra race matings, and 4.5 for the F_2 matings.

The distribution of litter sizes for matings within races is shown in Figure 26. Four was the commonest number of young, but litters with a greater number were less frequent than those with fewer young. The litters that were larger than normal were more productive of juveniles at weaning age; the optimum litter size may be near to, or even higher than, the maximum litter size that was found. The expectation of weaning improved with litter size (Figure 27), up to about 6 (from information on 523 young). The expectation of weaning for young which were F_1 hybrids (N = 238) was higher, but was not affected so much by the size of the litter in which they were born. When adult, however, the F_1 hybrid animals were less successful at rearing litters of more than five (Figure 28 based on 761 offspring of pure race parents and 81 offspring of F_1 hybrids).

(iii) Length of life

The mean expectation of life of an F_1 hybrid at weaning is 6 months, and an F_2 hybrid 5 months, compared with a mean of 8 months for individuals belonging to the uncrossed races. The mortality of animals after weaning is illustrated in Figure 29. At birth the mean expectations of life are 5, and 2 months, respectively, for the F_1 and F_2 hybrids, but 6 months for the pure race animals.

The significance of the differences in mortality curves has been tested by the maximum likelihood method (see appendix A). The probability of an F_1 hybrid animal dying between one age interval and the next is significantly greater than the probability that a member of one of the races of Clethrionomys will do so. The force of mortality acting on the F_2 is slightly greater than that on the F_1 hybrids ($P = .05$).

Hybrids were more frequently noticed to be fighting than were other bank voles. This probably contributed to their shorter expectation of life. Fighting was rarely sufficiently acute to have been recorded as the cause of death of a vole however. All cases in which juvenile voles were recorded as having so died within a week of weaning involved the hybrid offspring of skomerensis females (Table 23). That such deaths occurred more often when the skomerensis parent of the hybrids was the female is significant (P less than .01). The way that the cross had been made had no apparent effect on the expectation, at birth, of weaning among the skomerensis hybrids which were produced.

B. Information on mortality in wild populations

In order to estimate the effect of captivity on the fitness of bank voles it seemed worthwhile trying to make a rough comparison of the life table in the laboratory with that in the wild conditions to which voles have presumably become adapted.

In a small patch of woodland, in agricultural land at Wytham, near Oxford, intensive live trapping for small mammals was carried out at two-month intervals between September 1948 and September 1952 (Southern, unpublished[x]). The interval between the first and the last time that each bank vole, first caught before September 1951, was trapped has been obtained from these data. The bank voles first caught during the last year's trapping were omitted, because of the possibility that they were still living after the work had been discontinued. Not more than the last year's newcomers were left out because, from the data published by Turček (1953), it seems clear that few bank voles live much more than a year (Figure 30). The distribution

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[x] Mr. H. N. Southern has kindly given me access to his data on <u>Clethrionomys</u> which were caught and recaptured during this survey. He is naturally not responsible for any errors in my analysis, or wrong conclusions to which I may have come.

of weights is strikingly bimodal in the earlier part of the breeding season, but the heavier weight class, presumably representing the animals born in the previous year, has disappeared by September. This is confirmed by a study made in Scotland (Corbet, unpublished).

From the weight of animals when first trapped it appears probable that most of the animals used were caught when young. The data are shown in Figure 31 in comparison with the frequency with which various ages were obtained by Clethrionomys in captivity. If the Clethrionomys in the wild died soon after they were last known to be alive, it is clear that the force of mortality is greater in the field than that imposed upon domestic bank voles.

The chance of a vole surviving from one two-month period to the next has been estimated as 0.54 by the method given in appendix B; this is significantly less than the probability of 0.78 estimated from the captive material.

Howard (1949) found that less than one fifth of a population of Peromyscus maniculatus bairdii reached sexual maturity, and he doubts if any attain old age.

Predation, and cold weather accompanied by a shortage of food, appeared to be the principal causes of this high mortality. Blair (1948) estimates that the mean life span of this mouse is 4.88 ± .20, although in captivity many survive for three years of more. Under optimal conditions, in the laboratory, rodents commonly continue to live in age classes not known to be represented in the wild (Leslie and Ranson 1940, Leslie, Tener, Vizoso and Chitty 1955). The death rate among small birds is well known to be so high that evidence of senility (Medawar 1952) in the wild is lacking (Haldane 1953 b). This is probably true of small mammals also.

C. Discussion

(i) Significance of litter size

As deaths of female Clethrionomys were rare during pregnancy, or while rearing young, it is surprising, at first sight, that the mean litter size is much less than that which was most productive. The proximate determining factors are presumably physiological; what the ultimate significance may be is suggested by comparing the environmental pressure exerted on the captive animals, to which the figures apply, with that likely to have been exerted on their ancestors in the wild. The selective value of various litter sizes probably varies from season to season and year to year (Chitty 1952). The mechanisms determining the size of particular litters may not be geared to aspects of the environmental situation which are correlated with its selective effect on litter size, as they are in short eared owls (Elton 1942, Lockie, unpublished). At any rate the litter size at birth, in captivity, is closely similar to the mean late foetus number of 4.1 (with a maximum of 6, in 70 late pregnancies) found for animals in the wild by Brambell and Rowlands (1936). If the litter size is stable to environmental fluctuations it would be expected, on grounds of evolutionary expediency, to approximate to that which is optimal in the wild (Lack

1948 a and b, 1954, 1956). Food was available in abundance in captivity. This may have increased the chance of large litters being reared successfully, and would be expected to have done so from the extensive work on birds (Lack, *loc. cit.*). The longer breeding season of bank voles in captivity (Steven 1957a) than that which has been recorded as normal in the wild (Baker 1930, Brambell and Rowlands 1936) is in accordance with this interpretation, as is the evidence (presented in this section) that the expectation of life is better in captivity.

(ii) Inbreeding on islands and in captivity

Mayr (1954) has argued that the colonization of island habitats involves adaptation to an increase in the rate of inbreeding. This is likely to make island races preadapted to captivity, in which inbreeding also occurs (Spurway 1955a). From the work of Carson (1955 b), it seems possible that marginal populations are also more adaptable than the more genetically specialized central populations. One is lead to predict that the mainland animals would be the least fit in the environment of captivity, and that the animals from Skomer would do best. Skomer has an area of about one square mile. Raasay is about thirty times this size, and Mull three hundred times as large. The data on the races taken separately, and particularly on britannicus, is not felt to be adequate for a satisfactory test of this hypothesis, but it is suggestive that britannicus females give birth to fewer young per year than the mean for all races (P less than .05), whereas skomerensis had more offspring (P less than .001).

(iii) Hybrid vigour and hybrid breakdown

The effects of hybridization on the components of fitness that are expressed early in the life of bank voles is different from that which it has on animals later in life. Hybrids are born in litters which are, in general, larger than those of the parental races, and the young survive better to weaning age, but after this they have a lower expectation of living from one age group to the next, and are less successful at rearing large litters.

Mayr (1942) considers that although hybridization indicates relationship, the fertility of the offspring does not indicate the degree of relationship. Sterility of hybrids between geographical races, of Cobitis taenia, has been demonstrated by Miamori (1950), and yet Hubbs and Strawn (1956) have found the hybrids between two sympatric species of fish to be as fertile as the parental types, and hybrids among species and genera of the Ethiostominae, to show heterosis for viability (1957 a). The differences in criteria used to classify groups of animals makes this result difficult to interpret. Working with local populations of *Drosophila pseudoobscura*, Vetukhiv finds that the viability (1953) and fecundity (1956) of F_1 hybrids is improved, but that hybrid breakdown follows in subsequent generations; and that this transient heterosis is not found when geographically remote, or isolated, populations are crossed. Liu's (1953) data on prenatal mortality in *Peromyscus* show a higher foetal death rate in species hybrids than in their parental races, but, although he does not himself conclude this, intra-uterine heterosis in sub-specific hybrids.

Maynard Smith, Clarke and Hollingsworth (1955) argue that both excessive inbreeding and distant outcrossing may lead to a breakdown of developmental homeostasis. It is well known that inbreeding usually leads to a decrease in fertility and vigour (Reeve 1957). The situation described in *Clethrionomys* suggests that the optimum degree of outbreeding may vary during the process of individual development. This may be due to a change, during ontogeny, in the sensitivity of an animal to the two conflicting results which follow outbreeding.

Firstly heterozygosity is increased. This will tend to result in the masking of deleterious or lethal genes, which are usually recessive in the natural populations in which they are known to be common (see Zimmerman 1941 for Clethrionomys, Dobzhansky, Holz and Spassky 1942 for Drosophila, and Penrose 1957 for man), by the relatively dominant alleles which are normally more frequent in a species (Haldane 1930, 1939). In so far as each allele of a heterozygous pair produces its product independantly, it is becoming generally accepted (Robertson and Reeve 1952) that the biochemical diversity resulting from this is likely to be associated with a versatile phenotype. Some heterozygotes can however, synthesize substances not found in either homozygote (Wurmser et al. 1953, Miller 1956). This is discussed by Haldane (1955), and has been investigated by Maynard Smith (1956) who finds that hybrids between inbred lines have a greater capacity for regualtion during development than do inbred animals.

Secondly, the crossing of populations results in the disbanding of different groups of genes, which accumulated in each population during evolution because they often led to the development of fit individuals. The great variability of the F_1 hybrids between Ethiostoma spectabile and Percina caprodes (Hubbs and

Strawn 1957b) may be due to breakdown of such coadapted systems. Interactions between alleles, leading to the suppression of unfavourable traits, is one way that deleterious mutants may have become recessive in the course of repeated appearance in a population (Fisher 1928). These may express themselves when the gene background is changed.

The distinction which has been made here, is similar to that of Dobzhansky (1950), who termed the adaptively acquired aspects of hybrid vigour, euheterosis; and phenotypic increases in size, or some other trait, in heterozygotes, which can not be ascribed to the work of natural selection, luxuriance.

Some evidence has been presented here that hybrids may resemble neither parental race, nor be intermediate between them. The most striking examples are the lack of discrimination by hybrid males between potential mates, and the absence of a short term activity rhythm in hybrids. Tebb and Thoday (1956) have shown that the females of two strains of Drosophila both prefer males marked by one of a pair of alleles, but that their hybrids prefer males with the alternative allele. Few comparable results have been reported. A possible explanation of this is that most of the rather small number of studies which have been made sought behaviour characters determined in a simple Mendelian way. There is no evidence that the behavioural novelties which have been reported are of selective advantage to the hybrids in which they were found.

Lorenz (1941) describes how the sexual inciting behaviour of a female *Mareca sibilatrix* x *Anas platyrhynchos* hybrid closely resembled that of *Chaulelasmus strepera*, although the rest of its behavioural repertoire did not. Poulsen (1950) states that a hybrid between a domestic duck and goose has morphological and ethological characteristics of both parents, but is sterile. This may be due to a change in the response to hormones, as specifically sexual behaviour could not be induced, even when injections were given that were known to be effective in producing sexual activity of immature, or castrated, normal birds.

Spurway (1953) reports that F_2 hybrids between subspecies of newts form a rigid peck order, that is not found in either parent, if more than four individuals are kept in one tank, and that this impairs the normal development of the subordinate individuals. On the other hand Clarke, Arenson and Gordon (1954), studying the hybrids between *Xiphophorus maculatus* and *X. helleri*, have found intermediate behaviour in the F_1 for characters distinguishing the species. Similar results were obtained by Hinde (1956b) working on Carduelinae finch inter-species F_1 hybrids, and are general in birds (Hinde *loc. cit*). He concludes from the similarity of the hybrids for characters which do not differ between the parental species, that these features depend on similar hereditary factors. He says that if the similarity were superficial (i.e. that the characters were not homologous, see below) then hybrid breakdown in complex responses would be expected. From the intermediate behaviour of specific characteristics in hybrids he concludes that the differences are due to multiple genes with similar effect - this he considers evidence for the adaptive origin of the characters. When the species differ widely the hybrids show evidence of dominance, or of breakdown.

It is suggested that the later developmental stages, particularly when social interactions between individuals become important, are most sensitive to the disruption of co-adapted systems which is one result of crossing between relatively isolated populations. If the adaptive significance of a piece of behaviour lies in the specific response it induces in another individual, then any large change in it is likely to prove disadvantageous, even if it would be of advantage were it performed in the presence of an audience of another species. Similarly, it seems probable that the recently evolved characters, distinguishing populations which are sufficiently closely related for viable hybrids to be produced between them, are the ones most likely to undergo hybrid breakdown. This argument is a corollary of that used by

Hinde (1956b) in support of the use of motor patterns as indicators of the historical affinity of groups of animals.[x] He says "With complex behaviour which is similar in the parent species, the whole organization of motor patterns and associated motivational conditions is likely to depend on basically similar hereditary factors

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[x] Lorenz (1941) has used similarity of the form of movements as evidence for the common ancestry of the animals showing them; and this method has been generally accepted as valid. Lorenz argues that display movements are conservative features in evolution. Independent evidence in support of this is lacking. Blest (in press) shows that convergence has been important in the evolution of protective displays in the Saturniidae. but Faber (1953) has shown that, although most of a group of the Orthoptera produce two types of song, by stridulating a tympanic membrane with the hinde legs, one species produces the same song patterns by movements of the mandibles. Although the hind legs do move at these times they do not cause the sound production. Less easily observed differences in the development of behaviour are likely to be missed. This suggests that the genetical control of homologous structures may become changed (Harland 1933, Spurway 1949); that is, two related animals may develop a character, which they share with their common ancestor, in different ways.

in each case. If the similarity were only superficial (i.e. characters not homologous), then the complex mechanisms leading from stimulus to response would be likely to break down in the hybrid".

If this argument is valid, one can expect some of the differences in behaviour between hybrids, and bank voles belonging to a pure race, to be related to the higher death rate of the former. This difference in death rate is probably minimized by the hybrids being maintained in captivity, where the force of mortality has been shown to be less severe than that to which they would be subject in the wild state. For instance, the lack of regularity in the distribution of activity in hybrids may be associated with ill coordinated behaviour. The lack, in hybrid males, of olfactory discrimination between potential mates, would probably reduce the fitness of hybrids in natural conditions. It is unlikely that such highly specific behaviour would have developed in all the populations which were tested unless it had selective value. The increased tendency of hybrids to fight would probably be disadvantageous in most environments. Tinbergen (1951, p.177) has argued cogently that ritualization of aggressive behaviour is of selective advantage to individuals in a group.

The tendency for genetic interactions, which influence the ontogeny of characters, to breakdown in hybrids has been discussed. It is likely that hybrid offspring will be influenced differently by traditional factors also. As well as being less aggressive, <u>skomerensis</u> individuals did not show either of the submission signals found in other voles. Hybrid offspring of <u>skomerensis</u> mothers tended to die at weaning age as a result of fighting among themselves. The reciprocal cross led to less fighting and no deaths. It is suggested that the development of submissive responses depends on specific behaviour by the mother (Godfrey, in press).

VIII. GENERAL DISCUSSION

Recent European work on behaviour, which was reviewed by Tinbergen in 1951, has been concerned chiefly with instinct, and it seems worthwhile to outline briefly some of the problems associated with the use of this term. No attempt will be made here to summarize the literature as the views of workers in this field on a number of crucial issues are currently changing. 'Instinct' is almost always used so as to imply at least one of the following ideas, the first of which is descriptive, and the others to do with causation on three different time scales.

α-instinct. Instincts are behaviour patterns common to a group of animals. As animals in natural populations grow up in different circumstances, and are not genetically uniform, this implies that instincts are stable to the normal range of genetical and environmental variation. Variations in behaviour in response to age or sex are not however excluded. An α-instinctive movement is a fixed action pattern or Erbkoordination (Thorpe 1956). Spurway (1955a) quotes James (1890) as saying "Instincts are the functional correlatives of structure". Lorenz (1955) makes what is essentially the same point. It is this which renders instincts suitable as taxonomic characters (Lorenz 1941).

The apparent precision with which behaviour patterns may be adapted to the peculiar conditions of an animal's life is not easy to account for by the past accumulation of mutants which modified favourably the form which was taken by the equivalent behaviour in the animals' progenitors. This is the difficulty, pointed out so forcibly by Lamarkians, that a small step, which can be seen in retrospect to have been towards an obviously favourable end, may be of little or no selective advantage to the animals exhibiting it. Environmentally controlled differences in behaviour from a related animals may be of advantage to an individual. That is, learning may increase this individual's fitness. It is easy to see what advantage would be a gene increasing, if only slightly, an individuals chance of carrying out this learning process. As suggested by Waddington for comparable morphological situations a genocopy of the developmental process may occur: a less stringent set of environmental circumstances may become necessary. If this happens, a previously learned behaviour pattern may become α-instinctive in the sense that the conditions which are normally encountered during ontogeny by a group of animals may allow the development of the behaviour in question. It will then be a matter for experiment to inhibit the appearance of the behaviour. It can be investigated experimentally just how stable α-instincts are. Lizards normally have a twenty four hourly rhythm of activity. Hoffmann (1955) has shown that this behaviour appears in an approximately normal form even if the newly hatched young are reared in constant light or in constant darkness. It is probable that, if they were reared under cyclical illumination with a different periodicity to natural daylight, an abnormal rhythm corresponding to the experimental one would develop.

β-instinct. A number of terms to do with the origin of behaviour patterns during the life history of an animal, such as 'innate', 'genetically determined', 'unlearned', 'inborn' and 'inherited' are applied to instinct. These are often difficult to understand, and for the sake of clarity they are all taken to be coextensive. An example may help.

In his recent book on learning and instinct in animals, Thorpe (1956) reviews much of the work on the development of behaviour in mammals. His own view is that the pragmatic test for instinct in this order is the Kaspar Hauser experiment. He says (p.397): "Experiments upon the white rat have also provided a good deal of evidence about other instinctive behaviour patterns. 'Hoarding' - that is, retreiving into the cage or into a known territory and there, if possible, hiding food in excess of immediate needs - clearly has an innate basis in the rat, since no tuition from parents or elders is necessary to bring about its appearance (Wolfe 1939)." The use of this criterion is unsatisfactory from two points of view. Firstly, this usage is not in accordance with the discussion and definition of instinct given earlier in his work. The second consideration is far more serious; one of the factors often taken into consideration in defining instinctive behaviour is whether learning can be demonstrated to be important in its ontogeny. Hebb (1953), among others, has pointed out how unsatisfactory is the use of this concept. It is not possible to design an experiment to exclude the possibility that learning is necessary for the development of a piece of behaviour. The most subtle work along these lines has usually found that aspects of the environment, which would not have been thought, *a priori*, to be important, were so. Even if it were to be accepted that a condition for designating behaviour as instinctive is that it be unlearned, the Kaspar Hauser experiment would be inconclusive. The rearing of individuals in isolation from other members of the species can be expected to eliminate the development of traditions, which form only one category of learned behaviour.

Variability in most complex characters, such as temperament or intelligence, is due, as pointed out by Penrose (1954) for humans, to the interaction of the environment with a variety of genetical influences; a complex in which the components are very difficult to separate. It may be more profitable at the present state of knowledge to give an account of what behavioural changes follow genetically understood events, such as gene substitution (Bastock 1956), hybridization, or inbreeding, that to try to analyse the part inheritance plays in the developmental causation of particular behaviour patterns. The value of Kaspar Hauser and litter exchange experiments is that they allow the investigation of the part which tradition plays in the development of differences between animals.

It is possible to investigate what effect differences in the environment produce on the development of behaviour in otherwise similar animals; that is, what part learning plays. Similarly, one can hope to investigate what effect genetical differences between related individuals has in ontogeny. Unless there is considerable variation for a behaviour pattern within a population (that is, it is not an α-instinct) one cannot make an experiment to show whether or not it is a β-instinct.

<u>γ-instinct</u>. Instincts are often said to be purposeful or directive. If they have resulted from the action of natural selection on a lineage of animals in a relatively stable environment it is not surprising that instincts are adaptive (Dobzhansky 1956) in the sense of increasing the fitness, from an historical point of view, of individuals expressing the character. It is not a property by which a group of actions can be conveniently recognised as, so many properties of animals are adaptive.

<u>δ-instinct</u>. The concept of δ-instinct is concerned with motivation, and presents some of the most complex problems of behaviour. It will be considered only briefly here as voles do not seem to be particularly favourable material for its analysis. The factors

which are considered immediately responsible for the occurrence of an item of behaviour are sometimes used as criteria for instinctiveness. Thorpe (1956) distinguishes instincts from reflexes by the former being internally motivated; being due, that is, to internal or instinctive drive. By internal drive he means (p.14) the complex of internal states and stimuli leading to a given behaviour. If it is remembered that all behaviour is a physiological process, then the last part of the causal chain leading to the behaviour which one observes is clearly internal. Internal drive can not therefore be used to distinguish one category of behaviour from another. Although the proximate causation of behaviour is the concern of neuro-physiologists, it can also be investigated by other methods. Ethologists and psychologists have described models which they consider would generate behaviour resembling, in some critical respects, that of the organisms which they have observed (Lorenz 1950). These analogues are useful in so far as they suggest what properties of the system (such as reactive inhibition), which can be investigated by other methods, must underlie observable behaviour (Wells and Wells 1957).

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The polytypic genus Clethrionomys is particularly suitable for the investigation of two sorts of problem. Firstly, the bank vole races which have been discussed here show α-instincts which they do not share with one another. Reed, Williams and Chadwick (1942) have described a similar situation in Drosophila pseudoobscura, which has races and local populations each characterized by a different wing beat frequency. The fate which these α-instincts would have under changed conditions of natural selection depends on their developmental physiology. The appearance of the instincts of bank voles, but not of Drosophila, could be due to tradition. It might be thought that the behaviour of hybrids could be used to decide whether or not this is so. As it was found that there is a clear cut maternal effect in the inheritance of submission postures, it was suggested that they are traditional. This method is only useful however where a character is simply inherited (whether the difference in question is genetical or due to learning is not important). Where hybrids differ from either parent this could be due to a direct effect of heterozygocity on gene expression, or to an indirect effect of it on susceptibility to learning, or alternatively to confusion resulting from the abnormal environment of the animals. In order to find out how important the behaviour of its parents and siblings is to a maturing bank vole, it would be necessary to reciprocally exchange whole and part litters at birth between parents of one race and those of another, and to study the resulting animals. Suitable characters to observe would be racial recognition, rhythmic behaviour, and those individual and social behaviour patterns which differ in occurrence, or frequency of occurrence, between the races.

The second process which might well be investigated with the use of Clethrionomys is the selective improvement of a reproductive barrier between two sympatric populations.

The sexual isolation between the local races of Clethrionomys has, with the possible exception of that between the britannicus from Kintyre and those from Edinburgh, presumably arisen since they were isolated geographically from one another. This provides direct support for the theory due to Müller (1939, 1942) that sexual isolation is initiated by selection for the pleotropic effects of genes which modify sexual behaviour. Bastock (1956) has clearly shown that the mutation causing yellow body colour in Drosophila melanogaster also leads, in males, to abnormally short and infrequent bursts of wing vibration during courtship, and to a lack of success in fertilizing normal females. As she points out, this gene substitution parallels in its effects the differences in behaviour patterns which have been shown to distinguish closely related species of Drosophila (Spieth 1947, 1949), and provides a means whereby systematic changes in mating behaviour may become established in isolated populations.

Similarly, Waddington, Woolf and Perry (1954) find that habitat preferences vary in response to gene substitutions which were selected for their morphological effects. Variability for factors of this sort is probably widespread in natural populations (Knight, Robertson and Waddington 1956). The isolation of populations by distance, by ecological choice, and by sexual preference will tend to evolve together. Brown and Wilson (1956) suggest the term 'ecological displacement' for the selection of genetic variants which reduce ecological competition. Gause (1932) gave reasons to suppose that only species which do not compete, at least at some critical phase, can coexist indefinitely. Support for this has come from work on Drosophila (Merrel 1951), on graminivorous insects (Crombie 1945), and on birds (Lack 1944a, 1944b, 1945). It is probably because ecological specialization cannot normally be maintained among conspecific individuals in the same locality, that competition and aggression are often found between members of the same species.

Vaurie (1950) describes how Sitta neumayer, the rock nuthatches of Southern Europe and Asia Minor, are morphologically distinguished from the closely related Sitta tephronata of Central Asia merely by a difference in size; but how, in the Middle East, where the species overlap, much more striking differences are found. Here the species are distinct in bill length (which suggests ecological divergence), and the facial stripe found in each species elsewhere is lost in S. neumayer but broad and conspicuous in S. tephronata. Although no field study has yet been made of these birds, it seems likely that this mark is important in the species recognition which underlies their reproductive isolation. It was presumably facts of this sort which led Dobzhansky (1951) to emphasise more than did Muller (1939, 1942) the importance of natural selection in the origin of sexual isolation. He considered that isolation did not normally arise until insipient species, which had diverged when geographically separated, occupied the same locality once more and produced hybrids which were less fit than either parental races. Rendel (1945) and Koopman (1950) have demonstrated how susceptable is reproductive isolation to the action of selection. The development of this isolation may be stable to environmental change, as in that between Drosophila pseudoobscura and D. persimilis (Mayr 1946), or it may be readily modified by experience, as in that between strains of Lebistes reticulatus (Haskins 1950).

The effect of the racial discrimination which has been found among geographical races of Clethrionomys could be investigated in substancially natural conditions, using experimental populations of two races put together on an island not already occupied by members of the genus. At present the main unfulfilled requirement in bank voles is a satisfactory marker for distinguishing certainly between members of the races and their hybrids. Although there is disagreement about how speciation occurs, it is now generally held that it has a crucial phase of short duration (Dobzhansky 1951, Spurway 1953). This may be one of the few natural situations where directive selection (see VII, 1) rivals in strength that exerted commonly in captivity (Haldane 1954). As the inter-racial hybrids of Clethrionomys would probably be at considerable selective disadvantage in the wild compared with either of their parental races (VII, 3), it is possible that progress towards reproductive isolation could be observed.

IX. SUMMARY

1. Bank vole races from the mainland of Great Britain and those from the islands of Raasay, Mull and Skomer are morphologically distinct, but will interbreed if given no choice of mate, yielding fertile hybrids.

2. Members of each race were found to have a characteristic range of behaviour patterns which differed from that of the other races.

3. Geographical differences in rhythmic behaviour were found, both in the distribution of activity between day and night, and in the number of short term cycles during the twenty-four hour period.

4. The frequencies with which a vole occupied its favourite nest box, and defended it against intruders, were used as criteria for territoriality. Skomer voles were found to be markedly less territorial than the others. Cues from inside the cage, and from the nest itself, were less important than those from outside the cage in the recognition by a vole of its home site.

5. In small communities of voles from the same population there was a tendency for the members, especially if female, to be found in groups more frequently than would be expected by chance. This is considered to demonstrate gregariousness. Social groups consisting of a male and a female from the mainland and another pair from one of the island populations were less gregarious. The constitution of associations showed racial segregation. Males

from Raasay and Mull, but not from Skomer, were usually found in associations excluding the mainland male. Olfactory cues were sufficient for this racial discrimination.

6. The scent of female *Clethrionomys* was found to be sufficient for them to be recognised, by males, as females.

7. Male *Clethrionomys* approach females who originated from the same locality in preference to others.

8. No evidence was found that hybrid males discriminate between potential mates.

9. Male bank voles inseminate females of the same race more frequently than alternative mates.

10. A partially isolated group of bank voles were found to be larger and more variable than those from other parts of the mainland.

11. Matings made between races gave rise to more frequent and larger litters. The young produced had a higher expectation of weaning than did pure race babies. The hybrids were less successful at rearing large litters.

12. At all ages after weaning hybrids had a lower expectation of life than pure bred animals.

13. Reasons are given to suppose that this difference would be more marked in wild conditions.

14. *C. skomerensis* individuals did not show either of the submission signals found in other voles. Hybrid offspring of *skomerensis* mothers tended to die at weaning age as a result of fighting among themselves, but the reciprocal cross led to less fighting and no deaths.

It is suggested that the development of submission depends on specific behaviour by the mother.

15. The difference in the relative fitness of hybrids in early and in later life if considered in relation to heterosis and development.

16. Some problems of instinct and of speciation, which might be investigated using *Clethrionomys*, are outlined.

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Table 1 Collections of *Clethrionomys* used, or the ancestors of laboratory bred animals used

Name	Locality	Year	Number in collection
britannicus Edinburgh	Borthwick, Ratho	1949	10
	Bush Estate, Midlothian	1953	16
	Blackford Hill, Edinburgh	1954	7
	Morton Hall, Edinburgh	1955	12
britannicus Kintyre	Carradale, Argylshire	1955	10
	Carradale, Argylshire	1956	13
britannicus New Forest	Hampshire	1954	3
britannicus Whytham	Pasticks, Whythamwood Oxfordshire	1957	-
erica	Raasay	1949)	31
	Raasay	1952)	
	Raasay	1954	19*
alstoni	Mull	1949	3
	Mull	1950	30
	Mull	1955	16
	Mull	1956	8
skomerensis	Skomer	1949	31
	Skomer	1954	18
norvegicus	Bergen peninsula	1951	approx.12
rutilus	Rosta, Nr. Tromsø	1953	17
rufocanus	Rosta, Nr. Tromsø	1953	2

*including 9 conceived in the wild but born and raised in the laboratory.

Table 2
Test of the significance of some differences between groups of *Clethrionomys* in the frequency of occurrence of a particular rating for handling ability (see text, and fig. 2)

Type of vole	Compared with	For the rating number	Probability of the difference being due to chance
britannicus from Edinburgh	the rest	5	<.001
britannicus from Kintyre	*britannicus* from Edinburgh	1	<.001
britannicus from Kintyre	*britannicus* from Edinburgh	5	<.001
erica	the rest	4	<.001
alstoni	the rest	1	<.001
alstoni	*skomerensis* 1954 stock	1	>.900
skomerensis old stock	other than *skomerensis*	1	<.001
skomerensis 1954 stock	*skomerensis* old stock	1	<.001
britannicus x *skomerensis* hybrids	pure races	4	<.001
britannicus x *alstoni* hybrids	pure races	4	<.001
britannicus x *alstoni* hybrids	*britannicus* x *skomerensis* hybrids	4	<.100

Table 3 To show the reaction of voles to the lids of their respective cages being opened

RACE	Animal Number	FLIGHT REACTION		
		NONE	UP	DOWN
britannicus	1	7	0	12
	2	0	8	8
	3	5	3	22
	4	4	0	7
erica	1	5	14	5
	2	0	21	0
	3	4	18	4
	4	10	7	3
	5	13	1	2
alstoni	1	20	2	2
	2	5	4	1
	3	16	0	3
skomerensis	1	10	3	4
	2	21	0	6
	3	26	0	0
	4	23	1	2

Table 4

The entry of Longworth traps by Clethrionomys in captivity

	Not Caught	Caught
<u>britannicus</u>	16	7
<u>skomerensis</u>	1	12
<u>britannicus x skomerensis</u>	2	15
<u>britannicus</u> x <u>alstoni</u>	0	31

Table 5 I. ANALYSIS OF VARIANCE FOR RHYTHMIC BEHAVIOUR IN 28 *CLETHRIONOMYS*

A. GROUPS SEPARATELY

Group	Mean No. mins. with an excursion per period				l.s.d. where appropriate*	Standard error off mean
	Dawn	Day	Dusk	Night		
britannicus Kintyre	59.2	64.2	94.6	87.6	-	10.6
britannicus New Forest	37.7	23.7	28.3	52.0	11.3	3.3
britannicus Edinburgh	78.8	77.8	04.8	134.6	-	19.7
erica	57.5	32.0	35.0	58.5	-	8.1
alstoni	108.6	94.4	117.8	113.8	-	15.1
skomerensis	113.0	117.0	122.0	109.0	-	27.3
norvegicus	133.0	88.0	129.0	129.0	-	21.3
rutilus	130.0	113.0	112.0	77.0	-	22.3
rufocanus	68.0	48.0	64.0	106.0	-	24.6
Hybrids	83.7	45.0	78.0	120.3	40.3	11.6

*Least significant difference (5%) for those groups in which significant differences exist.

Table 5 II. ANALYSIS OF VARIANCE FOR RHYTHMIC BEHAVIOUR IN 28 CLETHRIONOMYS

B. ALL GROUPS (i)

	d.f.	s.s.	m.s.	F
Between groups	9	73509	8168	2.77*
Between animals within groups	18	53039	2947	-
Between animals	27	126548	-	-
Between periods	3	15918	5306	5.60**
Groups x periods	27	16973	629	-
Animals within species x periods	54	51145	947	-
Total	111	210584	-	-

Key: d.f. = degrees of freedom
s.s. = sum of squares
m.s. = mean square
* = 5% significance level
** = 1% significance level

Table 5 II. ANALYSIS OF VARIANCE FOR RHYTHMIC BEHAVIOUR IN 28 *CLETHRIONOMYS*

B. ALL GROUPS
(ii) Difference between group means

Group	Mean	Standard error	Number of observations
britannicus Kintyre	76.4	12.1	20
britannicus New Forest	35.4	15.7	12
britannicus Edinburgh	99.0	12.1	20
erica	45.8	19.2	8
alstoni	108.6	12.1	20
skomerensis	115.2	19.2	8
norvegicus	119.8	27.1	4
rutilus	108.0	27.1	4
rufocanus	71.5	27.1	4
Hybrids	81.8	15.7	12

Table of least significant difference (5%)

		No. of observations in the first mean			
		20	12	8	4
No. of observations in the second mean	20	36.0	41.6	47.7	62.4
	12	41.6	46.7	52.2	65.8
	8	47.7	52.2	57.0	69.8
	4	62.4	65.8	69.8	80.5

Table 5 II. ANALYSIS OF VARIANCE FOR RHYTHMIC BEHAVIOUR in 28 CLETHRIONOMYS

B. ALL GROUPS

(iii) Difference between period means

	Mean	Standard error
Dawn	81.0	5.8
Day	69.1	5.8
Dusk	90.1	5.8
Night	101.6	5.8

Least significant difference (5%) = 16.6

Table 6 Number of minutes during which named behaviour patterns were observed, in eight hour-periods, for several races of Clethrionomys

Name of behaviour	britannicus		erica		alstoni		skomerensis		TOTAL	
	R	V	R	V	R	V	R	V	Rs	Vs
Chase away from nest	46	9	31	13	18	4	11	1	106	27
Scuffling	13	0	18	2	0	0	0	0	21	2
Boxing	18	9	16	16	10	7	5	5	39	37
Pre-lunge position	17	4	16	4	11	3	1	1	45	12
Lunge	12	2	14	0	5	0	2	0	33	2
Hunched submission	0	0	0	21	0	3	0	0	0	24
Rigid submission	1	7	0	0	0	0	0	0	1	7

R = Resident male

V = Visiting male

Table 7 (i) Summed data for single race experimental communities

Aa	Bb	Total day records	Groups of animals found together in the morning														
			AaBb	AaB	Aab	ABb	aBb	Aa and Bb	AB, and ab	Ab, and aB	Aa	AB	Ab	aB	ab	Bb	none
b	b	45	39	2	0	0	4	0	0	0	0	0	0	0	0	0	0
e	e	46	14	3	8	0	0	8	0	1	2	0	0	0	7	0	3
a	a	25	16	2	0	3	0	1	0	0	0	0	0	0	1	0	2
s	s	51	11	1	2	2	15	1	0	4	2	1	1	3	2	5	1
O		167	80	8	10	5	19	10	0	5	4	1	1	3	10	5	6
E		167	2.6	7.8	7.8	7.8	7.8	7.8	7.8	7.8	15.7	15.7	15.7	15.7	15.7	15.7	15.7

Showing the total number of times particular types of association were found, and the expectation of these categories on chance grounds. A male and female are arbitrarily designated as A (male) and a (female), or as B (male) and b (female).

key: b = britannicus
e = erica
a = alstoni
s = skomerensis
O = observed
E = expected

Table 7 (ii) Summed data for bi-racial experimental communities

Aa	Bb	Total day records	Groups of animals found together in the morning														
			AaBb	AaB	Aab	ABb	aBb	Aa, and Bb	AB, and ab	Ab, and aB	Aa	AB	Ab	aB	ab	Bb	none
b	*e*	164	4	1	0	3	15	13	0	3	17	6	8	13	16	46	19
b	*s*	54	18	0	2	0	7	4	2	3	10	0	0	5	0	3	0
b	*a*	79	23	0	3	0	6	11	2	5	6	1	0	5	4	12	1
O		297	45	1	5	3	28	28	4	11	33	7	8	23	20	61	20
E		297	4.6	13.9	13.9	13.9	13.9	13.9	13.9	13.9	27.8	27.8	27.8	27.8	27.8	27.8	27.8

Showing the total number of times particular types of association were found, and the expectation of these categories on chance grounds. A male and female pair of the same race are arbitrarily designated as A (male) and a (female); or as B (male) and b (female).

key: *b* = *britannicus*
e = *erica*
a = *alstoni*
s = *skomerensis*
O = observed
E = expected

Table 8 (i) OLFACTORY CHOICE EXPERIMENTS, SERIES A.

The response of a male given the choice of a female of his own race (Female "A") and a female of another race (Female "B")

Male making the choice	britannicus 51			alstoni 102			alstoni 240/317			alstoni 240/317		
Female "A"	britannicus 256/407a			alstoni 240/313			alstoni 240/302c			alstoni 240/302c		
Female "B"	erica 227/283a			britannuicus 63			skomerensis 252/315			skomerensis 252/315		
Trial Number	Choice		Time before choice made in mins	Choice		Time before choice made in mins	Choice		Time before choice made in mins	Choice		Time before choice made in mins
	"A"	"B"		"A"	"B"		"A"	"B"		"A"	"B"	
1	+		2	+		22		+	90+37	+		10
2		+	1	+		3		+	42	+		4
3		+	3		+	2	+		25	+		4
4	+		6		+	4		+	32	+		90+1
5	+		5	+		5	+		8	+		6
6	+		9		+	14		+	16		+	15
7	+		2	+		82	+		1	+		5
8	+		½	+		¼		+	7	+		5
9	+		1		+	½		+	13		+	16
10		+	20		+	22	+		6		+	½
11		+	16	+		1	+		6		+	½
12	+		2	+		19		+	½		+	¾
13	+		1	+		1		+	1		+	21
14	+		1	+		4	+		1	+		4
15	+		1	+		4		+	36		+	½
16	+		½	+		1	+		½	+		1
17	+		6	+		1		+	18	+		1
18	+		2	+		18	+		10	+		1
19	+		½	+		5		+	4		+	½
20		+	14	+		1	+		2	+		5
21	+		18	+		1	+		2		+	2
22	+		¼	+		5	+		2	+		2
23	+		½	+		1	+		¼	+		1
24	+		1	+		1		+	¼	+		½
25		+	3	+		3	+		½	+		1
TOTALS	19	6	2h. 6¼	20	5	3h.40¾	13	12	1h.30+4h.31	16	9	1h.30+1h.48

Table 8 (ii) OLFACTORY CHOICE EXPERIMENTS, SERIES A. (cont'd)

The response of a male given the choice of a female of his own race (Female "A") and a female of another race (Female "B")

Male making the choice	alstoni 240/317			alstoni 102			skomerensis 239/303			skomerensis 239/303		
Female "A"	alstoni 240/302c			alstoni 104			skomerensis 252/314			skomerensis 252/314		
Female "B"	skomerensis 252/315			rutilus 231			britannicus 256/407			britannicus 256/407		
Trial Number	Choice		Time before choice made in mins	Choice		Time before choice made in mins	Choice		Time before choice made in mins	Choice		Time before choice made in mins
	"A"	"B"		"A"	"B"		"A"	"B"		"A"	"B"	
1		+	90+2	+		23		+	31	+		32
2	+		2		+	1	+		8	+		20
3		+	10		+	½	+		12	+		1
4		+	25	+		5		+	21	+		1
5	+		½	+		1		+	4	+		1
6	+		2		+	19	+		1	+		1
7		+	7	+		9	+		½	+		1
8	+		2	+		2		+	7	+		2
9	+		16	+		1		+	17	+		15
10		+	22		+	7	+		11	+		25
11	+		3	+		3	+		2		+	¼
12	+		½	+		1	+		1	+		¼
13	+		6	+		½		+	1	+		½
14	+		2	+		1		+	½	+		1
15	+		½		+	1		+	¼	+		1
16	+		¼		+	12		+	¼	+		¼
17	+		3		+	¼		+	¼	+		1
18		+	9	+		1	+		¼	+		8
19	+		3	+		6	+		1	+		11
20	+		1	+		2	+		3	+		10
21	+		4	+		1	+		7	+		2
22	+		6		+	9	+		4	+		4
23	+		1	+		1	+		½	+		6
24	+		¼	+		1		+	½	+		15
25	+		5	+		1		+	¾		+	½
TOTALS	19	6	1h.30+2h.12½	17	8	1h.49¼	13	12	2h.15	23	2	2h.39¾

Table 8 (iii) OLFACTORY CHOICE EXPERIMENTS, SERIES A. (cont'd)

The response of a male given the choice of a female of his own race (Female "A") and a female of another race (Female "B")

Male making the choice	skomerensis 252/315			skomerensis 252/315			skomerensis 252/315			rutilus 231		
Female "A"	skomerensis 222/278			skomerensis 222/278			skomerensis 222/278			rutilus 234		
Female "B"	alstoni 107			alstoni 107			alstoni 107			alstoni 240/317c		
Trial Number	Choice		Time before choice made in mins	Choice		Time before choice made in mins	Choice		Time before choice made in mins	Choice		Time before choice made in mins
	"A"	"B"		"A"	"B"		"A"	"B"		"A"	"B"	
1		+	28		+	78		+	1	+		78
2		+	23	+		17		+	6	+		23
3	+		½	+		41	+		4	+		30
4		+	1	+		9	+		1	+		1
5	+		2		+	2		+	2	+		2
6	+		4		+	16	+		1	+		4
7	+		1	+		23	+		1	+		½
8	+		10		+	5		+	1	+		1
9		+	3	+		¼	+		10	+		1
10	+		2	+		1	+		3	+		¼
11	+		2		+	14	+		3	+		¼
12	+		¼	+		½		+	½	+		¼
13	+		3		+	2	+		¼	+		¼
14	+		1	+		27	+		½	+		¼
15	+		6	+		12	+		1	+		¼
16		+	4	+		12	+		2	+		3
17	+		32		+	1	+		7	+		15
18	+		4		+	¼	+		1		+	27
19	+		¼	+		3		+	25		+	2
20	+		1	+		1	+		5	+		½
21	+		½	+		1	+		1		+	4
22		+	3	+		7	+		2	+		8
23	+		1	+		13	+		½	+		9
24	+		4	+		10	+		¼	+		20
25		+	11	+		1	+		3	+		5
TOTALS	18	7	2h.27½	17	8	4h.57	19	6	1h.22	22	3	5h.35½

Table 9 OLFACTORY CHOICE EXPERIMENTS, SERIES B.

The response of a male given the choice of a female of his own race (Female "A") and a female of another race (Female "B") but both females removed from the apparatus one hour before the experiment began.

Male making the choice	rutilus 231		
Female "A"	rutilus 234		
Female "B"	alstoni 240/317/c		
Trial Number	Choice		Time before choice made in mins
	"A"	"B"	
1	+		2
2	+		1
3	+		1
4	+		1
5	+		10
6	+		2
7		+	21
8	+		3
9	+		1
10	+		1
11		+	¼
12	+		½
13		+	½
14	+		7
15	+		2
16		+	1
17	+		1
18	+		1
19		+	13
20	+		1
21	+		1
22		+	¼
23	+		1
24	+		½
25		+	½
TOTALS	18	7	1h.13½

Table 10 OLFACTORY CHOICE EXPERIMENTS, SERIES C.

The response of a male given the choice of a female of his own race (Female "A") and a female of another race (Female "B") but both females removed and their boxes washed in soap and water before the experiment began.

Male making the choice	skomerensis 252/315			britannicus Kintyre		
Female "A"	skomerensis 222/278			britannicus Kintyre		
Female "B"	alstoni 107			britannicus 256/407b		
Trial Number	Choice		Time before choice made in mins	Choice		Time before choice made in mins
	"A"	"B"		"A"	"B"	
1		+	1		+	56
2	+		½		+	32
3	+		9		+	½
4	+		½		+	44
5		+	¼		+	5
6		+	¼	+		3
7	+		¼		+	8
8	+		1	+		1
9		+	¾	+		1
10	+		33	+		3
11		+	48		+	1
12	+		2	+		6
13		+	½		+	27
14	+		½	+		1
15		+	17		+	1
16		+	¼	+		10
17		+	½	+		1
18		+	1	+		4
19		+	¼	+		½
20	+		¼		+	1
21	+		½		+	9
22		+	4		+	12
23	+		¼		+	10
24	+		1		+	1
25		+	1		+	3
TOTALS	12	13	2h.3¼	10	15	4h.1

Table 11 OLFACTORY CHOICE EXPERIMENTS, SERIES D.

The response of a male given the choice of two females of his own race.

Male making the choice	<u>skomerensis 252/315</u>			<u>skomerensis 252/315</u>		
Female "A"	<u>skomerensis 239/323</u>			<u>skomerensis 239/323</u>		
Female "B"	<u>skomerensis 222/278</u>			<u>skomerensis 222/278</u>		
Trial Number	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins
1		+	7	+		1
2	+		15		+	3
3		+	1	+		6
4	+		20	+		2
5		+	10	+		2
6	+		11		+	5
7	+		¼		+	11
8	+		½		+	3
9	+		11	+		3
10	+		½		+	13
11	+		¼	+		1
12	+		13	+		2
13		+	9		+	1
14		+	7		+	1
15	+		1		+	4
16	+		1	+		1
17	+		5		+	4
18		+	3		+	2
19		+	2		+	1
20		+	¾		+	1
21	+		¼		+	½
22	+		8		+	½
23		+	1	+		1
24		+	5	+		1
25		+	1		+	¼
TOTALS	14	11	2h.13½	10	15	1h.10¼

Table 12 OLFACTORY CHOICE EXPERIMENTS, SERIES B.

The response of a male given the choice of two females of two different races not his own.

Male making the choice	britannicus 256/407		
Female "A"	erica 216/280		
Female "B"	alstoni 240/302c.		
Trial Number	Choice		Time before choice made in mins
	"A"	"B"	
1	+		1
2		+	10
3	+		½
4	+		¼
5	+		7
6	+		2
7	+		¼
8	+		¼
9		+	⅛
10	+		¼
11	+		4
12		+	24
13		+	¼
14		+	1
15		+	1
16	+		9
17		+	¼
18		+	¼
19	+		1
20	+		2
21		+	¾
22	+		6
23		+	14
24		+	½
25	+		2
TOTALS	14	11	1h.28

Table 13 OLFACTORY CHOICE EXPERIMENT, SERIES F.

The response of a male given the choice of a female of his own race (Female "A") and a female of another race (Female "B") but involving only *britannicus* animals (from Edinburgh, *britannicus*; and from Kintyre, *britannicus* kintyre)

Male making the choice	*britannicus* 51			*britannicus* 256/407			*britannicus* 256/407			*britannicus* 5 kintyre		
Female "A"	*britannicus* 256/407/a			*britannicus* 63			*britannicus* 63			*britannicus* 20 kintyre		
Female "B"	*britannicus* 19 kintyre			*britannicus* 18 kintyre			*britannicus* 18 kintyre			*britannicus* 256/407/b		
Trial Number	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins
1	+		1	+		20	+		1	+		90+7
2		+	¾		+	6	+		1	+		26
3	+		3	+		4	+		1	+		90+ ½
4	+		1		+	½		+	¼		+	4
5		+	3		+	½	+		2	+		8
6	+		1		+	1	+		1	+		3
7	+		6		+	¼		+	27	+		1
8		+	½	+		3	+		13		+	2
9	+		1	+		5	+		14	+		2
10	+		2		+	17	+		3		+	20
11	+		2		+	¼	+		¼	+		7
12		+	19	+		½	+		5		+	1
13	+		11	+		1	+		25		+	6
14		+	90+12	+		1	+		28	+		6
15		+	¼	+		1	+		22	+		15
16	+		11		+	1	+		8	+		1
17	+		1	+		19	+		15		+	23
18	+		1	+		¼	+		5	+		1
19	+		1		+	¼	+		4	+		1
20	+		3	+		2		+	43		+	¼
21		+	¼	+		2	+		3	+		1
22	+		6	+		1	+		½	+		1
23	+		1	+		1	+		23	+		10
24	+		1		+	¼	+		¼	+		2
25	+		5	+		¼		+	4	+		½
TOTALS	18	7	90+1h.33¾	15	10	1h.28	21	4	2h.9¼	18	7	3h.+2h.28¼

Table 14 (i) OLFACTORY CHOICE EXPERIMENT, SERIES G.

The response of a male given the choice of a female of his own type (Female "A") and a female of another type (Female "B") but involving hybrid animals

Male making the choice	britannicus 51			alstoni 247			alstoni 247		
Female "A"	britannicus 256/407/b			alstoni 105			alstoni 105		
Female "B"	britannicus x alstoni 502/402/a			britannicus x alstoni 500/400			britannicus x alstoni 500/400		
Trial Number	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins
1	+		9		+	90+19	+		9
2	+		18		+	10	+		24
3	+		2		+	18	+		18
4	+		1	+		½	+		6
5	+		5	+		6	+		½
6		+	12		+	5	+		3
7		+	5	+		½	+		1
8	+		1	+		1	+		½
9	+		2	+		11	+		1
10	+		2		+	90+16	+		6
11		+	15	+		4		+	4
12	+		3	+		1	+		¼
13	+		½	+		½	+		½
14	+		7	+		2		+	22
15	+		1	+		2	+		2
16	+		½		+	17	+		6
17	+		5	+		13	+		2
18	+		1	+		2	+		1
19	+		2		+	11		+	¼
20		+	10	+		18	+		3
21	+		3	+		1	+		½
22	+		1		+	¼	+		4
23	+		6	+		1	+		6
24	+		4	+		1	+		8
25	+		1	+		8		+	2
TOTALS	21	4	2h.7	17	8	3h.+2h. 48¾	21	4	2h.10½

Table 14(ii) OLFACTORY CHOICE EXPERIMENT, SERIES G. (Cont'd)

The response of a male given the choice of a female of his own type (Female "A") and a female of another type (Female "B") but involving hybrid animals

Male making the choice	skomerensis 222/278/a			britannicus x alstoni 508/416/b			britannicus x alstoni 501/401/e		
Female "A"	skomerensis 239/303			britannicus x alstoni 500/400/b			britannicus x alstoni 502/402		
Female "B"	skomerensis x alstoni 507/415/b			alstoni 240/313			alstoni 240/302/c		
Trial Number	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins	Choice "A"	Choice "B"	Time before choice made in mins
1	+		1	+		46		+	17
2	+		27	+		6	+		7
3	+		14	+		35		+	2
4		+	1	+		3		+	22
5	+		2	+		1		+	2
6	+		1		+	22		+	3
7	+		42	+		1		+	21
8		+	4	+		1	+		3
9	+		3	+		½		+	2
10		+	11		+	¼	+		3
11		+	½	+		1		+	4
12	+		2	+		1	+		2
13	+		1		+	13	+		2
14	+		12		+	1	+		1
15	+		4		+	10		+	¼
16		+	22		+	2		+	¼
17	+		2		+	½		+	½
18	+		6	+		5	+		½
19	+		½	+		4		+	½
20	+		1	+		¼	+		¼
21		+	45		+	1		+	2
22	+		4	+		5		+	2
23	+		1	+		5		+	1
24	+		3		+	2	+		4
25	+		4		+	2	+		1
TOTALS	19	6	3h.34	15	10	2h.48½	10	15	1h.43

Table 14(iii) OLFACTORY CHOICE EXPERIMENT, SERIES G. (cont'd.)

The response of a male given the choice of a female of his own type (Female "A") and a female of another type (Female "B") but involving hybrid animals

Male making the choice	skomerensis x alstoni 507/420		
Female "A"	skomerensis x alstoni 507/421		
Female "B"	skomerensis 254/326		
Trial Number	Choice "A"	Choice "B"	Time before choice made in mins.
1		+	4
2	+		13
3		+	4
4		+	25
5	+		1
6		+	19
7		+	3
8	+		3
9	+		1
10		+	25
11	+		5
12	+		3
13	+		½
14		+	1
15		+	¼
16	+		2
17	+		2
18		+	65
19	+		¼
20	+		2
21	+		4
22	+		3
23	+		2
24	+		1
25	+		½
Totals	16	9	3h.9½

Table 15 OLFACTORY CHOICE EXPERIMENTS, SERIES H.

The response of a hybrid male given the choice of one female of each parental race.

Male making the choice	britannicus x alstoni 502/402		
Female "A"	britannicus 63		
Female "B"	alstoni 240/313		
Trial Number	Choice		Time before choice made in mins.
	"A"	"B"	
1	+		2
2		+	25
3		+	1
4		+	2
5	+		½
6		+	½
7	+		2
8	+		5
9		+	¼
10		+	½
11		+	1
12	+		3
13		+	1
14	+		1
15	+		6
16	+		1
17	+		3
18	+		2
19	+		1
20		+	½
21	+		1
22		+	1
23	+		1
24		+	½
25	+		26
Totals	14	11	1h.25¾

Table 16 SIGNIFICANCE OF THE RESULTS OF OLFACTORY CHOICE EXPERIMENTS

(Tables 8 to 15).

Series		Male	Chooses Female "A"	Rather than Female "B"	Probability of the result found being due to chance
(i)	A	*britannicus*	*britannicus*	*erica*	less than .02
		alstoni	*alstoni*	*britannicus*	" " .01
		alstoni	*alstoni*	*skomerensis*	" " .005
		alstoni	*alstoni*	*rutilus*	" " .11
		skomerensis	*skomerensis*	*britannicus*	" " .005
		skomerensis	*skomerensis*	*alstoni*	" " .005
		rutilus	*rutilus*	*alstoni*	" " .0005
	F	*britannicus*	*britannicus*	*brit.* Kintyre	" " .001
		brit. Kintyre	*brit.* Kintyre	*britannicus*	" " .05
	G	*britannicus*	*britannicus*	*brit.* x *alstoni*	" " .005
		alstoni	*alstoni*	*brit.* x *alstoni*	" " .001
		skomerensis	*skomerensis*	*skom.* x *alstoni*	" " .02
		brit. x *alstoni*	*brit.* x *alstoni*	*alstoni*	greater" .9
		skom. x *alstoni*	*skom.* x *alstoni*	*skomerensis*	less than .3
(ii)	B	*rutilus*	*rutilus*	*alstoni*	" " .05
(iii)	C	*skomerensis*	*skomerensis*	*alstoni*	greater" .9
		brit. Kintyre	*brit.* Kintyre	*britannicus*	" " .4
(iv)	D	*skomerensis*	*skomerensis*	*skomerensis*	" " .9
(v)	E	*britannicus*	*erica*	*alstoni*	" " .6
(vi)	H	*brit.* x *alstoni*	*britannicus*	*alstoni*	" " .6

Table 17 Sexual isolation as measured by inseminations (see text)

Race of male	Five similar females		Five different females	
		Number of vaginal plugs	Race (or hybrid type)	Number of vaginal plugs
skomerensis	*skomerensis*	2	*alstoni*	0
skomerensis	*skomerensis*	5	*erica*	3
alstoni	*alstoni*	5	*britannicus (Edinburgh)*	2
alstoni	*alstoni*	1	*britannicus* x *alstoni*	0
skomerensis	*skomerensis*	4	*britannicus* x *skomerensis*	1
britannicus (Kintyre)	*britannicus (Kintyre)*	3	*alstoni*	1
TOTAL		20		7

Table 18 The weight of *Clethrionomys*

Author	Population	No. adults	Mean wt. ± S.D. of mean	Variance
D.M. Steven	*erica*	33	36.1 ± 1.34	-
D.M. Steven	*alstoni*	23	25.83 ± 1.62	-
W. Phillips & L.H. Matthews	*skomerensis*	42	30.59 ± 0.773	-
L.E. Adams	*britannicus* Reigate (BH)	40	19.20 ± 0.433	-
G. Dunnet	*britannicus* Aberdeenshire	112	16.79 ± 0.306	-
W. Phillips	*britannicus* Ramsey	12	17.67 ± 0.859	-
J. Godfrey	*britannicus* Kintyre	11*	22.47 ± 0.931	9.526
J. Godfrey	*britannicus* Edinburgh	8*	15.00 ± 0.493	1.944

*both these collections were made in September.

Table 19 To show the distribution between habitats of britannicus and other small mammals near Edinburgh.

Habitat	Trap Nights	Clethrionomys	Microtus	Apodemus	Shrews
Ungrazed grass	350	0.0	5.1	3.4	5.1
Bushes and bank of stream	240	2.1	0.0	9.2	3.3
Wood	275	1.5	0.0	8.4	6.5

Numbers of animals caught expressed as animals per trap night.

Table 20 To show the distribution between habitats of <u>britannicus</u> and other small mammals in Kintyre.

Habitat	Trap Nights	Clethrionomys	Microtus	Apodemus	Shrews
Grass bank near shrubs	100	8.0	10.0	16.0	3.0
Wood edge	126	7.9	0.8	9.5	4.0
Wood	45	0.0	0.0	42.2	0.0

Numbers of animals caught expressed as animals per 100 trap nights.

Table 21 To show the distribution between habitats of <u>skomerensis</u> and other small mammals.

Habitat	Trap Nights	Clethrionomys	Apodemus	Shrews
1 Rock outcrop	112	0.9	4.5	0.0
2 Heath	252	3.6	0.0	2.4
3 Bracken	336	0.3	1.5	0.0
4 Marsh	168	1.2	0.6	0.0
5 Old buildings walls & gardens	168	3.6	0.6	4.2

Numbers of animals caught expressed as animals per 100 trap nights.

Table 22 Mean consumption and S.E. of mean of various items for thirteen days.

Item	Individual	*britannicus*	*erica*	*alstoni*	*skomerensis*
HAY	1	0.63 ± .65	0.42 ± .096	0.86 ± .51	0.37 ± .41
	2	0.38 ± .096	0.52 ± .071	0.41 ± .55	0.43 ± .33
	3	0.47 ± .50	0.79 ± 1.08	0.42 ± .096	0.32 ± .09
TURNIP	1	9.6 ± 5.41	9.7 ± 1.94	8.9 ± 3.12	8.7 ± 1.31
	2	6.2 ± 1.32	12.0 ± 4.91	9.0 ± 2.13	12.3 ± 2.58
	3	8.1 ± 2.51	9.0 ± 2.95	11.0 ± 2.06	8.1 ± 1.80
CORN	1	4.0 ± .88	7.0 ± 1.13	4.3 ± .89	4.6 ± .64
	2	3.4 ± .80	4.2 ± .96	4.8 ± .75	4.1 ± .80
	3	3.1 ± 1.30	4.8 ± .81	4.5 ± .69	4.9 ± 1.10
WATER	1	1.4 ± 1.08	1.9 ± 1.06	0.8 ± .09	0.7 ± .07
	2	2.2 ± .71	1.4 ± 1.88	0.6 ± .10	0.6 ± .39
	3	0.6 ± .06	0.8 ± .44	0.7 ± .34	0.8 ± .38

Table 23 All the cases recorded of juveniles having died of fighting after weaning, when the members of a litter are put into a cage by themselves.

Parents of cross		Number of young born	Number of juveniles weaned	Number of juveniles died of fighting
Male	Female			
alstoni	*skomerensis*	26	22	2
erica	*skomerensis*	36	29	9
norvegicus	*skomerensis*	13	13	3
skomerensis	*britannicus*	35	18	0
skomerensis	*alstoni*	18	13	0
skomerensis	*erica*	6	6	0

Appendix A. The difference between the mortality of *Clethrionomys* races, F_1 hybrids and F_2 hybrids by the maximu likelihood method

Where $\hat{P}$ is an estimate of the likelihood of surviving from one two month interval to the next

$$\hat{P} = \frac{\sum(r-1)f(r)}{\{N+\sum(r-1)f(r)\}}$$

when $F(r)$ = No. dying in the rth period
N = total population
when $Q = 1 - P$ = probability of dying

$$\text{var. of } \hat{P} = \frac{PQ^2}{N}$$

The probability of as good a fit to the theoretical expectation being found by chance (see below*)

For *Clethrionomys* races: Chi-squared for 10 degrees of freedom = 15.01 P greater than .1
" " F_1 : " " " 4 " " " = 6.25 P approx. .2
" " F_2 : " " " 4 " " " = 2.66 P approx. .6

Clethrionomys races: $\hat{P} = 686/880 = 0.7795$ var $\hat{P} = 0.000195$
" F_1 : $\hat{P} = 158/236 = 0.6695$ var $\hat{P} = 0.000938$
" F_2 : $\hat{P} = 146/251 = 0.5817$ var $\hat{P} = 0.000969$

S.E. of the difference for *Clethrionomys* races V. F_1 t = 0.1100/0.034 = 3.24 P less than .01
" " " " " F_1 V. F_2 t = 0.0878/0.044 = 2.00 P approx. .05

* 6

Age at death in months	-2	-4	-6	-8	-10	-12	-14	-16	-18	-20	-22	-24	-26	-28	-30 to -40
***Clethrionomys* races**															
observed	47	34	13	23	19	12	14	7	2	9		10			4
expected	42.78	33.34	25.99	20.26	15.79	12.31	9.60	7.48	5.83	8.09		6.59			5.94
***Clethrionomys* F_1**															
observed	26	20	8	3	7	14									
expected	25.78	17.26	11.55	7.74	5.18	10.49									
***Clethrionomys* F_2**															
observed	49	26	10	8	4	8									
expected	43.92	25.55	14.86	8.65	5.03	6.99									

Appendix B. The survival of *Clethrionomys* from recapture data

Let $Q = 1 - P$

$q = 1 - p$

$f(r)$ be the observed frequency in the table below for time r,

and N be the total number of animals marked.

where p is an estimate of the chance of capture,

and P is the chance of survival from one two month period to the next,

$$p = \left\{\sum_{1}^{\infty} f(r)\right\}^2 \Big/ \left\{(0)\sum_{1}^{\infty}(r-1)f(r)\right\}$$

$$\text{var } \hat{p} = \frac{p(1-Pq)(1-P^2q)}{NP^2Q}$$

and the expected values of $f(r)$ are given by,

$$Ef(r) = NP^rQp/(1-Pq) \text{ for } r \neq 0$$

$$Ef(o) = NP/(1-Pq)$$

$$p = 0.119 \pm 0.010$$

The χ^2 for the fit of this with the observed figures (given below*) is 12.4 (with 5 degrees of freedom, $P = .05$)

*

	Time (in two month periods) to last recapture.							
	0	1	2	3	4	5	6	7 or more
observed	3672	202	131	70	37	15	5	3
expected	3672	225	116	59	30	16	8	9

The expected total number of recaptures is 521 compared with the observed 572 P=0.514 ± 0.016. This applies to a time scale measured in two calendar month units; correcting it to apply to an eight week period, for comparison with the value of P = 0.7795 (with a variance of .000195) obtained from the data on voles in captivity,

we have P = 0.543 ± 0.016

Correction to figure 1 : For "*norvegicus* NORTH NORWAY" read "*norvegicus* WEST NORWAY"

CR 17

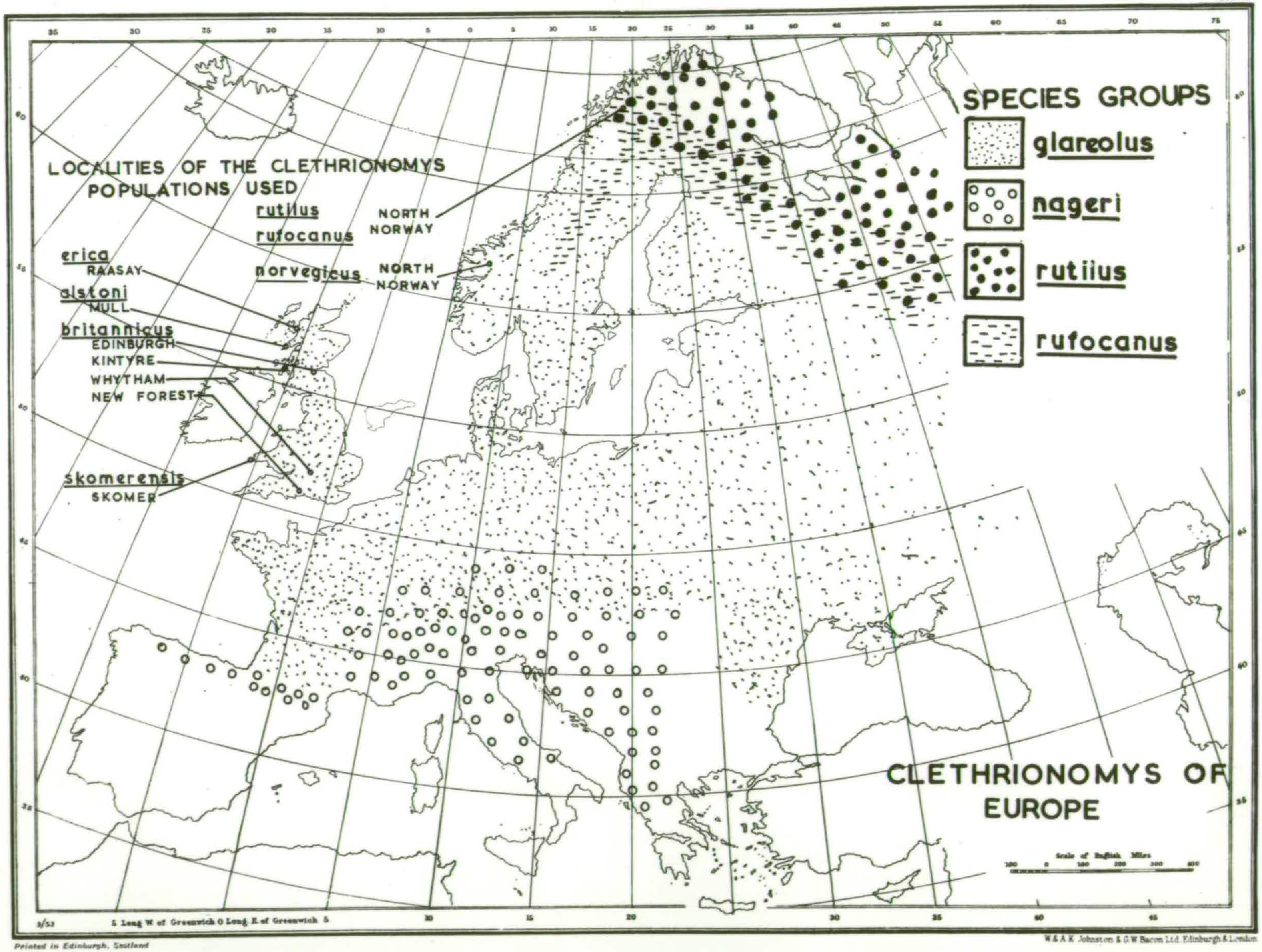

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Figure 2 Five individuals of each of eight categories of Clethrionomys scored for the ease with which they can be handled (see text) for each of ten days in November 1955.

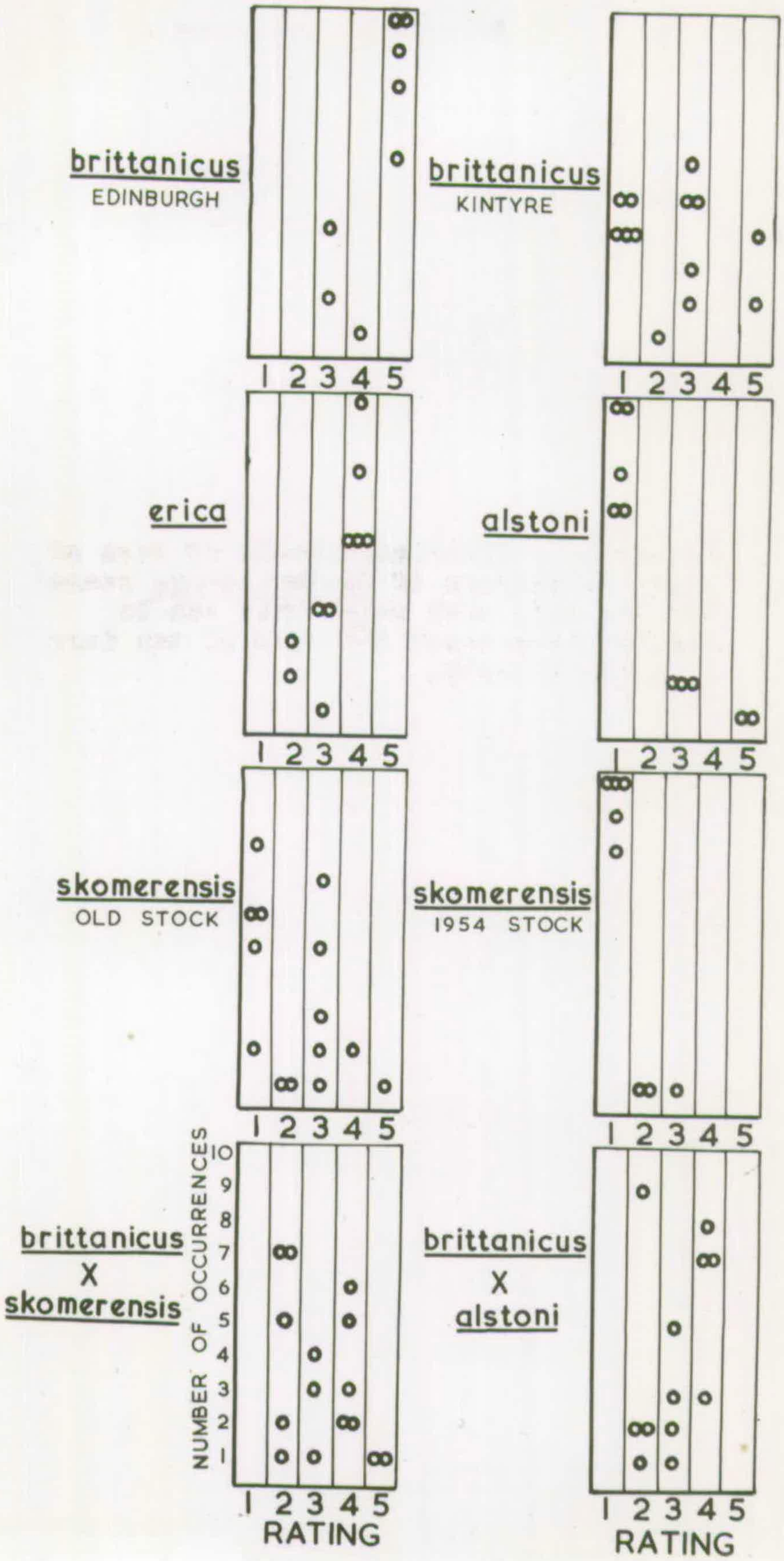

brittanicus
EDINBURGH
brittanicus
KINTYRE
erica
alstoni
skomerensis
OLD STOCK
skomerensis
1954 STOCK
brittanicus
X
skomerensis
brittanicus
X
alstoni
NUMBER OF OCCURRENCES
1 2 3 4 5 6 7 8 9 10
1 2 3 4 5
RATING
1 2 3 4 5
RATING

Fig. 3

Upward and downward flight reactions of voles, in response to the opening of the lids of their respective cages, plotted as percentages of the total trials (shown in table 3).

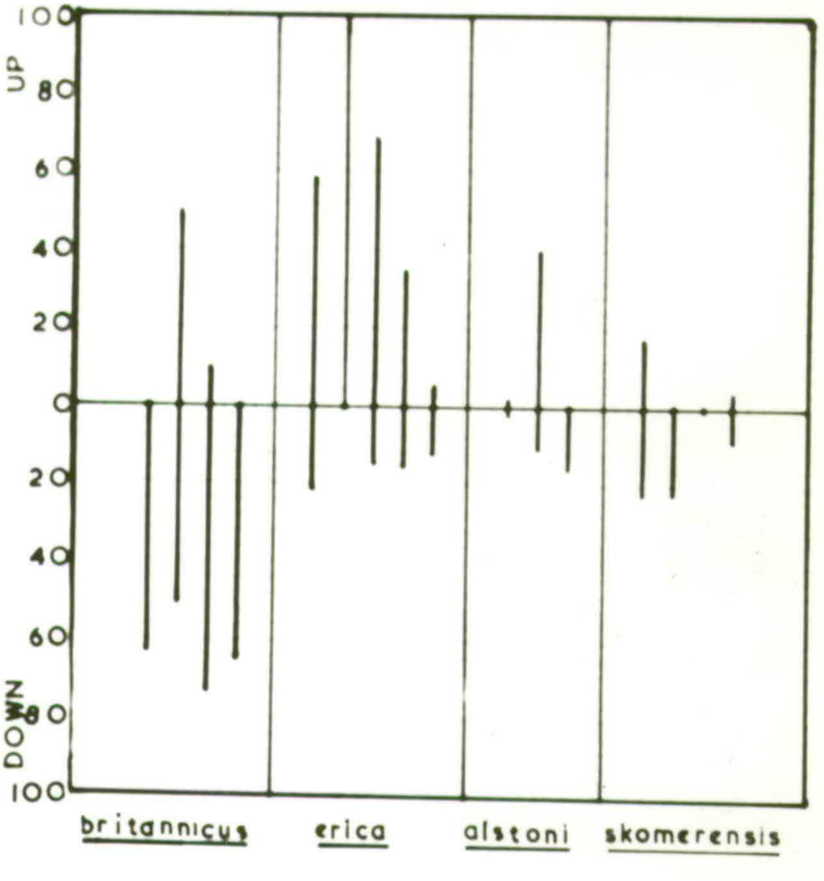
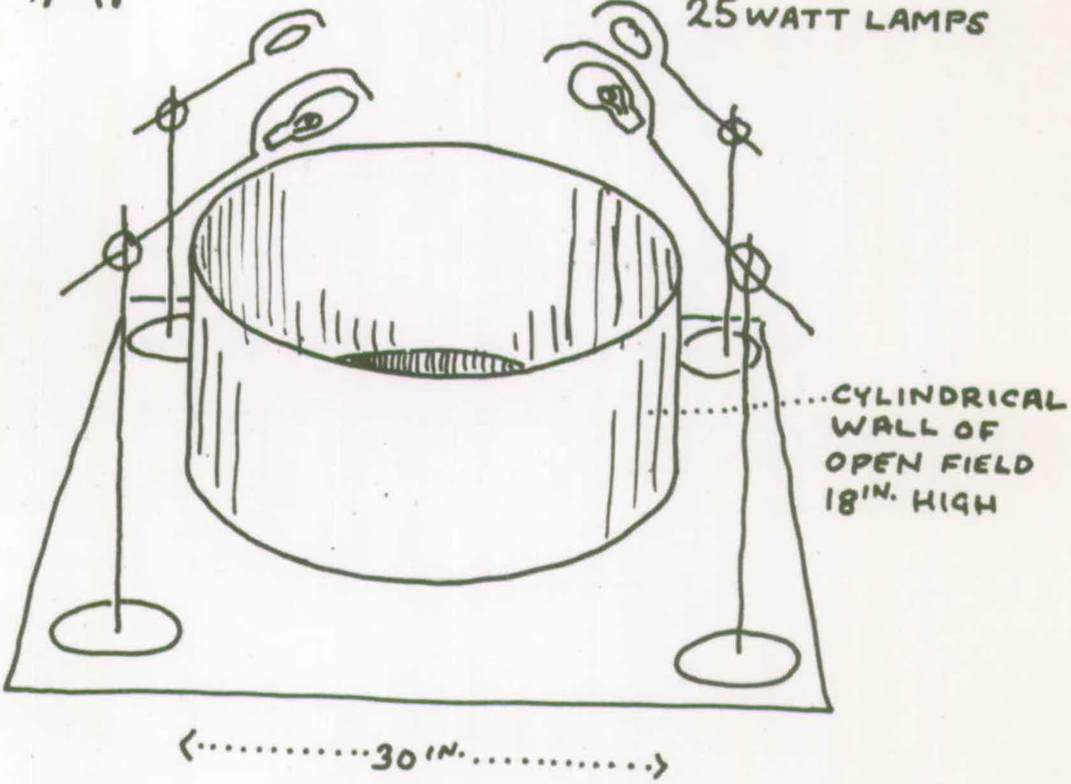

UP
100
80
60
40
20
0
20
40
60
80
100
DOWN
britannicus
erica
alstoni
skomerensis

Fig. 4 Apparatus used in the open field experiment.

A sketch of the design

B plan view of floor to show the central position where the animal was released, and the sections marked on the floor which were used in scoring movement.

A.


25 WATT LAMPS
CYLINDRICAL WALL OF OPEN FIELD 18 IN. HIGH
30 IN.

B.

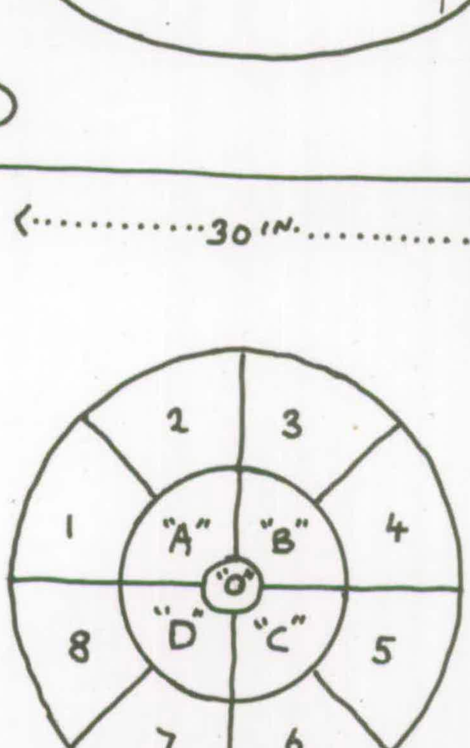

2
3
1
"A"
"B"
4
"O"
8
"D"
"C"
5
7
6

Fig. 5 OPEN FIELD EXPERIMENT

1 MOVEMENT

Number of movements* made in a ten minute period by five individuals of each of eight categories of *Clethrionomys* (dots), and the means (crosses), and the Standard Deviation of the means of these groups.

key: *bE* = *britannicus* Edinburgh
bK = *britannicus* Kintyre
e = *erica*
a = *alstoni*
s1 = *skomerensis* (Old stock)
s2 = *skomerensis* (1954 stock)
bXs = hybrid between *britannicus* and *skomerensis*
bXa = hybrid between *britannicus* and *alstoni*

---

*number of times that a line drawn on the experimental area (see fig.   ), was crossed.

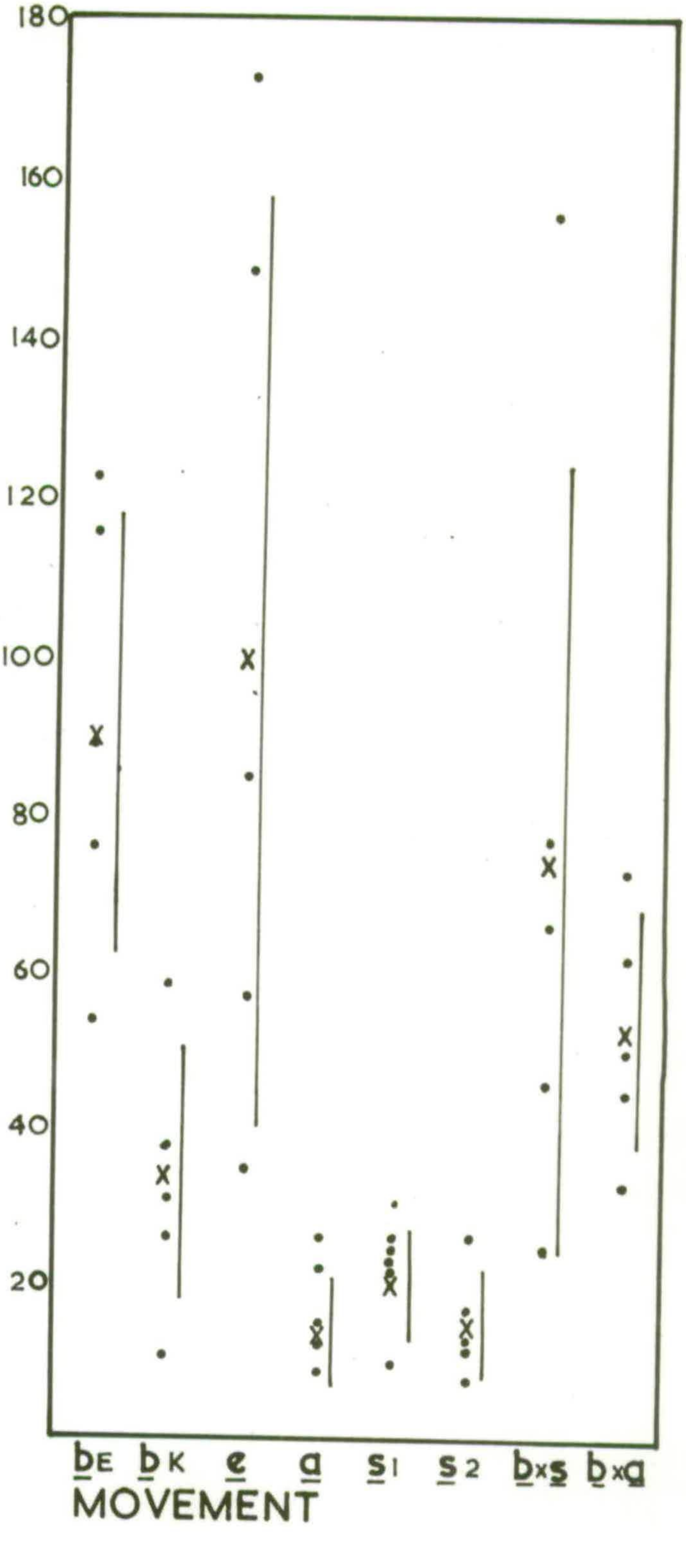

180
160
140
120
100
80
60
40
20
bE
bK
e
a
s1
s2
bxs
bxa
MOVEMENT

Fig. 6 OPEN FIELD EXPERIMENT

2 RUNNING

Number of minutes, out of ten, in which running* occurred for five individuals of each of eight categories of *Clethrionomys* (dots), and the means of these groups (crosses).

key: *bE* = *britannicus* Edinburgh
bK = *britannicus* Kintyre
e = *erica*
a = *alstoni*
s1 = *skomerensis* (Old stock)
s2 = *skomerensis* (1954 stock)
bXs = hybrid between *britannicus* and *skomerensis*
bXa = hybrid between *britannicus* and *alstoni*

*locomotion too rapid for all the positions occupied to have been recorded.

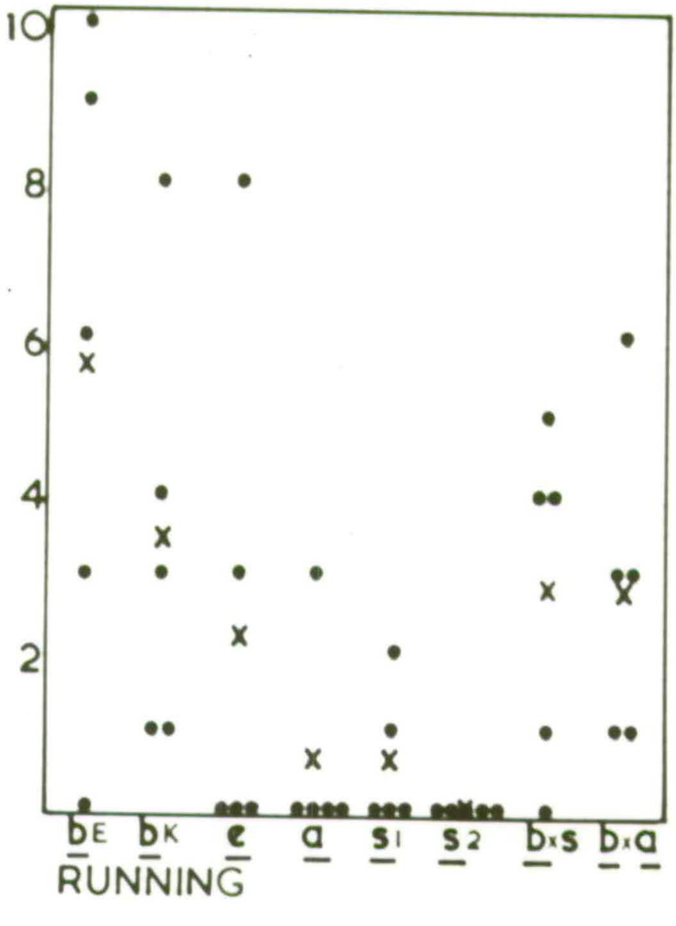

10
8
6
4
2
bE
bK
e
a
s1
s2
bxs
bxa
RUNNING

Fig. 7 OPEN FIELD EXPERIMENT

3 JUMPING

Number of minutes, out of ten, in which jumping* occurred for five individuals of each of eight categories of _Clethrionomys_ (dots), and the means of these groups (crosses).

key: _bE_ = _britannicus_ Edinburgh
_bK_ = _britannicus_ Kintyre
_e_ = _erica_
_a_ = _alstoni_
_s1_ = _skomerensis_ (Old stock)
_s2_ = _skomerensis_ (1954 stock)
bXs = hybrid between _britannicus_ and _skomerensis_
bXa = hybrid between _britannicus_ and _alstoni_

*when there is clearly no contact between the vole and the floors, (but usually there is contact with the wall) during an activity scored as jumping. This category excludes back flip (see next figure).

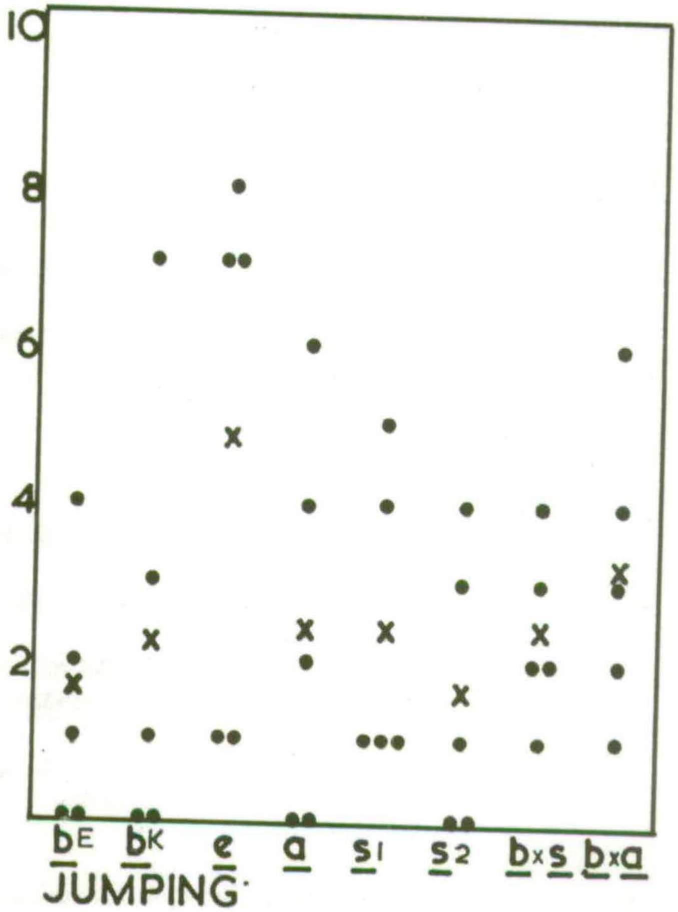

10
8
6
4
2
bE
bK
e
a
s1
s2
bxs
bxa
JUMPING

Fig. 8 OPEN FIELD EXPERIMENT

4 BACK FLIP

Number of minutes, out of ten, in which a back flip* occurred for five individuals of each of eight categories of *Clethrionomys* (dots), and the means of these groups (crosses).

key: bE = *britannicus* Edinburgh
bK = *britannicus* Kintyre
e = *erica*
a = *alstoni*
s1 = *skomerensis* (Old stock)
s2 = *skomerensis* (1954 stock)
bXs = hybrid between *britannicus* and *skomerensis*
bXa = hybrid between *britannicus* and *alstoni*

*the execution of a jump (see previous figure) in which the vole turns a back somersault before landing.

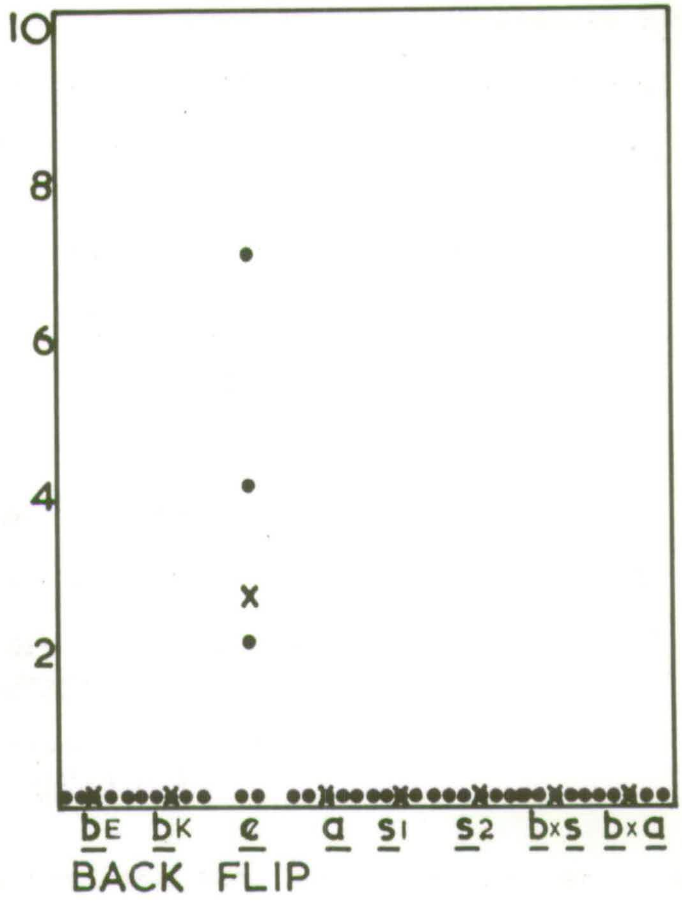

10
8
6
4
2
bE
bK
e
a
s1
s2
bxs
bxa
BACK FLIP

Fig. 9 OPEN FIELD EXPERIMENT

5 WASHING

Number of minutes, out of ten, in which washing* occurred for five individuals of each of eight categories of *Clethrionomys* (dots), and the means of these groups (crosses).

key: *bE* = *britannicus* Edinburgh
bK = *britannicus* Kintyre
e = *erica*
a = *alstoni*
s1 = *skomerensis* (old stock)
s2 = *skomerensis* (1954 stock)
bXs = hybrid between *britannicus* and *skomerensis*
bXa = hybrid between *britannicus* and *alstoni*

*rapid movement by the fore paws over the face, the vole sitting on its hind quarters.

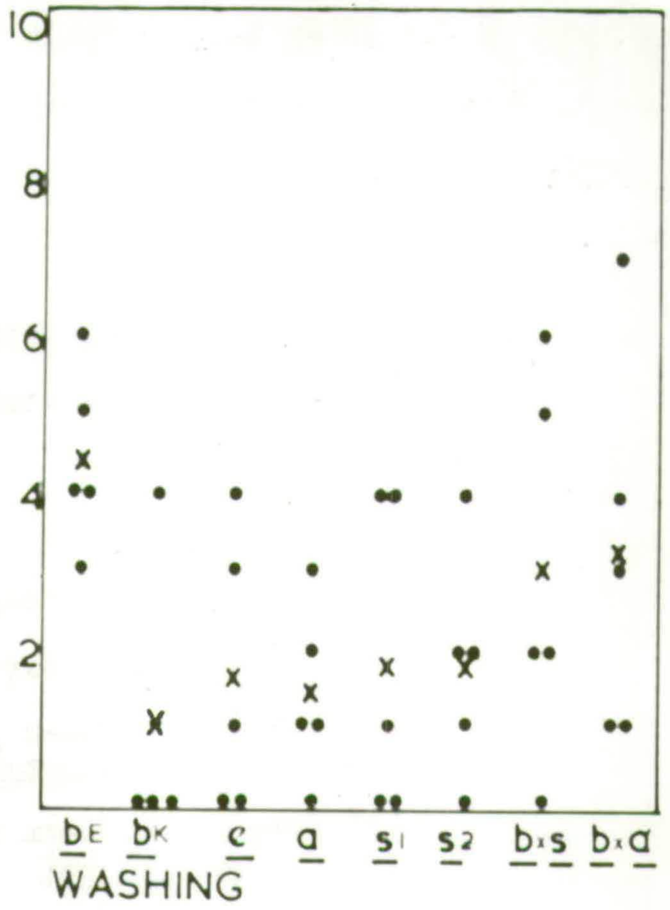

10
8
6
4
2
bE
bK
c
a
s1
s2
b×s
b×a
WASHING

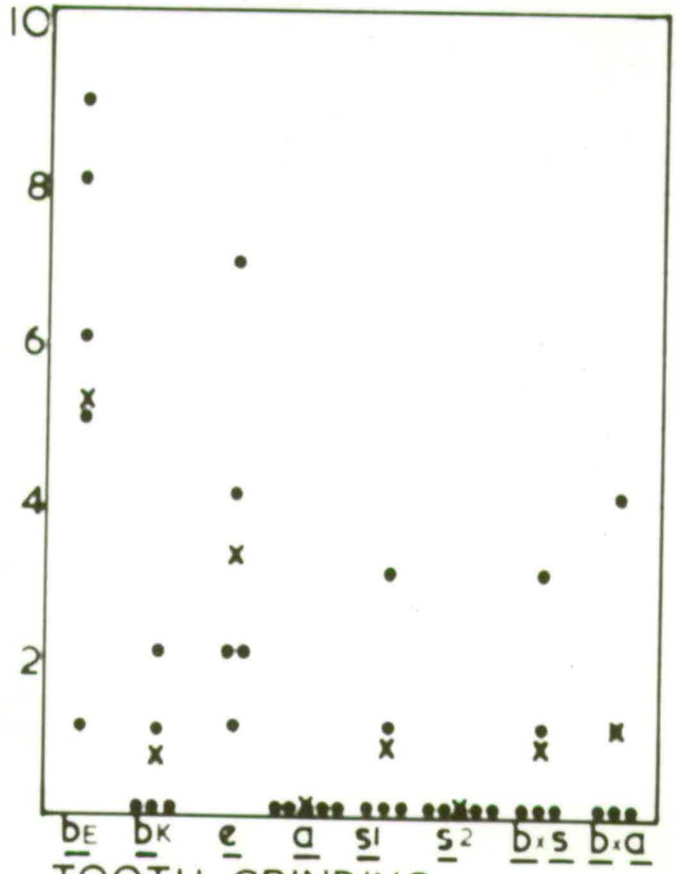
Fig. 10 OPEN FIELD EXPERIMENT

6 TOOTH GRINDING

Number of minutes, out of ten, in which tooth grinding° occurred for five individuals of each of eight categories of Clethrionomys (dots), and the means of these groups (crosses).

key: bE = britannicus Edinburgh
bK = britannicus Kintyre
e = erica
a = alstoni
s1 = skomerensis (Old stock)
s2 = skomerensis (1954 stock)
bXs = hybrid between britannicus and skomerensis
bXa = hybrid between britannicus and alstoni

°this is accompanied by very rapid jaw movements but is recognised by the sound. The mechanism implied by the name has not been demonstrated.



TOOTH GRINDING

Fig. 11 OPEN FIELD EXPERIMENT

7 WALL CONTACT

Number of minutes, out of ten, in which wall contact* occurred for five individuals of each of eight categories of Clethrionomys (dots), and the means of these groups (crosses).

key: bE = britannicus Edinburgh
bK = britannicus Kintyre
e = erica
a = alstoni
s1 = skomerensis (Old stock)
s2 = skomerensis (1954 stock)
bXs = hybrid between britannicus and skomerensis
bXa = hybrid between britannicus and alstoni

*continuously for more than about five seconds (estimated).

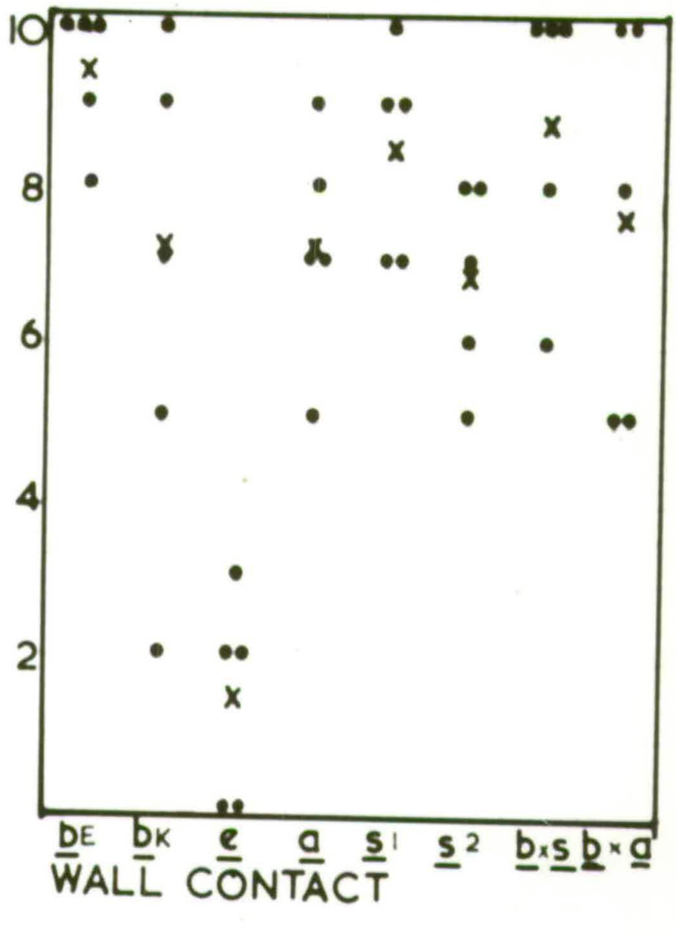

10
8
6
4
2
bE
bK
e
a
s1
s2
bxs
bxa
WALL CONTACT

Fig. 12 Diagram of the apparatus used to investigate rhythmic behaviour.

Each time the vole steps onto or off the floor of the cage (on left) the pen moves to the on, or off, position.

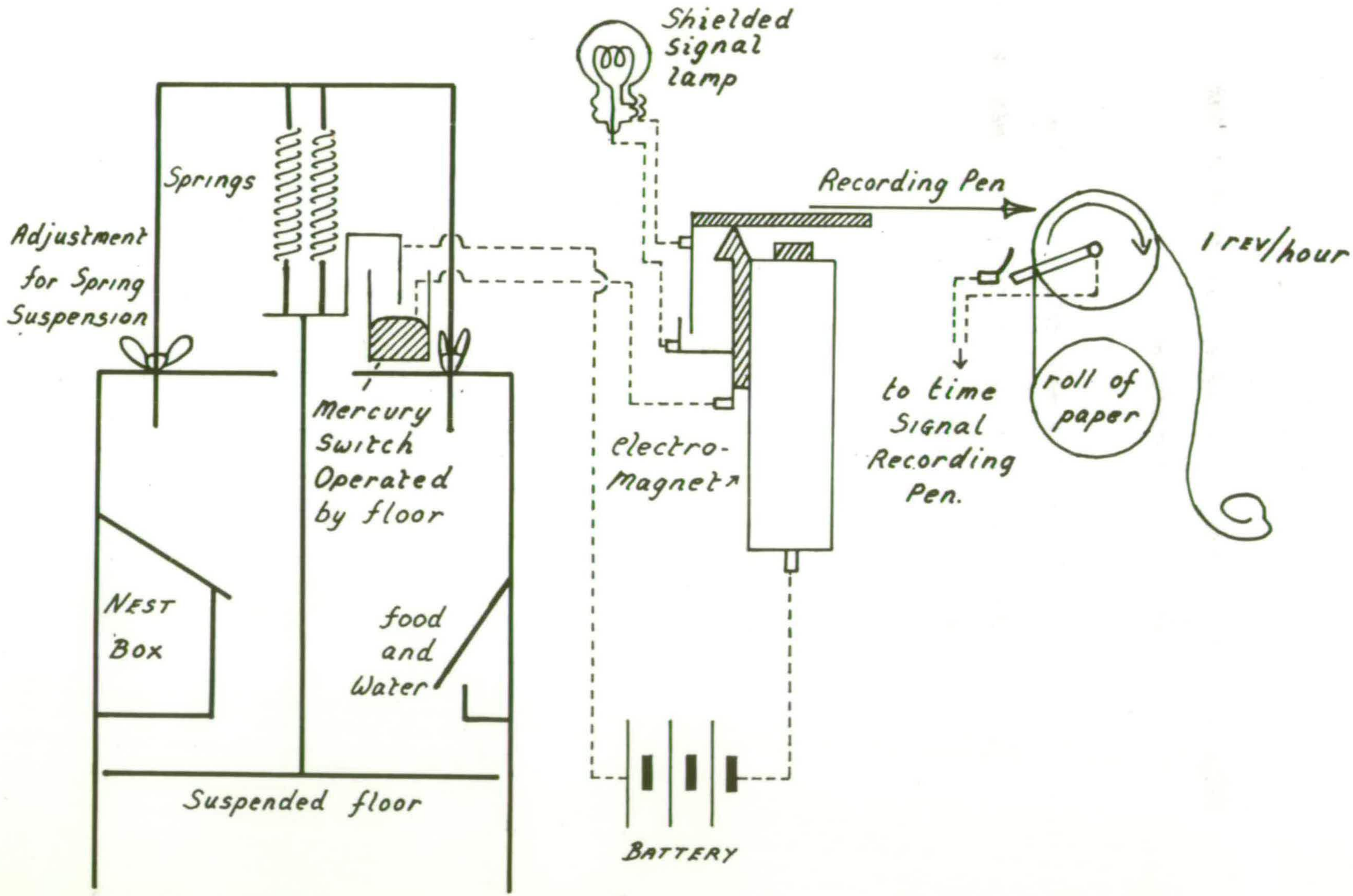

Shielded
Signal
lamp
Springs
Adjustment
for Spring
Suspension
Recording Pen
1 rev/hour
Mercury
Switch
Operated
by floor
electro-
Magnet
to time
Signal
Recording
Pen.
roll of
paper
Nest
Box
food
and
Water
Suspended floor
BATTERY

Fig. 13 Circuit diagramme of the voltage supply unit for the infra red image convector device.

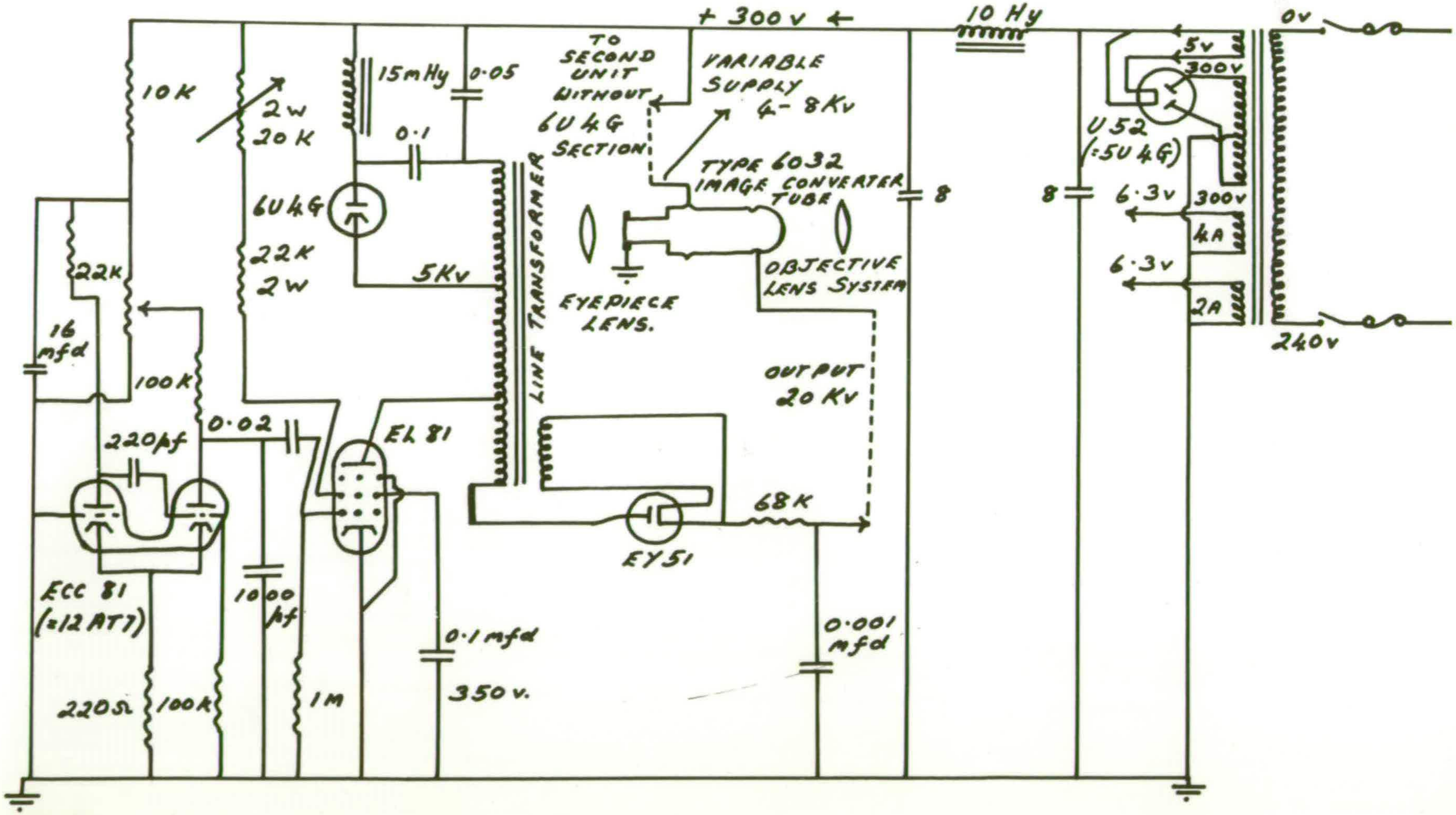

+ 300v ←
10 Hy
0v
5v
300v
TO SECOND UNIT WITHOUT 6U4G SECTION
VARIABLE SUPPLY 4- 8Kv
15mHy
0·05
10K
2w
20K
0·1
6U4G
TYPE 6032 IMAGE CONVERTER TUBE
8
8
U52 (=5U4G)
6·3v
300v
4A
6·3v
2A
240v
22K
2W
5Kv
LINE TRANSFORMER
EYEPIECE LENS.
OBJECTIVE LENS SYSTEM
22K
16 mfd
100K
OUTPUT 20 Kv
0·02
220pf
EL 81
68K
EY51
ECC 81 (=12AT7)
1000 pf
0·1 mfd
350v.
0·001 mfd
220Ω
100k
1M

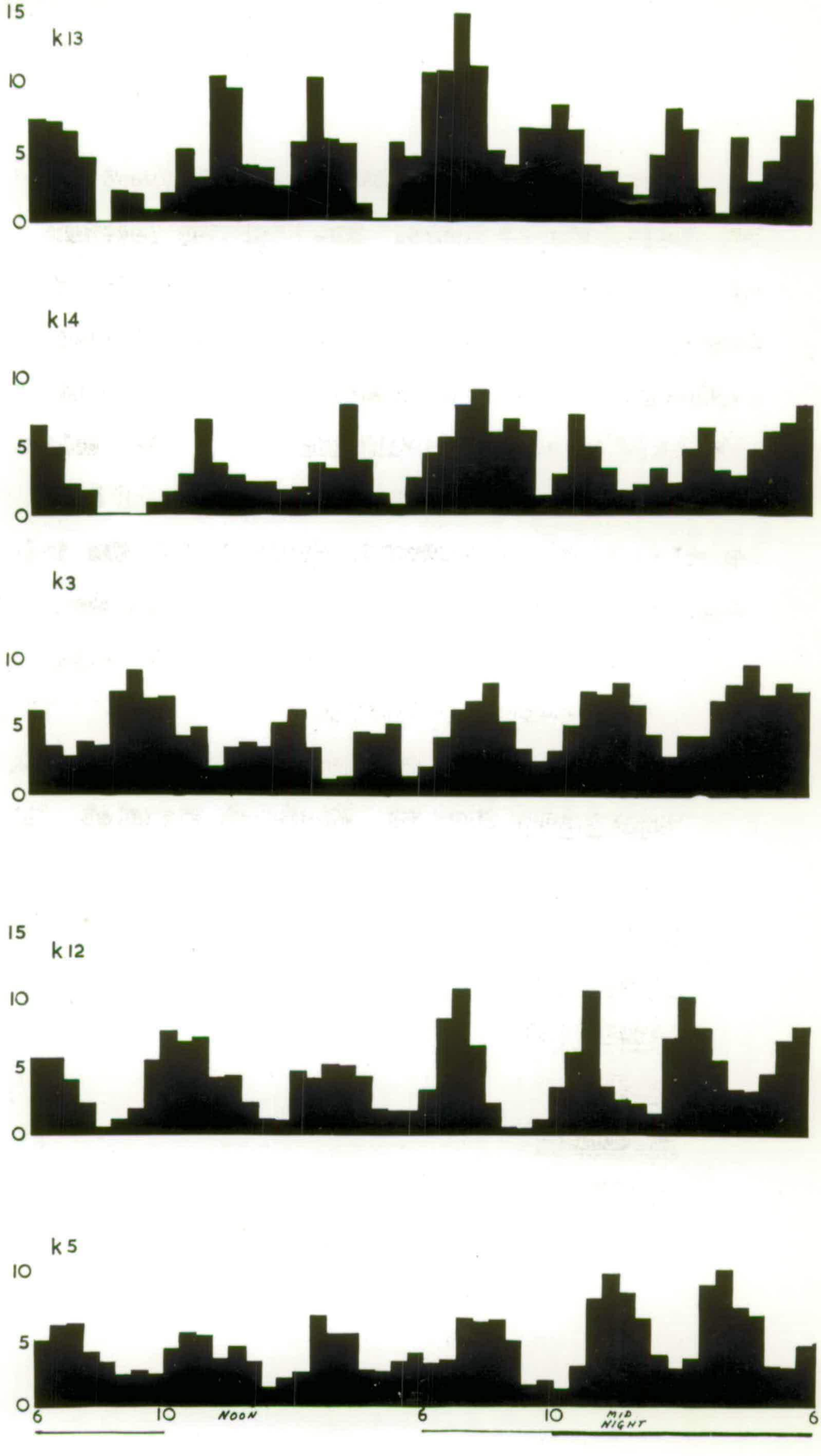
Fig. 14

Showing the distribution of excursions out of the nest box during the 24 hours. The lighting schedule is indicated, at the bottom of each figure, by a thin line for dim illumination (simulating dawn and dusk); by a thick line for darkness; and by the absence of a line for the bright illumination period (artificial day). The columns represent the mean number of minutes, per clock half hour, for the duration of the experiment, during which the individual being recorded spent some time outside its nest box.

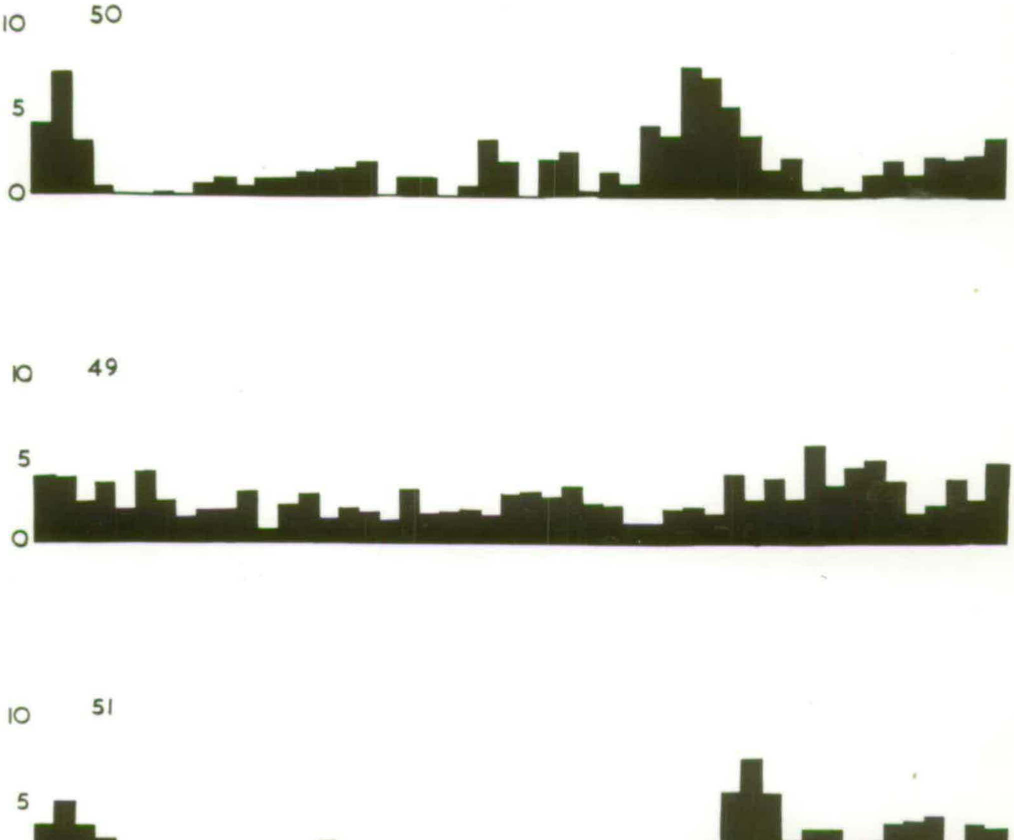
The categories of animals are as follows:-

britannicus from Kintyre	(i)
britannicus from the New Forest	(ii)
britannicus from the Edinburgh district	(iii)
alstoni	(iv)
erica	(v)
skomerensis	(v)
norvegicus	(vi)
rutilus	(vi)
rufocanus	(vi)
Hybrids	(vii)

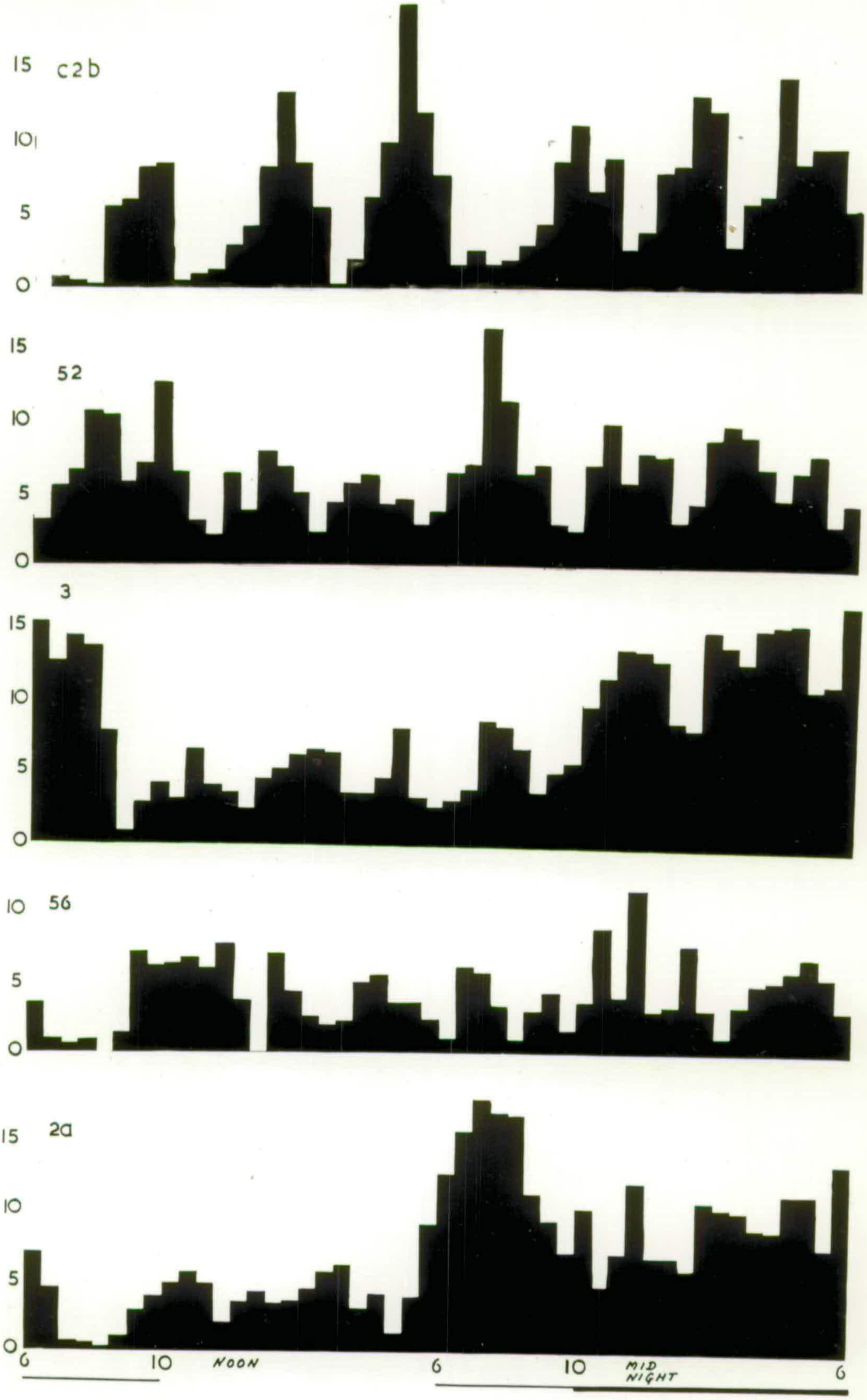
britannicus KINTYRE

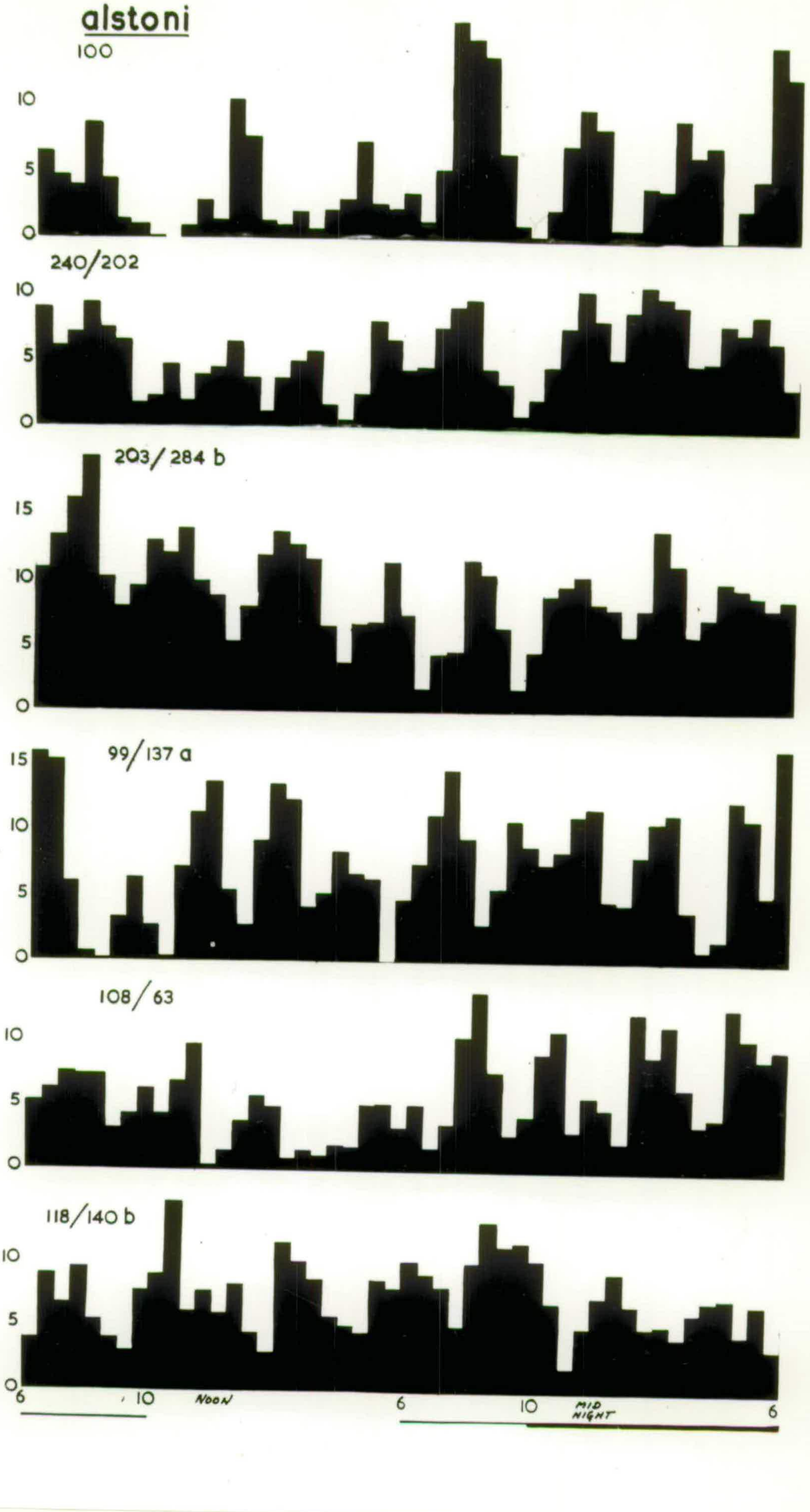


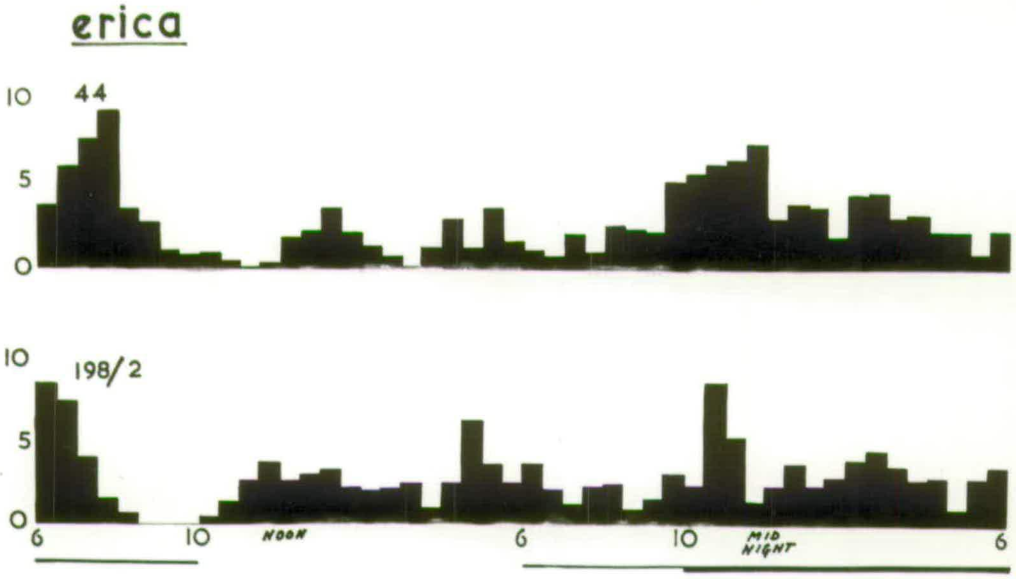
britannicus NEW FOREST

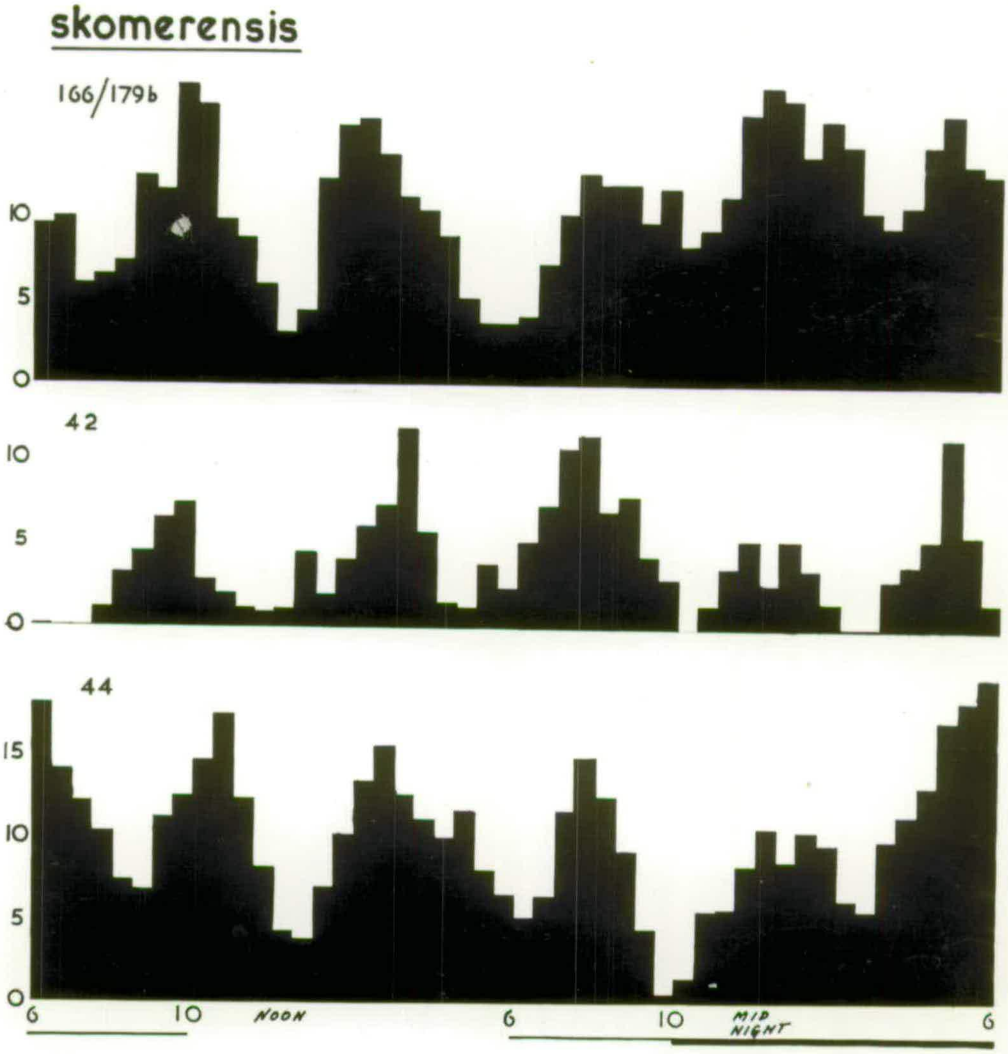


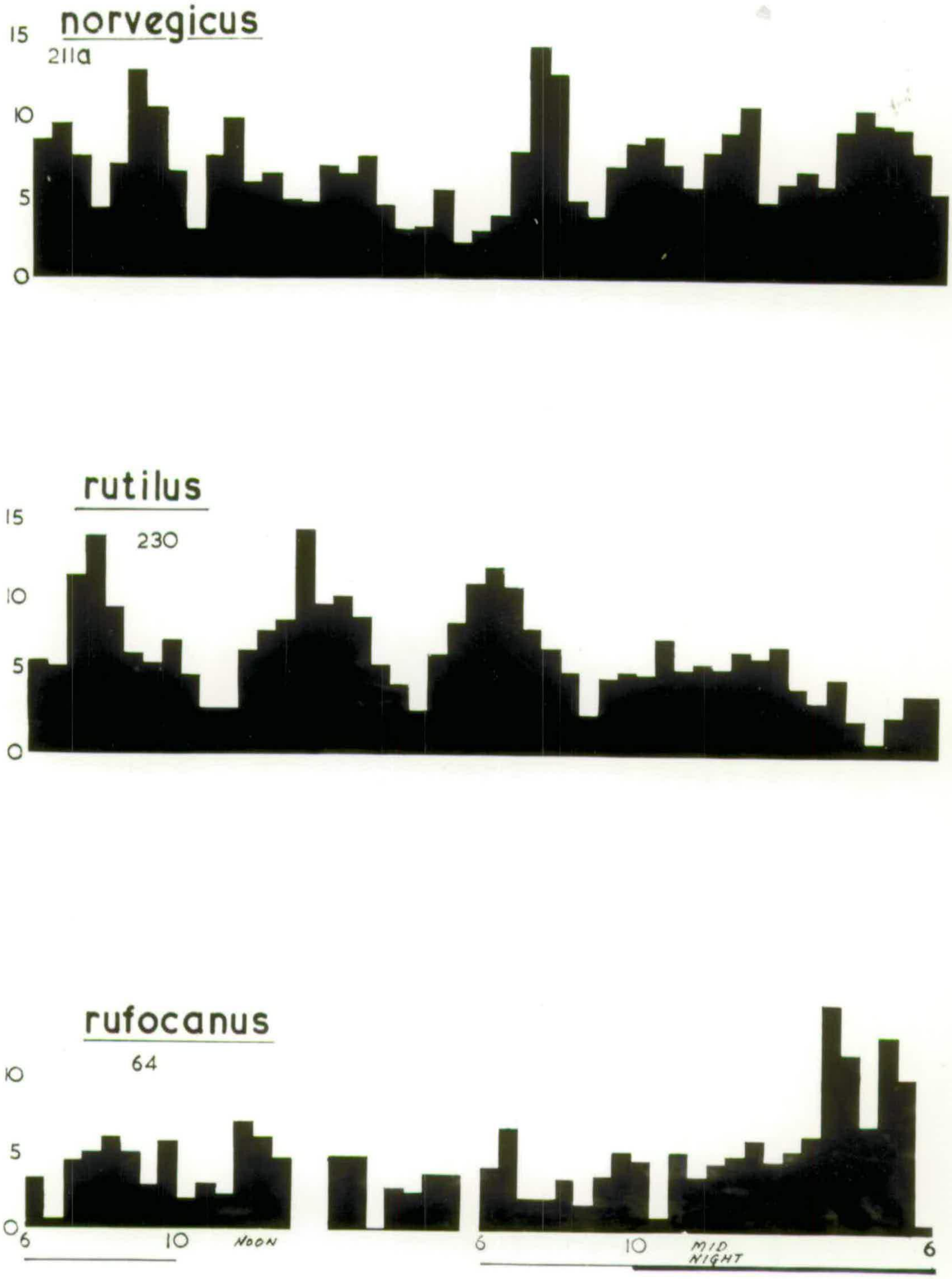
britannicus EDINBURGH



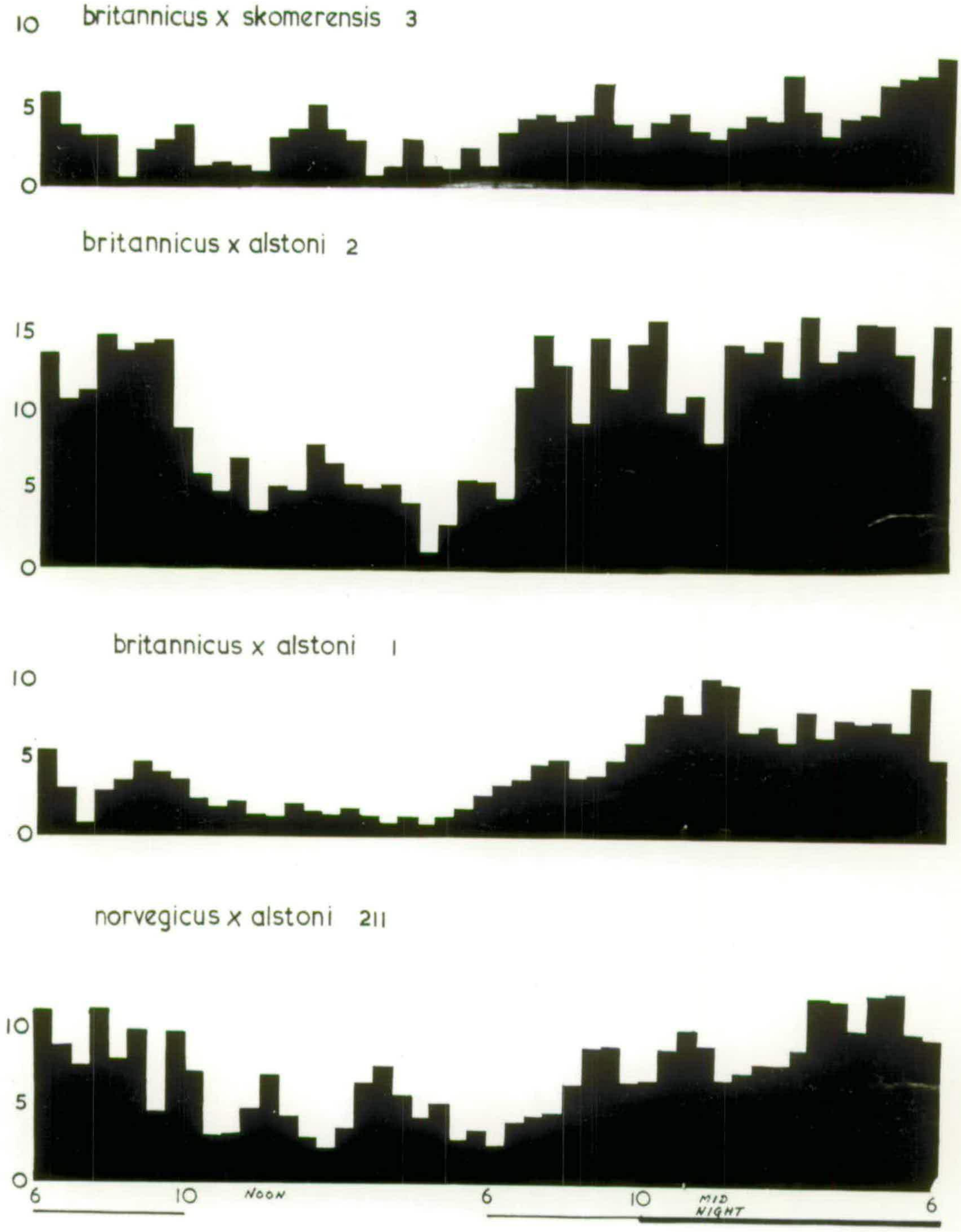

alstoni
100
10
5
0
240/202
10
5
0
203/284 b
15
10
5
0
99/137 a
15
10
5
0
108/63
10
5
0
118/140 b
10
5
0
6
10
NOON
6
10
MID NIGHT
6


erica
44
10
5
0
198/2
10
5
0
6
10
NOON
6
10
MID NIGHT
6


skomerensis
166/179b
10
5
0
42
10
5
0
44
15
10
5
0
6
10
NOON
6
10
MID NIGHT
6


norvegicus
211a
15
10
5
0
rutilus
230
15
10
5
0
rufocanus
64
10
5
0
6
10
NOON
6
10
MID NIGHT
6

HYBRIDS



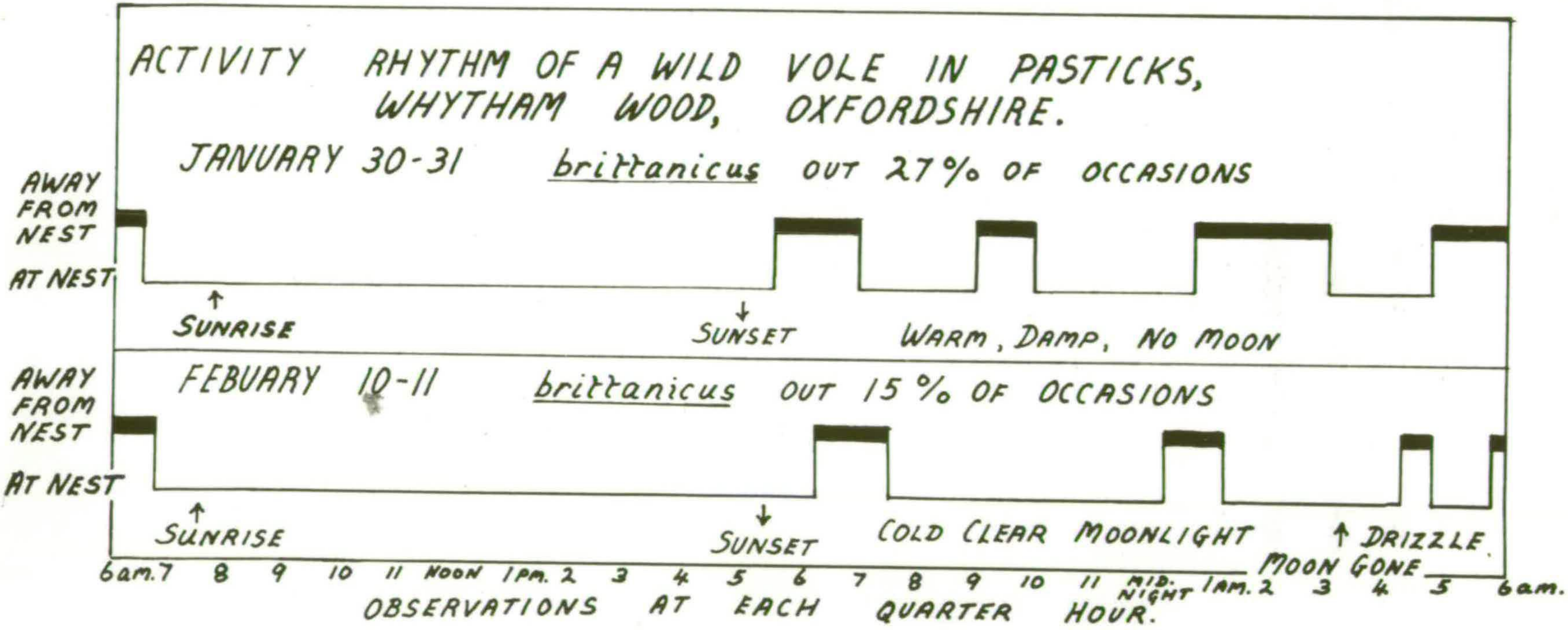
britannicus x skomerensis 3

britannicus x alstoni 2

britannicus x alstoni 1

norvegicus x alstoni 211

Fig. 15 The rhythmic behaviour of a specimen of *britannicus* which had been marked with a leg ring bearing radioactive cobalt.



ACTIVITY RHYTHM OF A WILD VOLE IN PASTICKS, WHYTHAM WOOD, OXFORDSHIRE.

Fig. 16 NEST BOX CONSTANCY

The number of times the favourite nest box was occupied is arbitrarily scored as 100, and the number of times each of the other nest boxes was occupied is given as a percentage of this.

Number of observations:	*britannicus*	220
	erica	92
	alstoni	92
	skomerensis	129

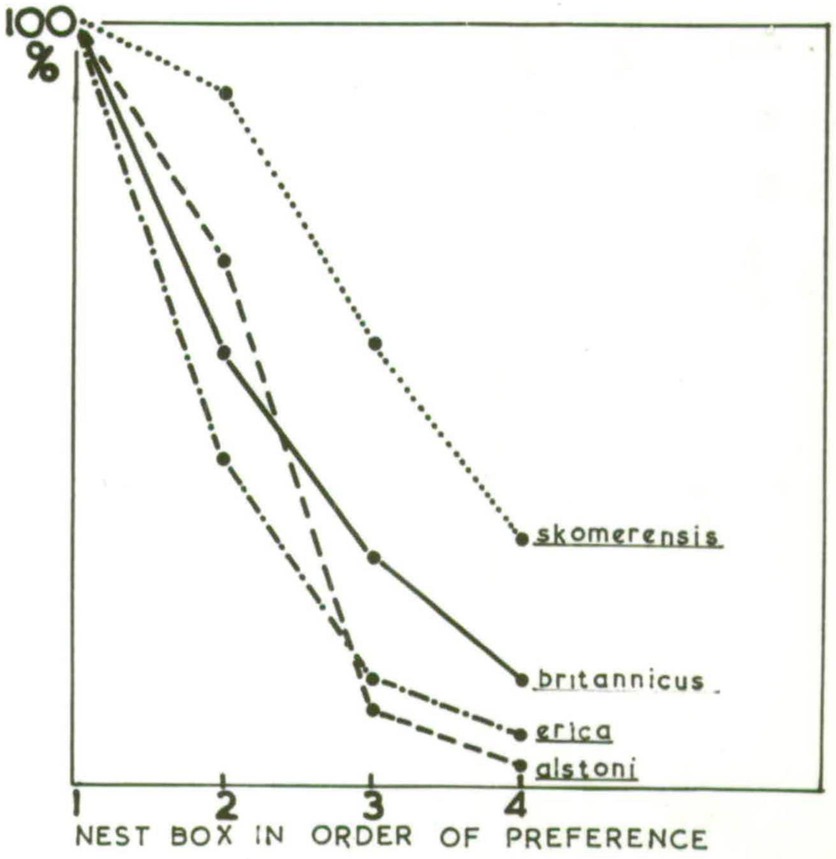

100
%
skomerensis
britannicus
erica
alstoni
1
2
3
4
NEST BOX IN ORDER OF PREFERENCE

Fig. 17 THE RELATIVE IMPORTANCE OF CUES FROM WITHIN THE CAGE AND FROM OUTSIDE IT IN THE RECOGNITION BY A VOLE OF ITS HOME.

The number of times the favourite nest box or position in the room was occupied is arbitrarily scored as 100, and the number of times each of the others was occupied is given as a percentage of this.

Nest + Cage + Room - the results when the nests and cage remained in the same position in the room for each trial (533 observations).

Nest + Cage - results when the nest and cage were rotated between observations (192 observations).

Room - numbers of times the favourite position in the room was occupied regardless of which nest box was in that position (123 observations).

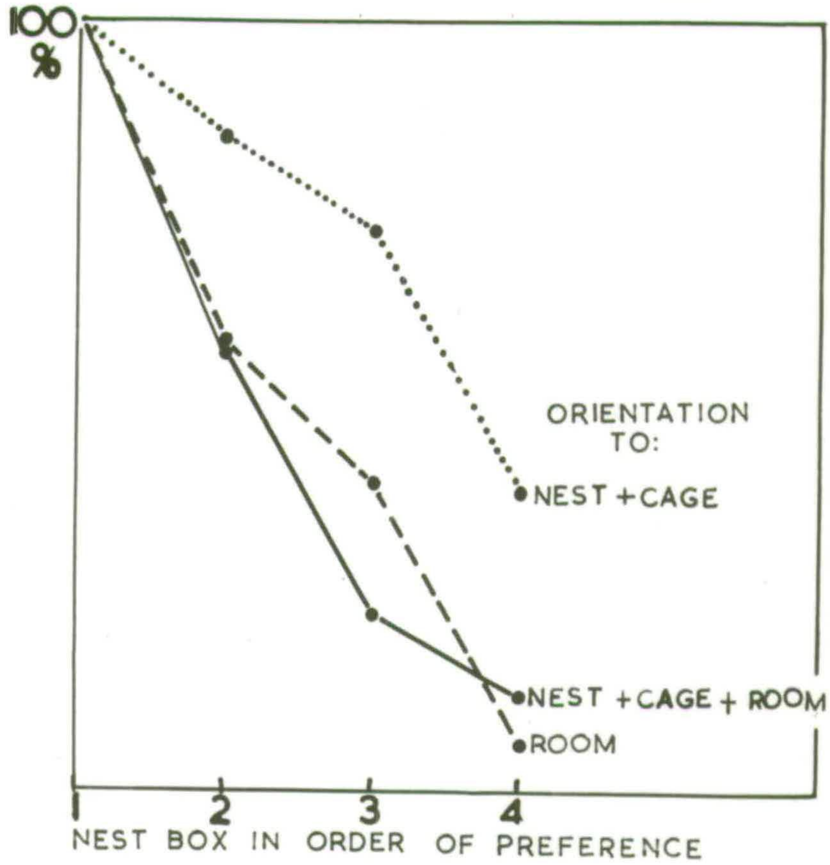
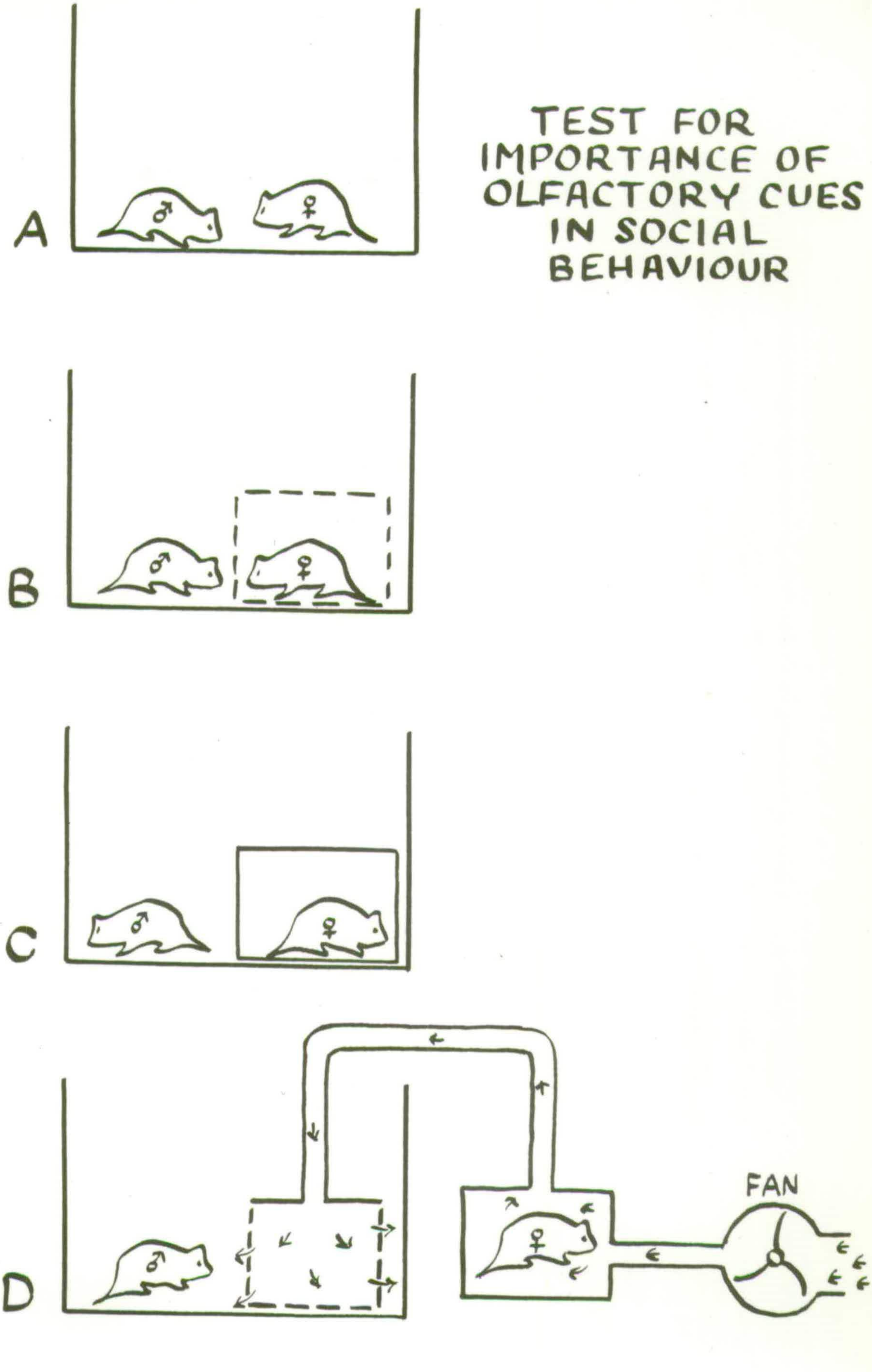

100
%
ORIENTATION
TO:
NEST + CAGE
NEST + CAGE + ROOM
ROOM
1
2
3
4
NEST BOX IN ORDER OF PREFERENCE

Fig. 18 Test for the importance of olfactory cues in social behaviour.



TEST FOR IMPORTANCE OF OLFACTORY CUES IN SOCIAL BEHAVIOUR

Fig. 19 Diagram to illustrate the design of the Y-tube apparatus which allows the simultaneous presentation of the odours of two female bank voles to a male. The choice of the male is recognised by his entry of the box in front of either A or B.

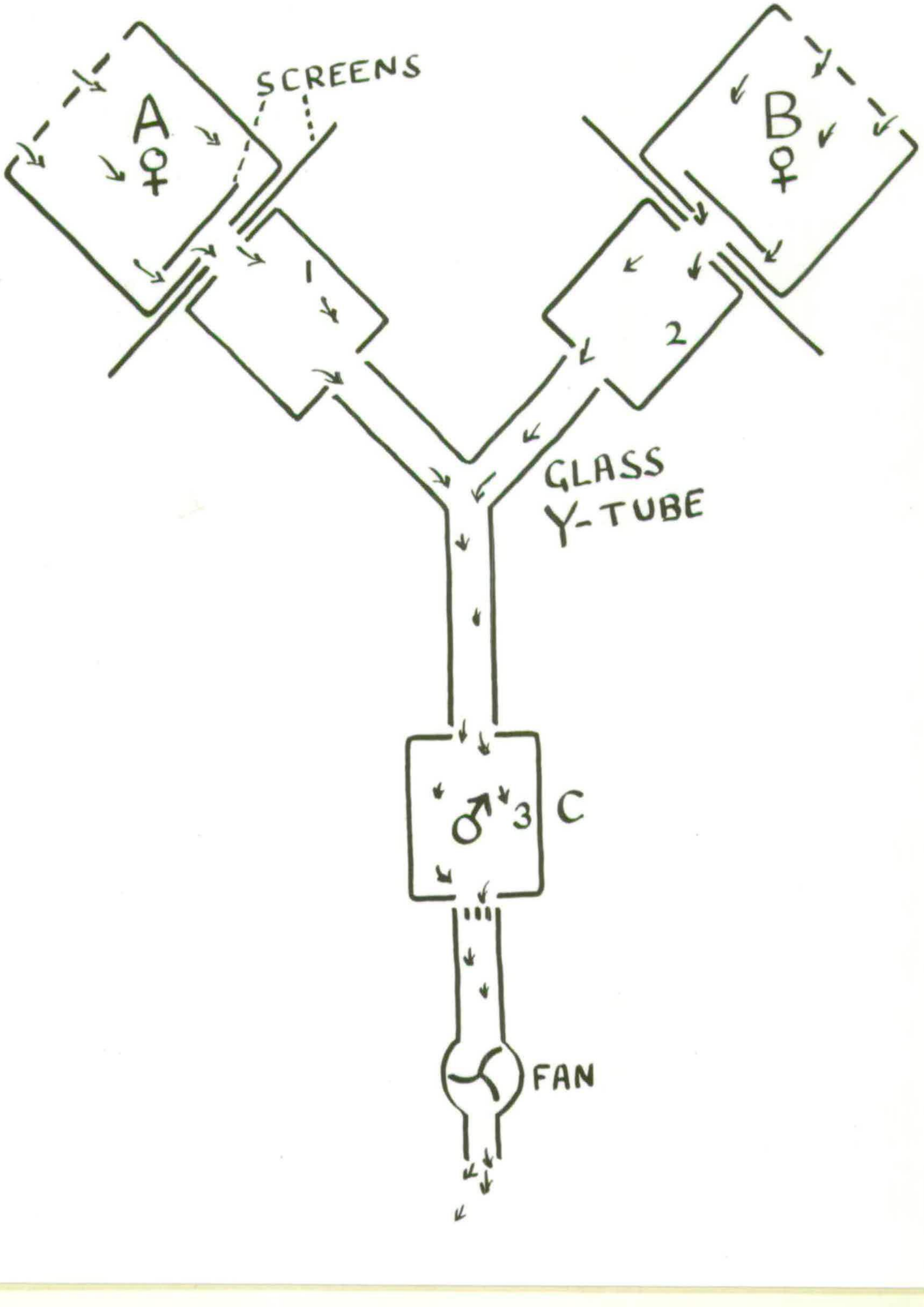

SCREENS
A
♀
B
♀
1
2
GLASS
Y-TUBE
♂
3
C
FAN

Fig. 20

The change in the mean success achieved by males, given an olfactory choice between a female of the same race, and a female of another race, during the first twenty-five trials.

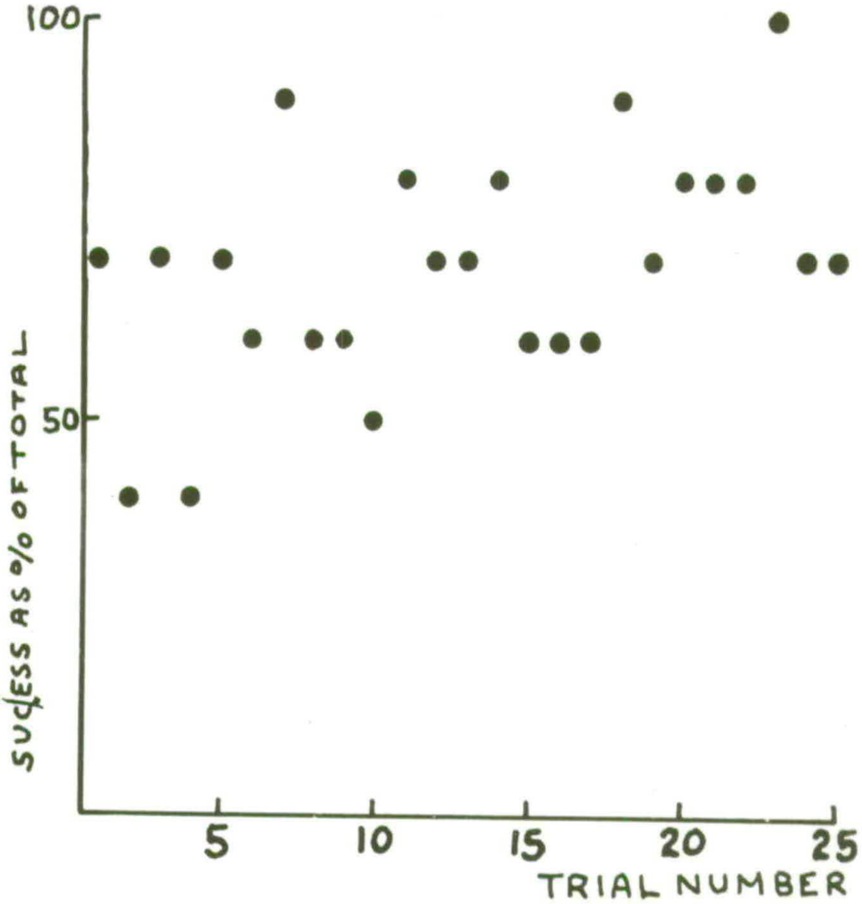

100
50
SUCCESS AS % OF TOTAL
5
10
15
20
25
TRIAL NUMBER

Fig. 21

The change in the mean time spent at the Y-junction for each male which was offered an olfactory choice between a female of his own race, and a female of another race, during the first twenty-five trials.

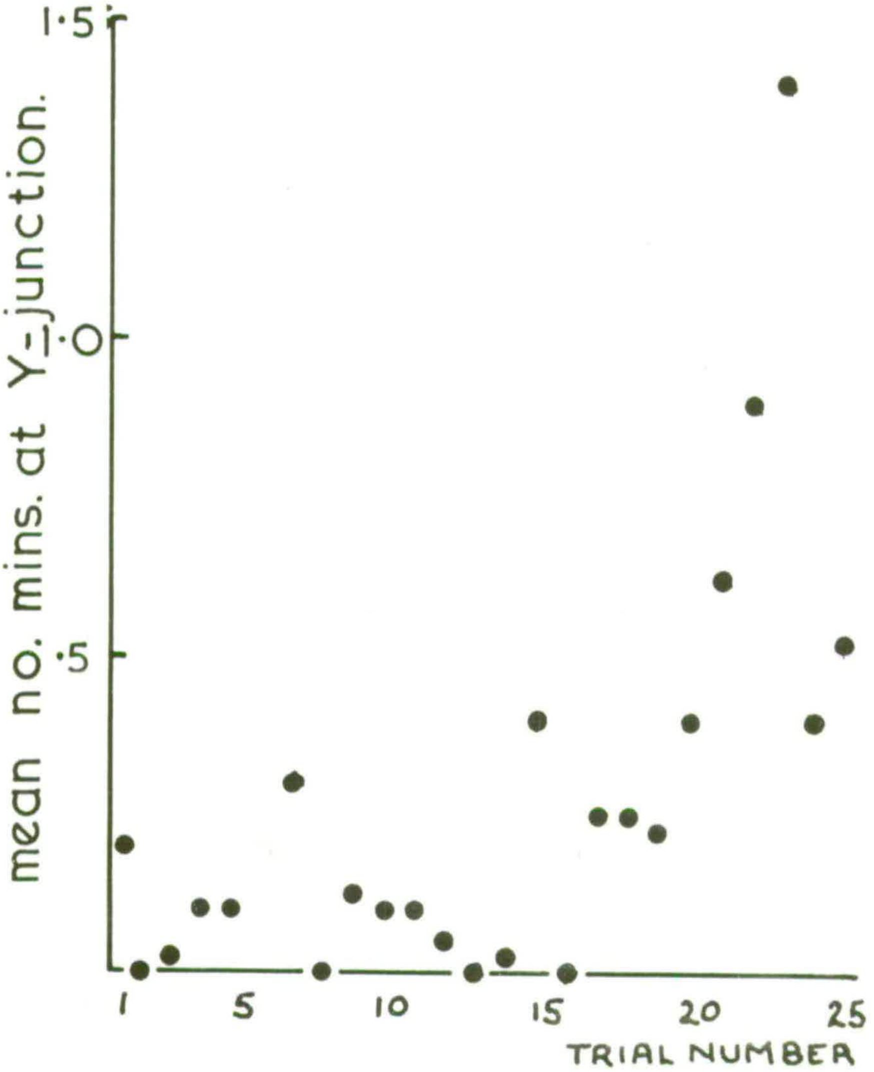
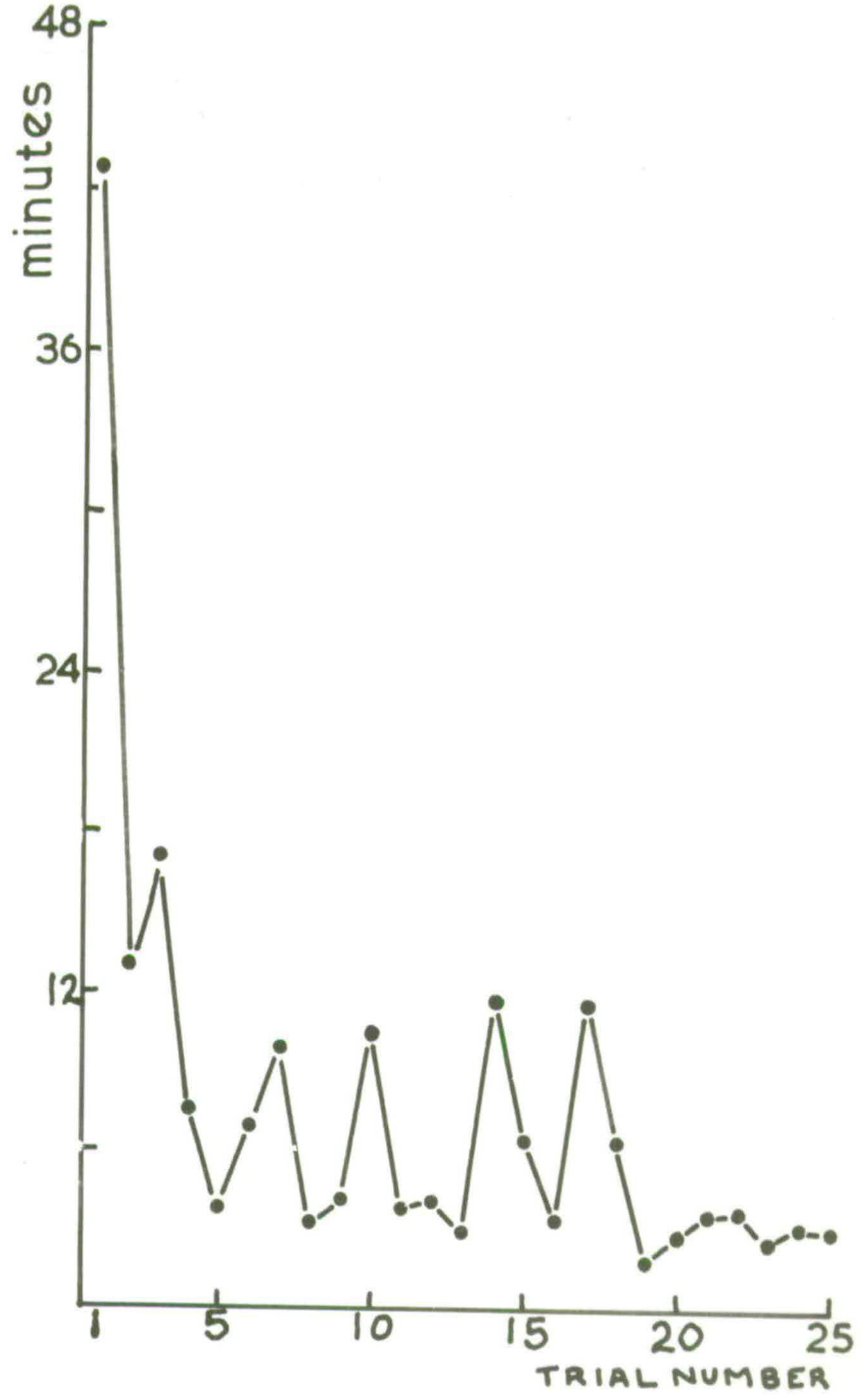

mean no. mins. at Y-junction.
1·5
·0
·5
1
5
10
15
20
25
TRIAL NUMBER

Fig. 22

The change in the mean time taken by each male to make an olfactory choice between a female of his own race, and a female of another race, during the first twenty-five trials.


48
36
24
12
minutes
1
5
10
15
20
25
TRIAL NUMBER

SKOMER

Fig. 23 Showing the habitats in which trapping was done.

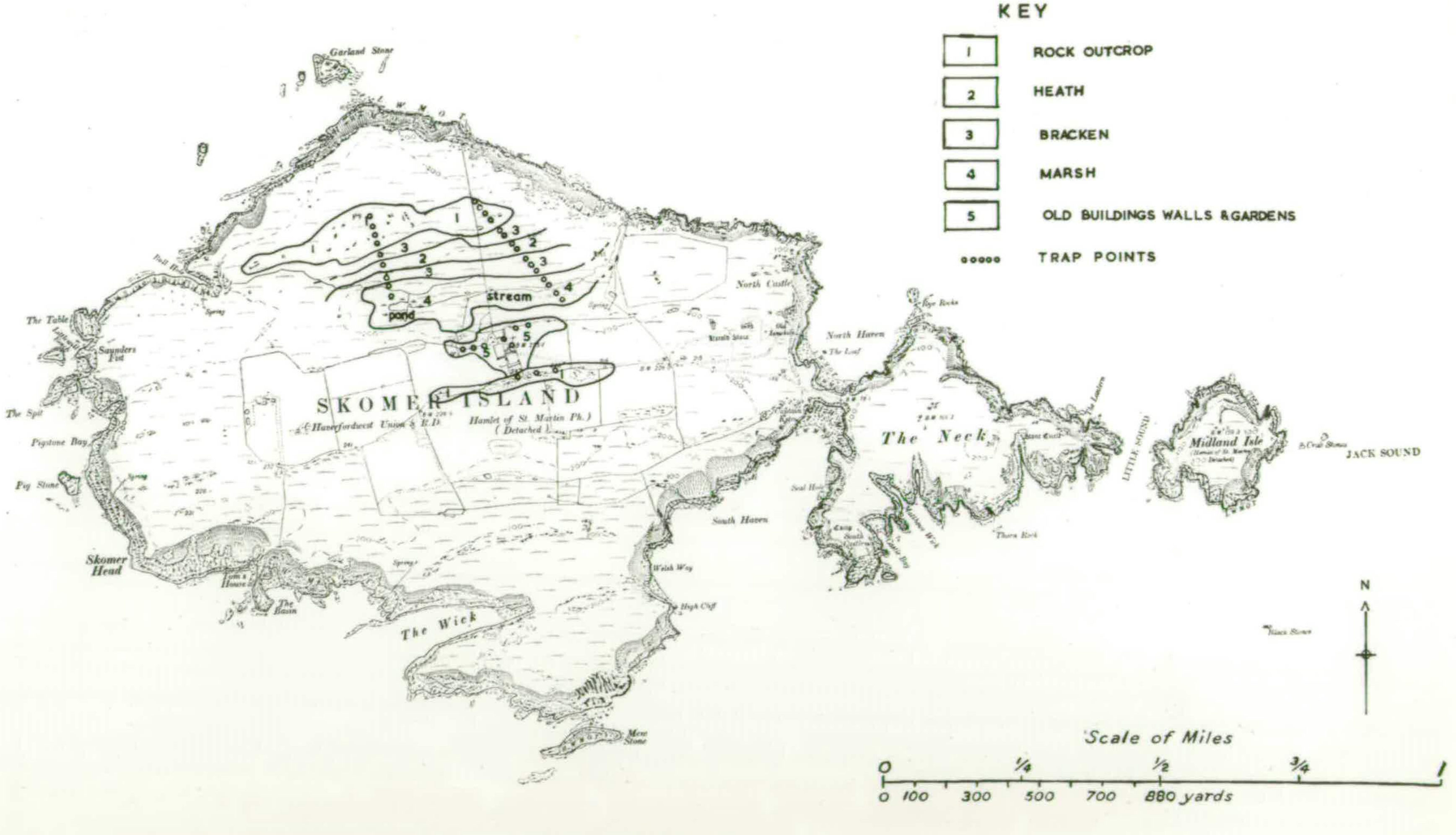

KEY
1 ROCK OUTCROP
2 HEATH
3 BRACKEN
4 MARSH
5 OLD BUILDINGS WALLS &GARDENS
ooooo TRAP POINTS
SKOMER ISLAND
(Haverfordwest Union & R.D. Hamlet of St. Martin Ph.) (Detached)
Garland Stone
The Table
Saunders Pit
The Spit
Pigstone Bay
Pig Stone
Skomer Head
The Basin
The Wick
Mew Stone
stream
pond
North Castle
North Haven
The Lorf
South Haven
Seal Hole
Welsh Way
High Cliff
The Neck
Thorn Rock
LITTLE SOUND
Midland Isle
Crab Stones
JACK SOUND
Black Stones
N
Scale of Miles
0 ¼ ½ ¾ 1
0 100 300 500 700 880 yards

Fig. 24

To show the mean consumption (with its standard deviation) of water, turnip, hay and corn by three individuals of four races of Clethrionomys, for a 13 day period.

Note of the method used:

The animals were isolated in metal cages, and weighed quantities of food and water, much in excess of that used, were added to the cleaned cage each morning. The following morning what remained of each was weighed. The weights of water and turnip plotted have been corrected by deducting the loss of weight, due to evaporation, of control samples placed in uninhabited cages. In each cage there was present a turf approximately 15 x 10 x 4 cm., placed in a tin 6 cm. deep. This was replaced each day by a freshly dug specimen.

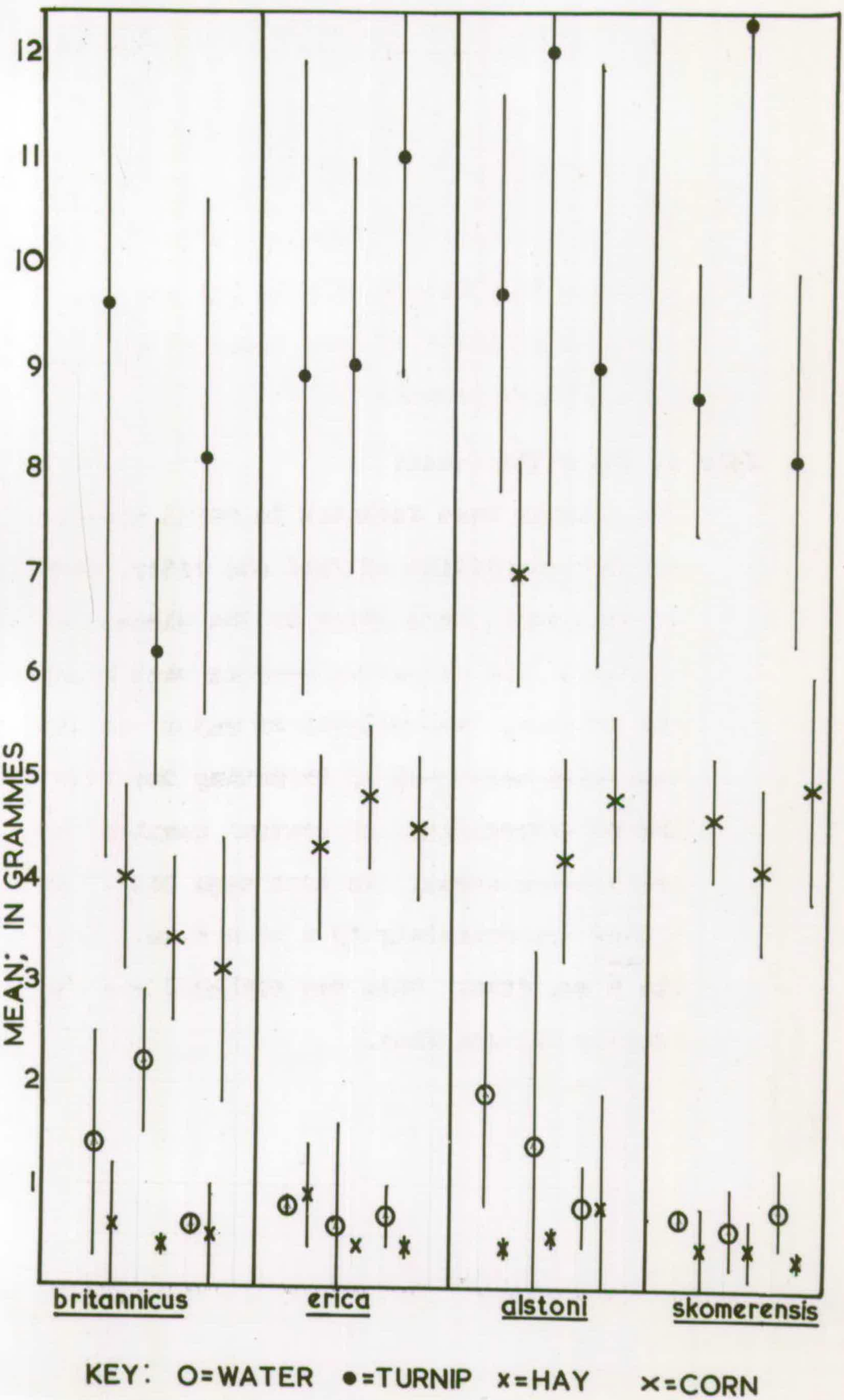

MEAN; IN GRAMMES
12
11
10
9
8
7
6
5
4
3
2
1
britannicus
erica
alstoni
skomerensis
KEY: O=WATER ●=TURNIP x=HAY ✕=CORN

Fig.25

The occurrence of bed shredding in several categories of *Clethrionomys*.

The mean number of performances* per day during all recordings made with the apparatus for measuring rhythmic behaviour is shown in the following groups of bank voles.

bK = *britannicus* Kintyre
bNF = *britannicus* New Forest
bE = *britannicus* Edinburgh
e = *erica*
a = *alstoni*
s = *skomerensis*
n = *norvegicus*
r = *rutilus*
ruf = *rufocanus*
bxa = *britannicus* (Edinburgh) x *alstoni*
bxs = *britannicus* (Edinburgh) x *skomerensis*
nxa = *norvegicus* x *alstoni*

*The criterion for a performance is the recording of a rapid series of excursions (at least eight) from the nest box for three or more consecutive minutes. A bout of ten or more such consecutive minutes is counted as two performances.

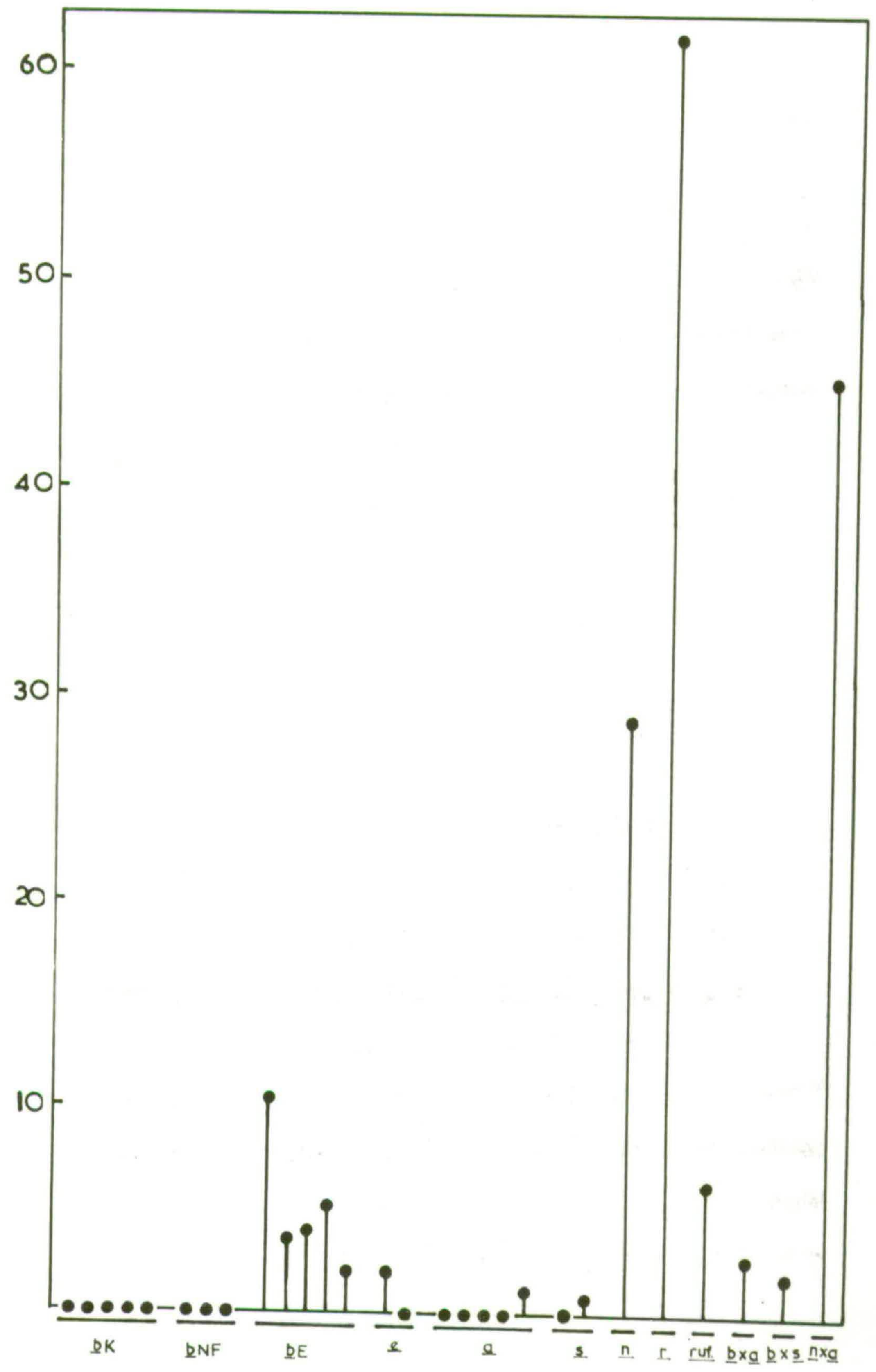

60
50
40
30
20
10
bK
bNF
bE
e
a
s
n
r
ruf
bxa
bxs
nxa

Fig. 26 A comparison of the frequency of occurrence of various litter sizes in intra-race matings in captivity with their productivity of juveniles at weaning age.

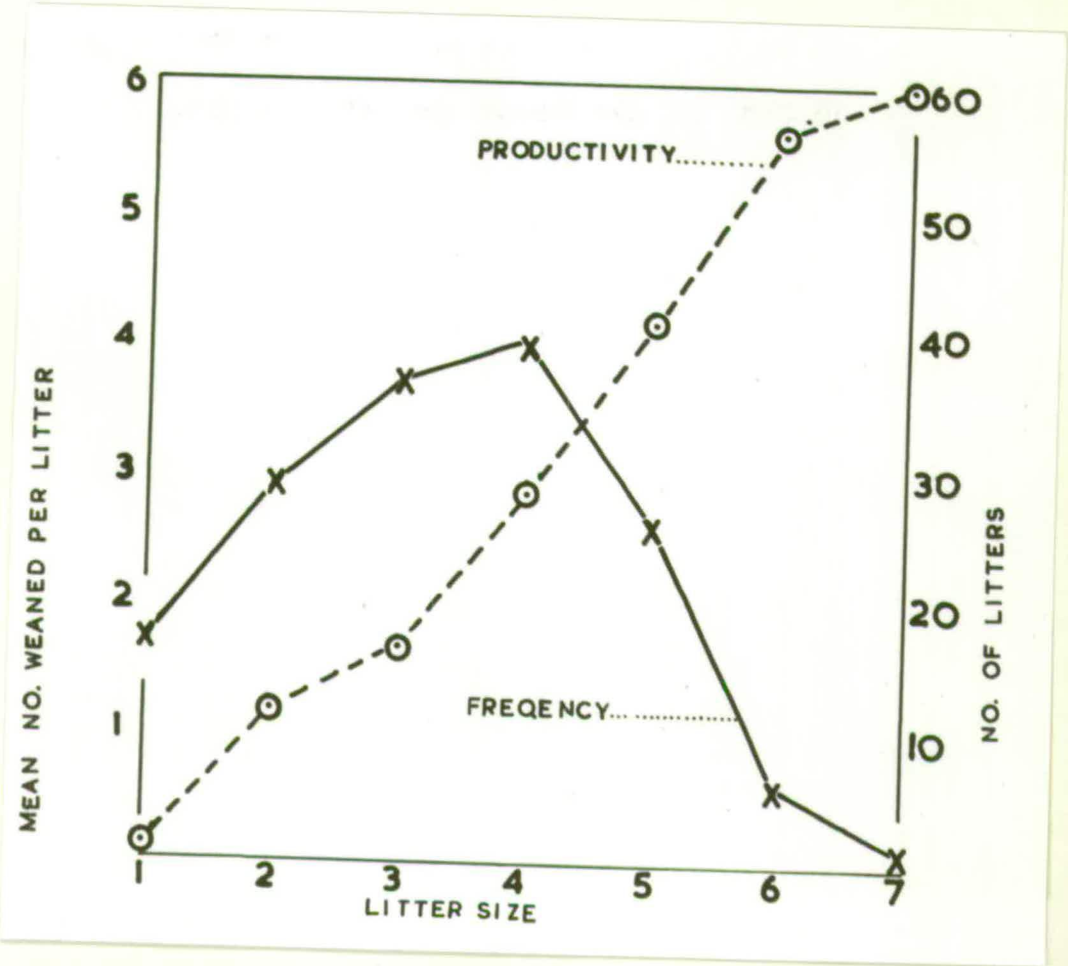
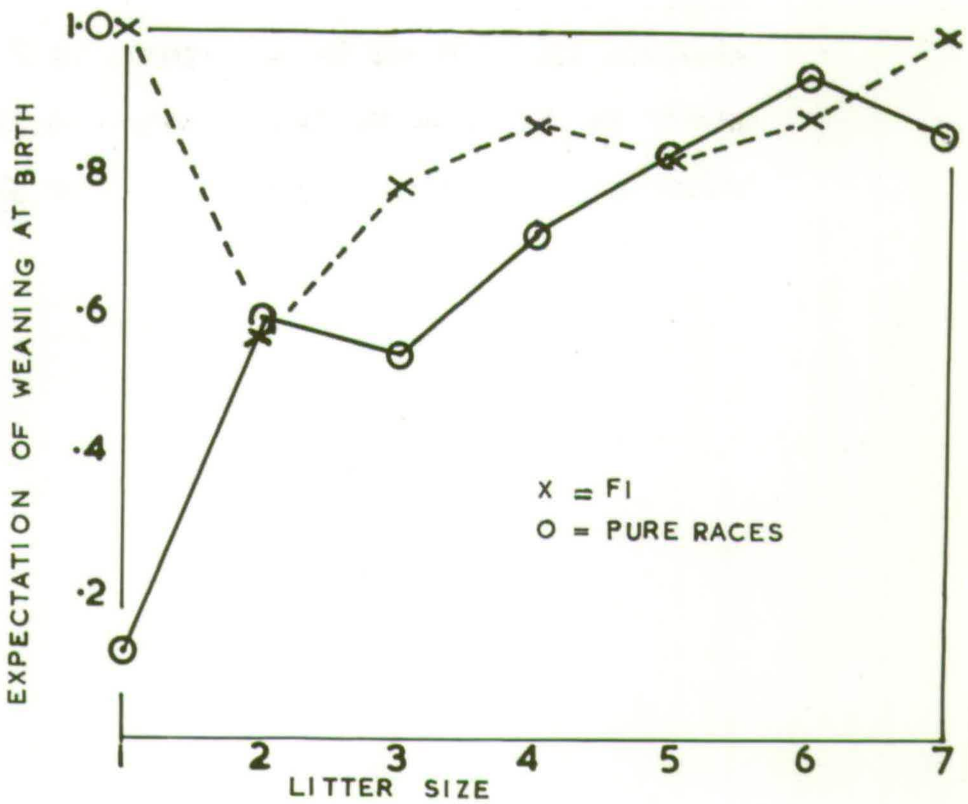

PRODUCTIVITY..........
FREQENCY... ....
MEAN NO. WEANED PER LITTER
NO. OF LITTERS
LITTER SIZE
1
2
3
4
5
6
7
10
20
30
40
50
60

Fig. 27 A comparison of the likelihood of weaning, for various litter sizes, in F_1 hybrid babies in relation to the expectation for young which have been bred within a race of Clethrionomys.



1·0
·8
·6
·4
·2
EXPECTATION OF WEANING AT BIRTH
1
2
3
4
5
6
7
LITTER SIZE
X = F1
O = PURE RACES

Fig. 28 A comparison of the likelihood of weaning, for various litter sizes, in the progeny of pure race parents (pure race and hybrid offspring) in relation to the expectation for the progeny of hybrid parents (F_2 and backcross offspring).

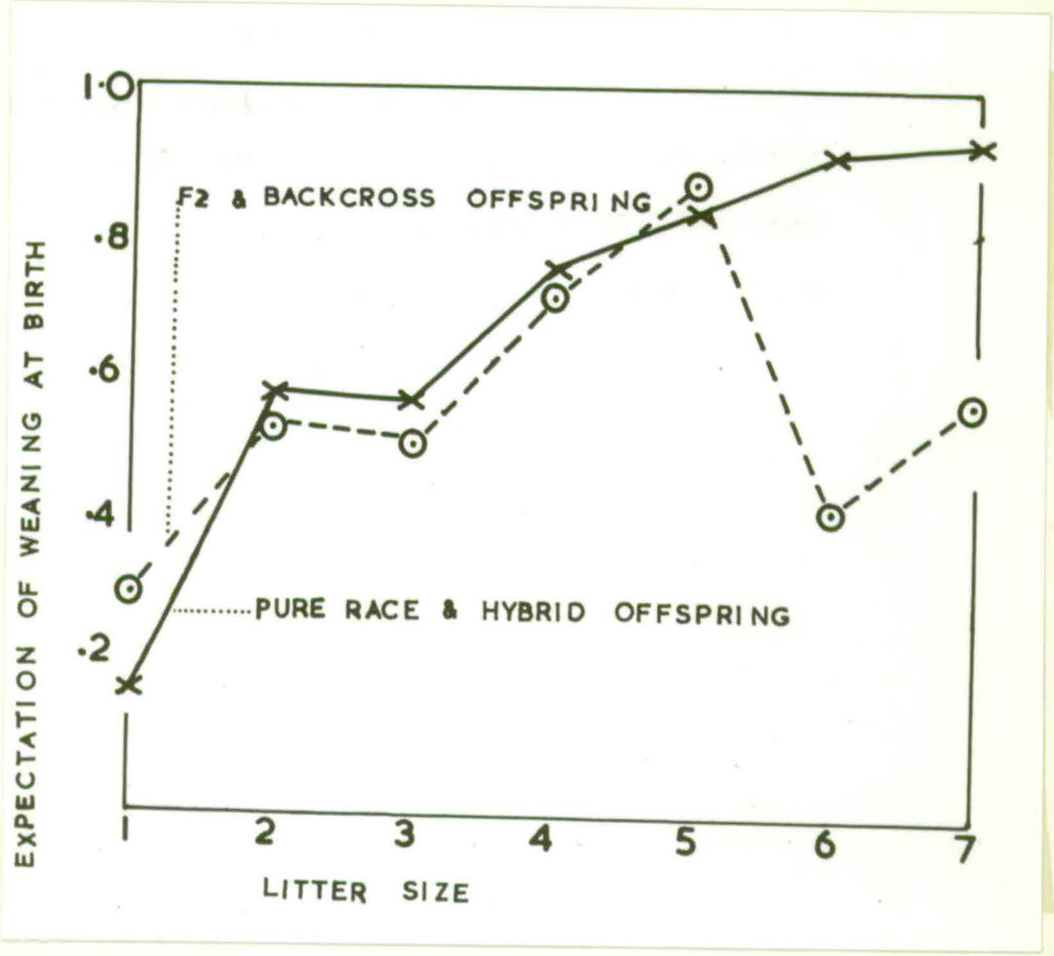
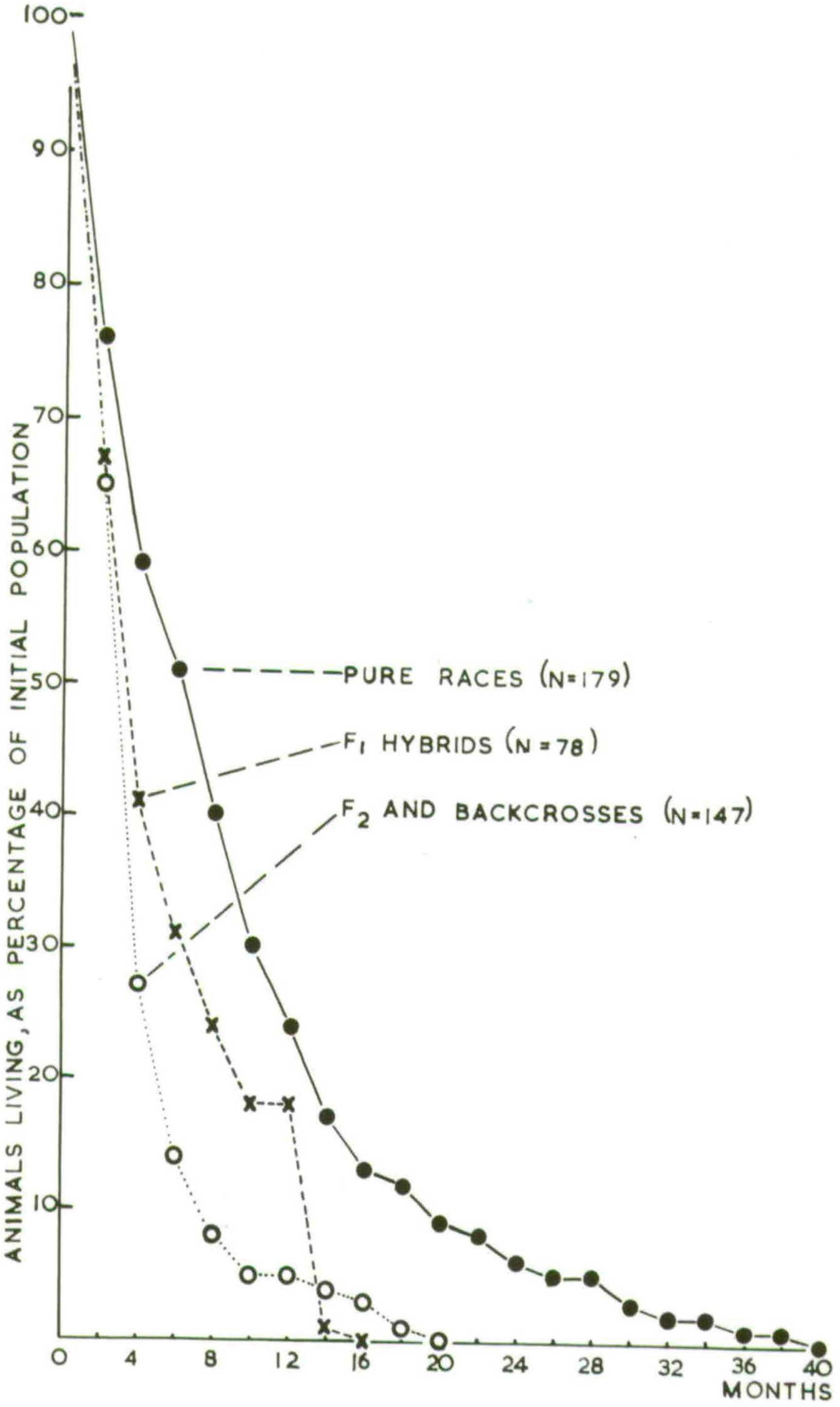

1·0
·8
·6
·4
·2
EXPECTATION OF WEANING AT BIRTH
F2 & BACKCROSS OFFSPRING
PURE RACE & HYBRID OFFSPRING
1
2
3
4
5
6
7
LITTER SIZE

Fig. 29 To show the effect of hybridization on the longevity of <u>Clethrionomys</u> after weaning, in captivity.



100
90
80
70
60
50
40
30
20
10
0
4
8
12
16
20
24
28
32
36
40
MONTHS
ANIMALS LIVING, AS PERCENTAGE OF INITIAL POPULATION
PURE RACES (N=179)
F_1 HYBRIDS (N=78)
F_2 AND BACKCROSSES (N=147)

Fig. 30 The change in weight distribution of a population of Clethrionomys glareolus in Slovakia during the breeding season (from the data published by Turček 1953).

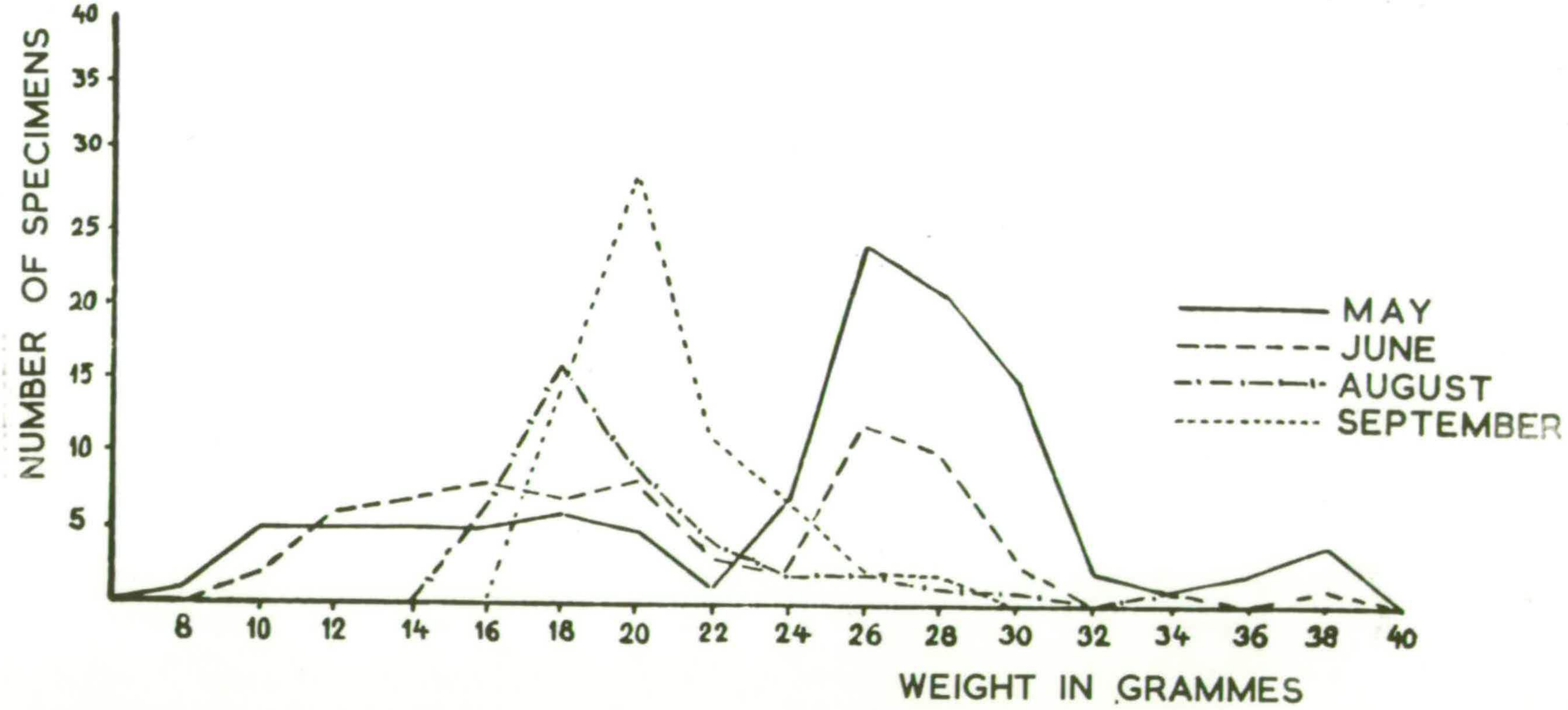
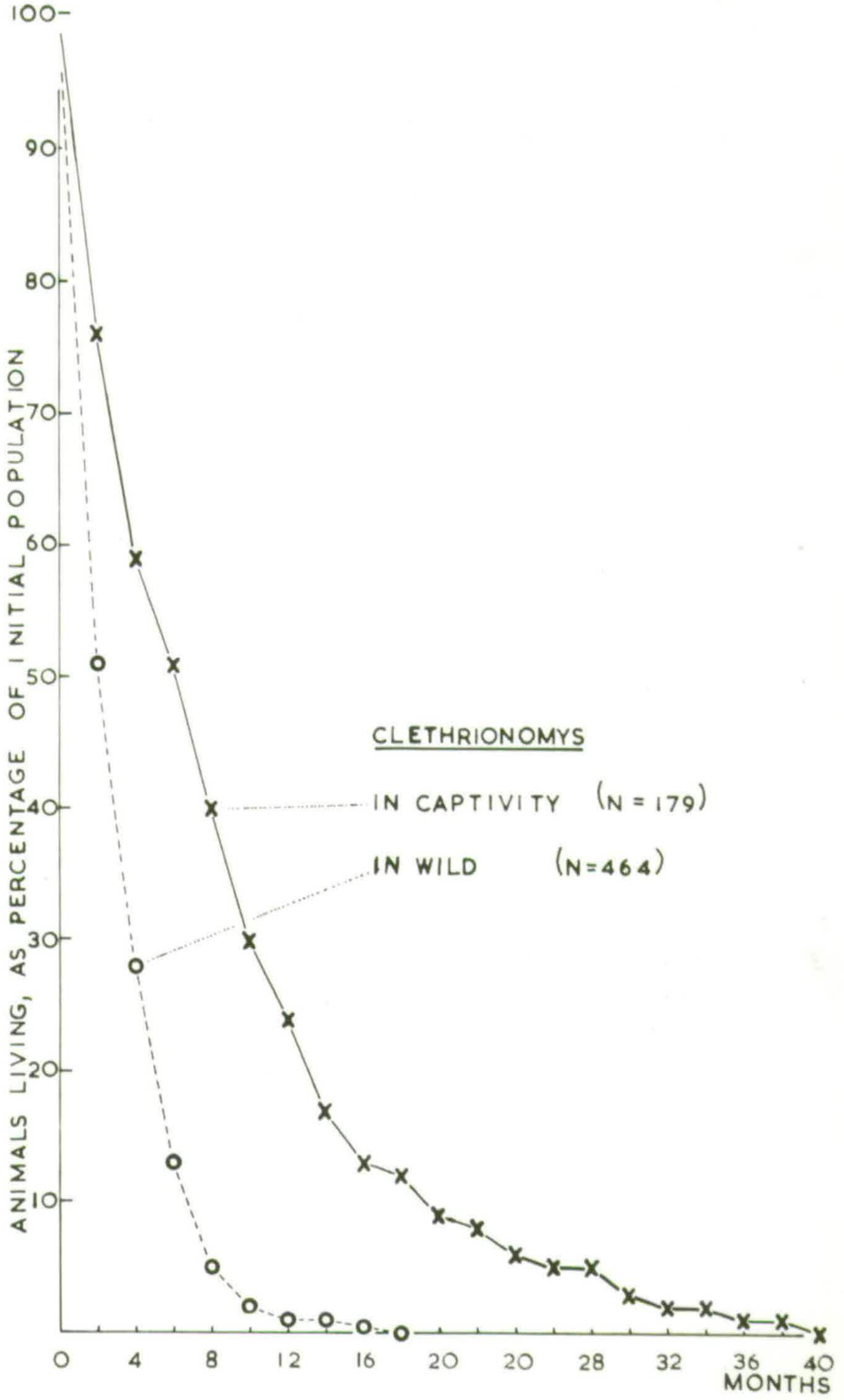

NUMBER OF SPECIMENS
40
35
30
25
20
15
10
5
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
WEIGHT IN GRAMMES
MAY
JUNE
AUGUST
SEPTEMBER

Fig.31 To show the longevity of <u>britannicus</u> in captivity and in the wild.

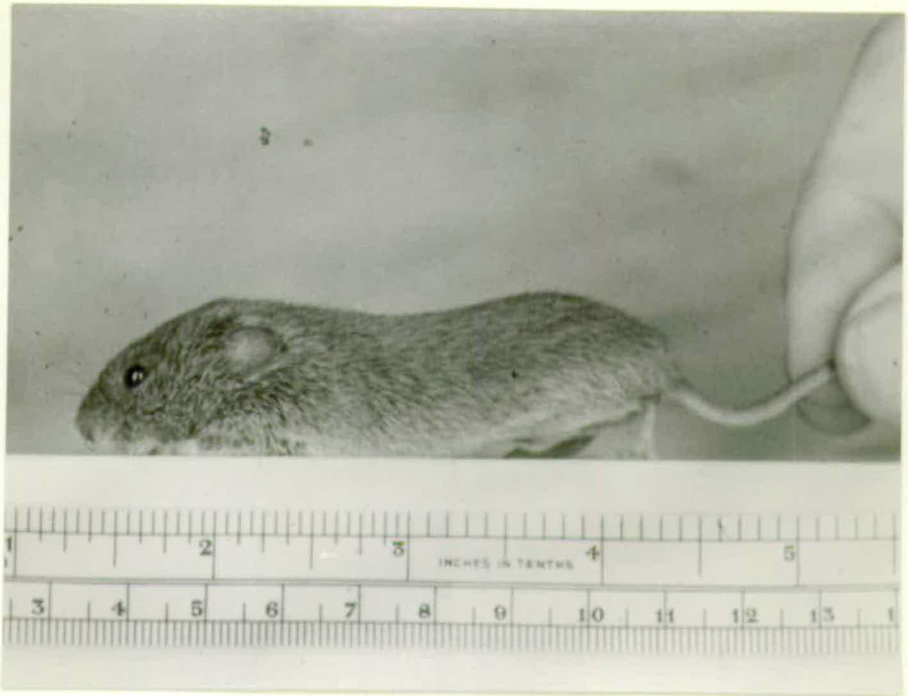
The captive animals life is recorded from weaning. The life of the wild animals as plotted is the interval between the first and the last time the individuals were trapped. (see text).

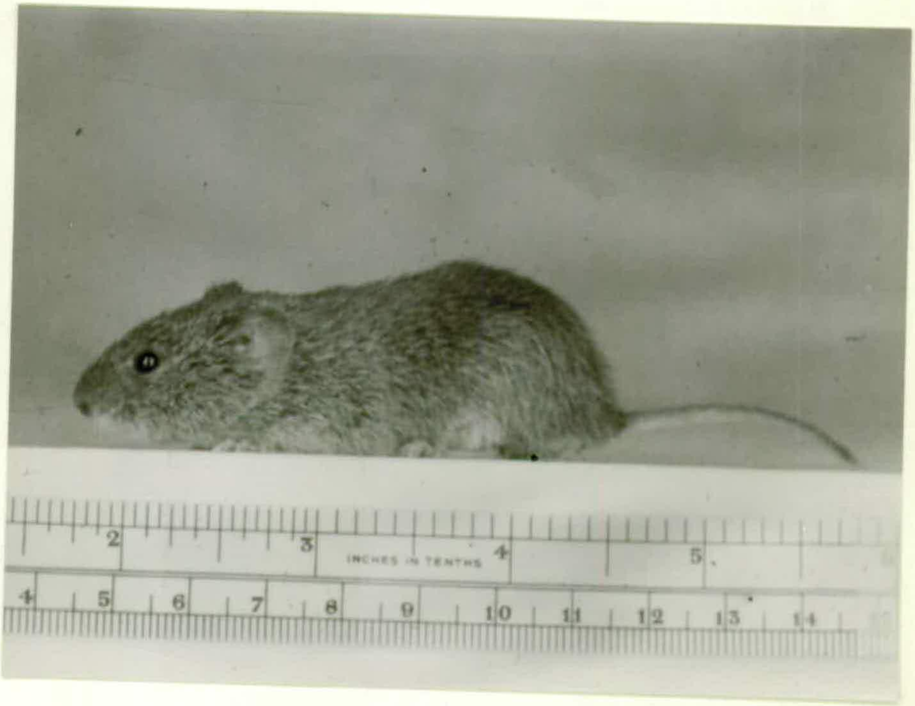

100
90
80
70
60
50
40
30
20
10
ANIMALS LIVING, AS PERCENTAGE OF INITIAL POPULATION
CLETHRIONOMYS
IN CAPTIVITY (N = 179)
IN WILD (N=464)
0
4
8
12
16
20
20
28
32
36
40
MONTHS

BRITISH FORMS OF *CLETHRIONOMYS* (1)

Plate 1 *britannicus* from the Edinburgh district.

Plate 1a *britannicus* from Kintyre.

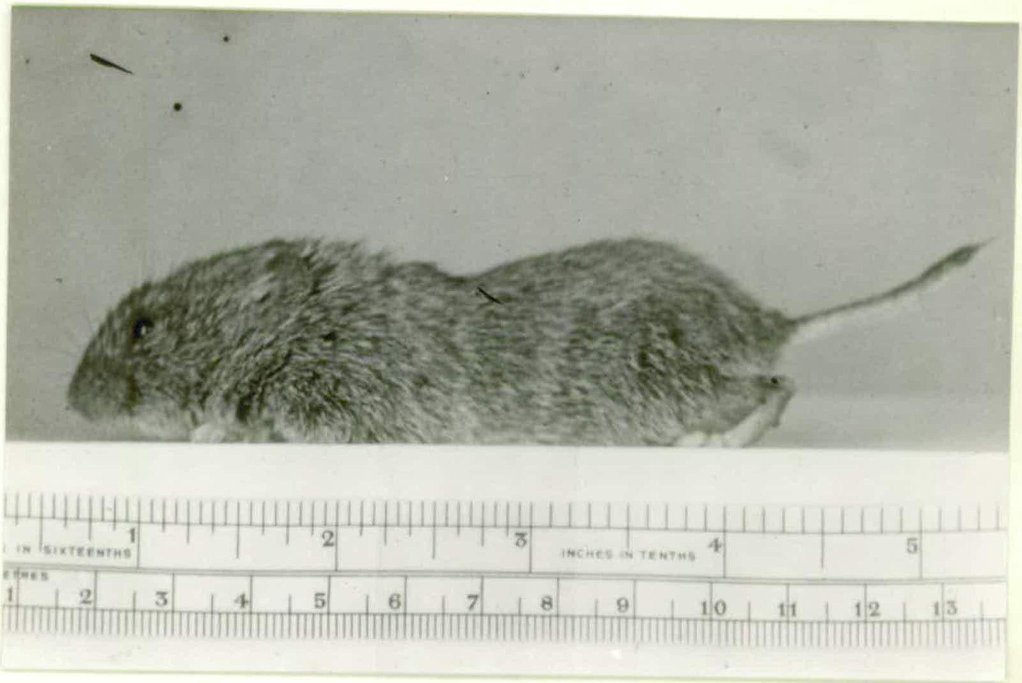

1 2 3 INCHES IN TENTHS 4 5
3 4 5 6 7 8 9 10 11 12 13


2 3 INCHES IN TENTHS 4 5
4 5 6 7 8 9 10 11 12 13 14

BRITISH FORMS OF *CLETHRIONOMYS* (ii)

Plate 2 *erica*

Plate 2a *erica* - an individual carrying the recessive gene for greyness. Note also the rough coat texture and shorter tail.


IN SIXTEENTHS
INCHES IN TENTHS
1
2
3
4
5
1
2
3
4
5
6
7
8
9
10
11
12
13

BRITISH FORMS OF *CLETHRIONOMYS* (iii)

Plate 3 *alstoni*

Plate 4 *skomerensis*


IN SIXTEENTHS
INCHES IN TENTHS

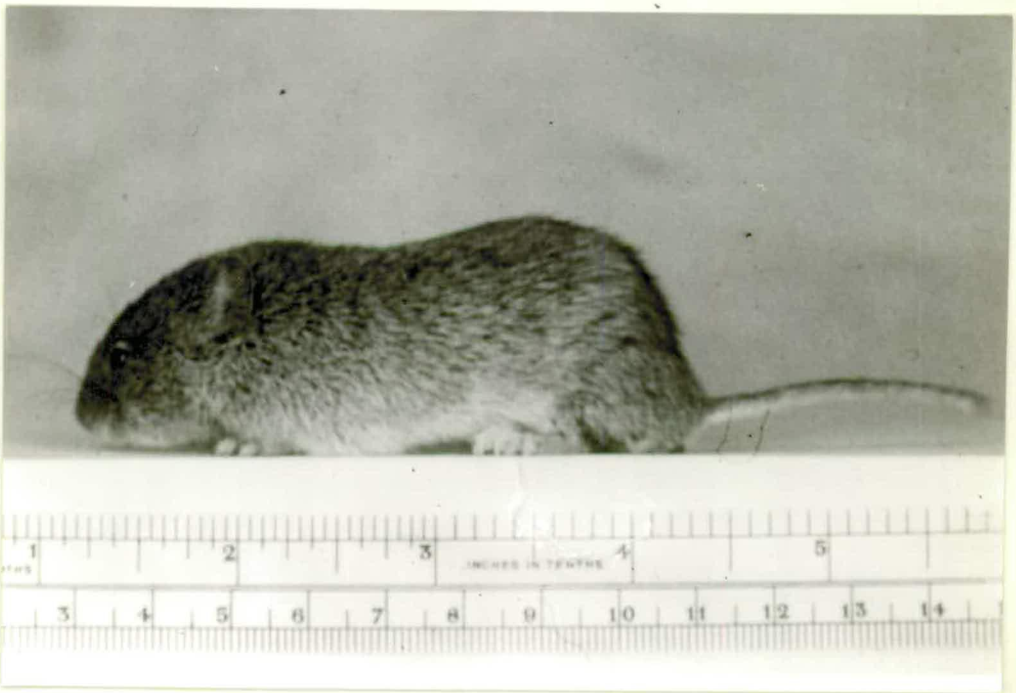

INCHES IN TENTHS

Plate 5 To show the design of the Longworth live trap which was used to test the reaction of bank voles to a strange object.

When the nest box is entered from the tunnel a treddle releases a self locking door, which falls to close the mouth of the tunnel.

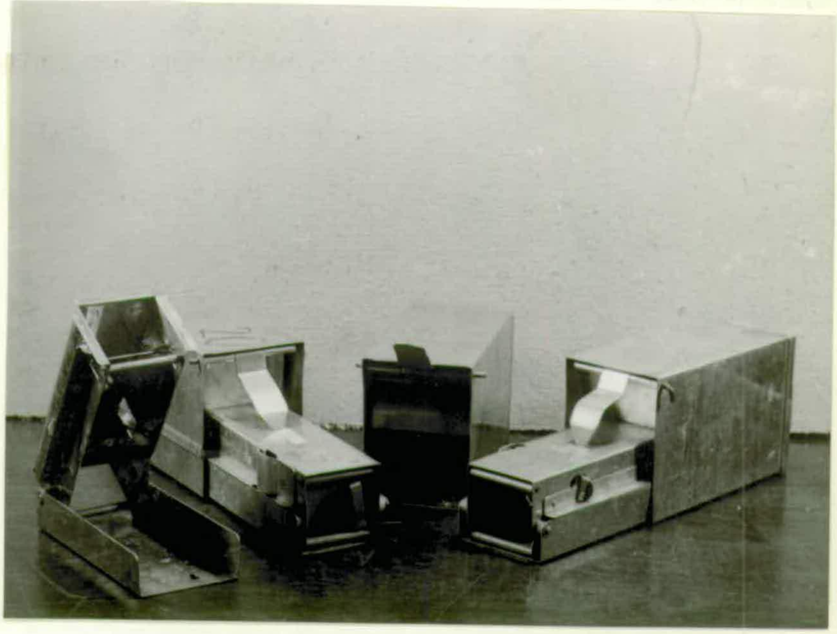


Plate 6 A pair of reels of paper with the records of rhythmic behaviour of four voles.

It can be determined whether a vole spent any part of each minute on the floor of its cage

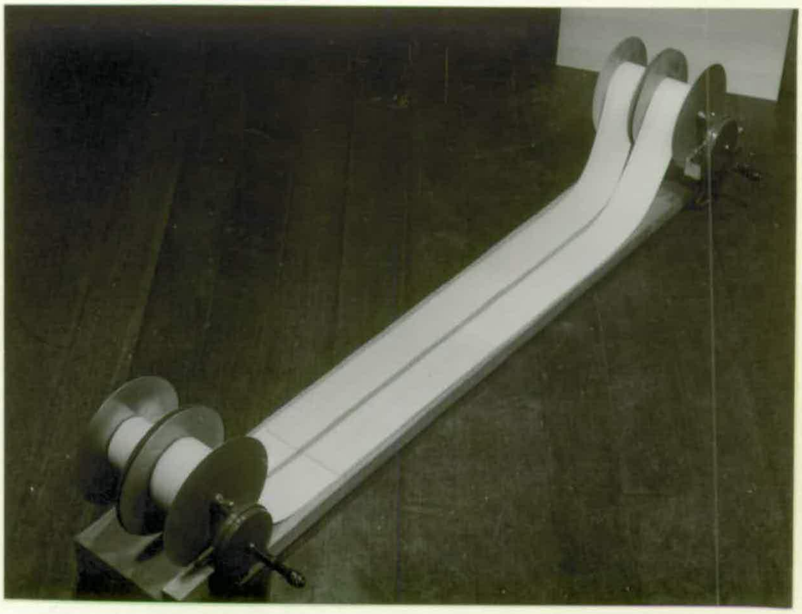
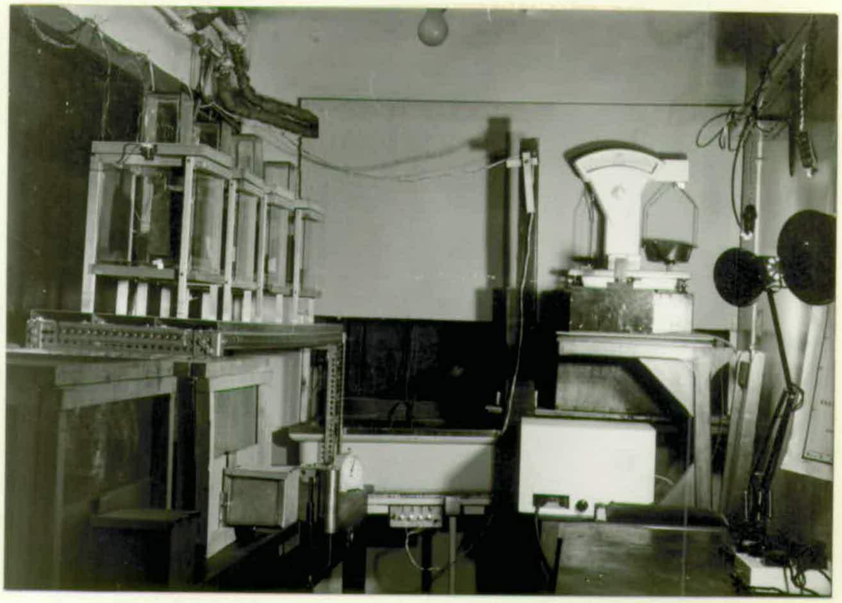


Plate 7. Apparatus used for studying rhythmic behaviour. Cages with moveable floors, on the left; place from which visual and infra-red observations were made, on the right.
A screen shielding the cages from direct illumination, and partly hiding the observer from the voles, have been removed.

Plate 8 Cages used to investigate rhythmic behaviour.

The nest box, and food and water container, of the nearest cage have been removed and opened. The floor is hung from springs. The suspension operates a mercury switch.



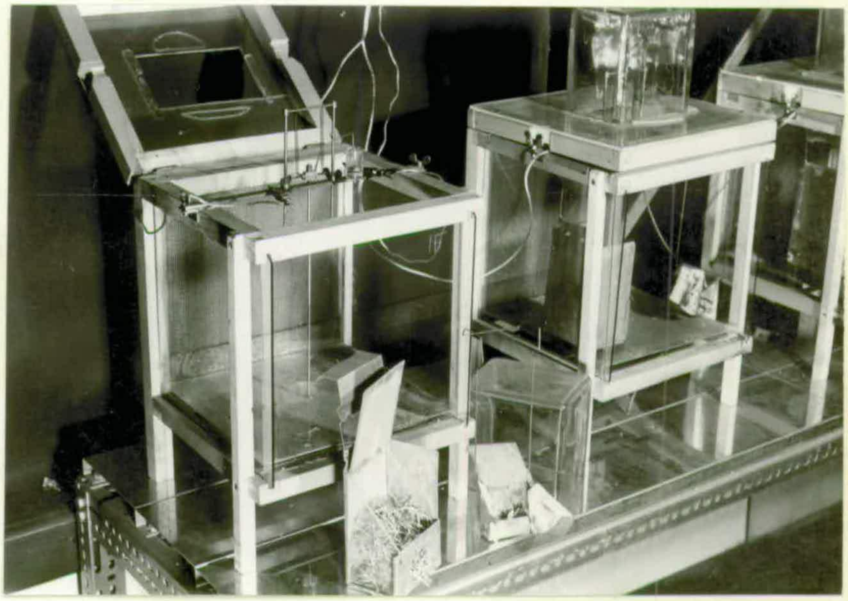
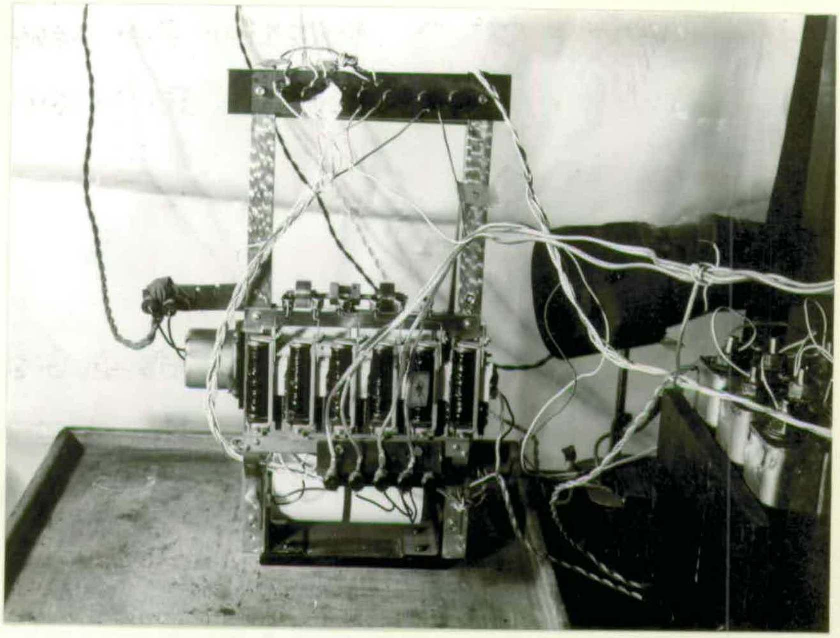
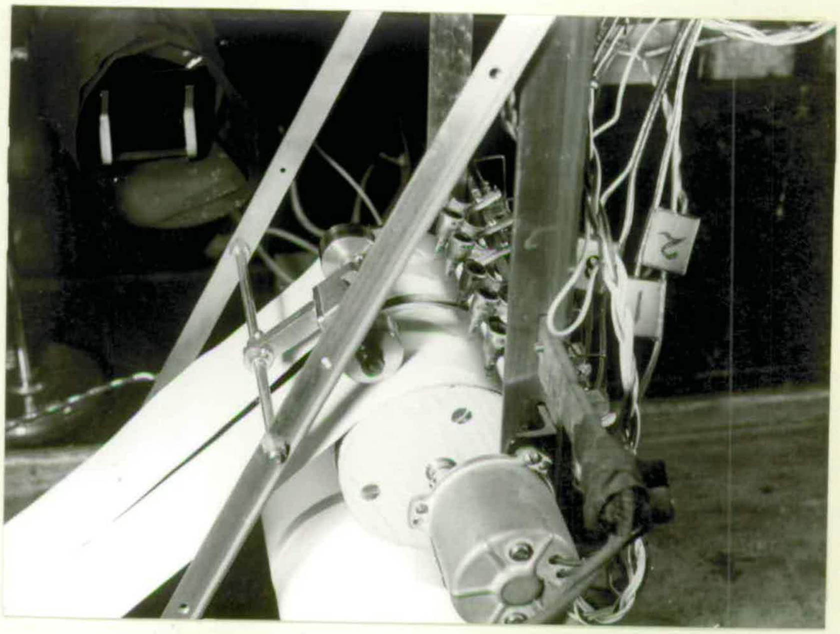


Plate 9 and 10 Apparatus for recording each time four voles step onto, and off the floor of their respective cages.

The upper roller, on which the uno pens write, rotates once each hour, and a time mark is made. The relays operate signal lamps as well as the pens.



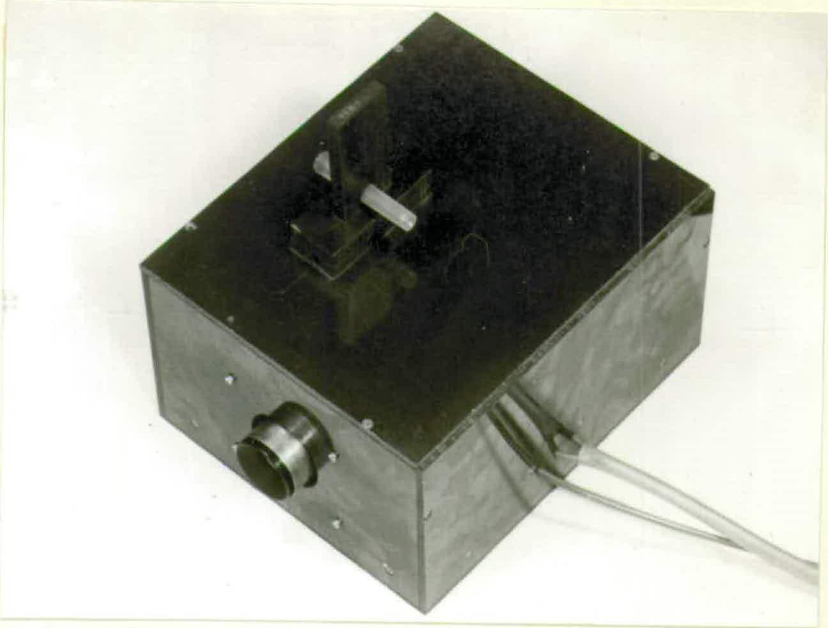

2
1

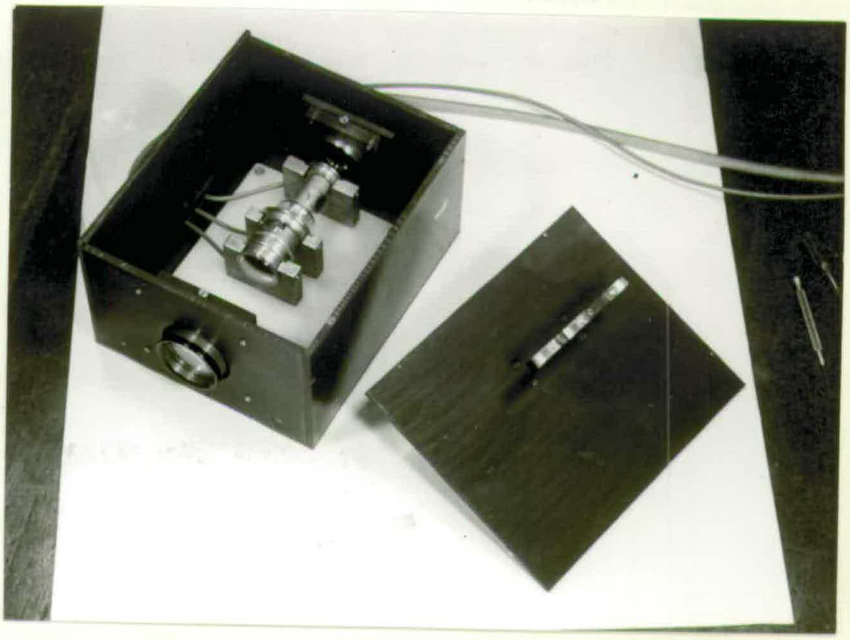
Infra-red image converter for the observation of bank voles in darkness.

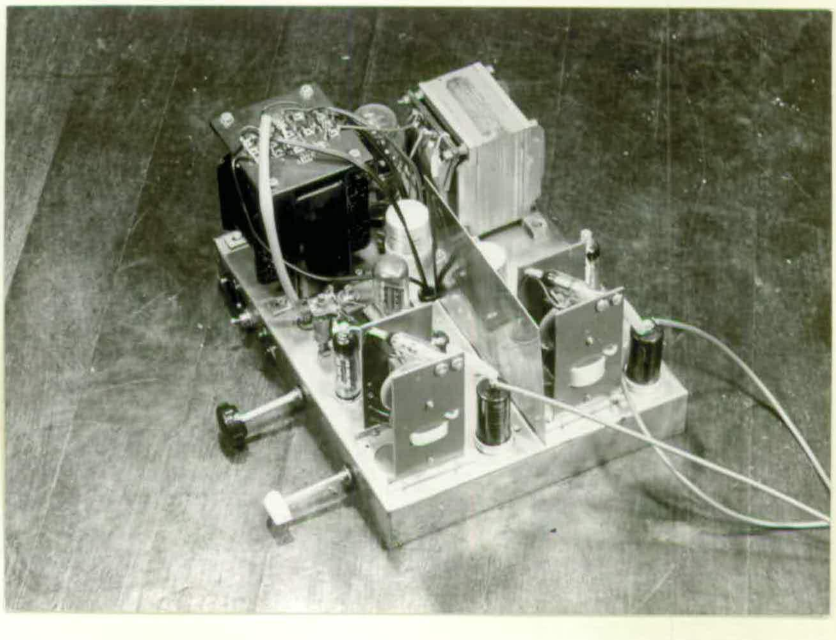
Plate 11 The viewing end of the apparatus showing the eyepiece and earthing device.

Plate 12 The apparatus opened to show the image converter tube, from the objective end.

Plate 13 The supply for 20 Kv and 4-8 Kv.

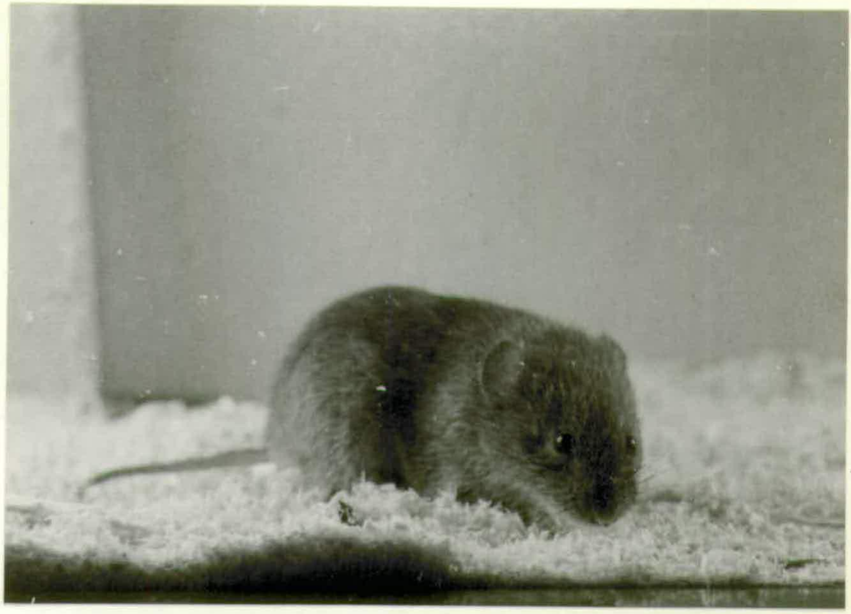


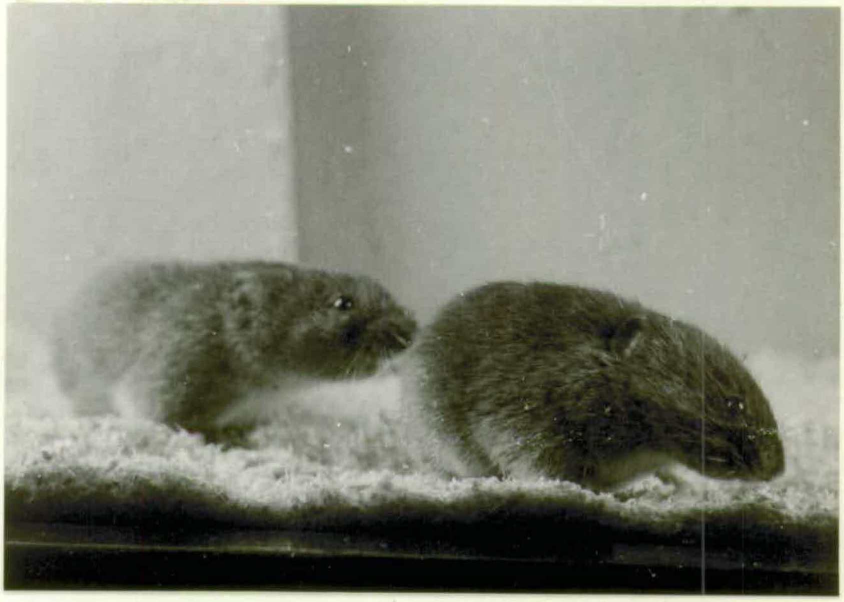




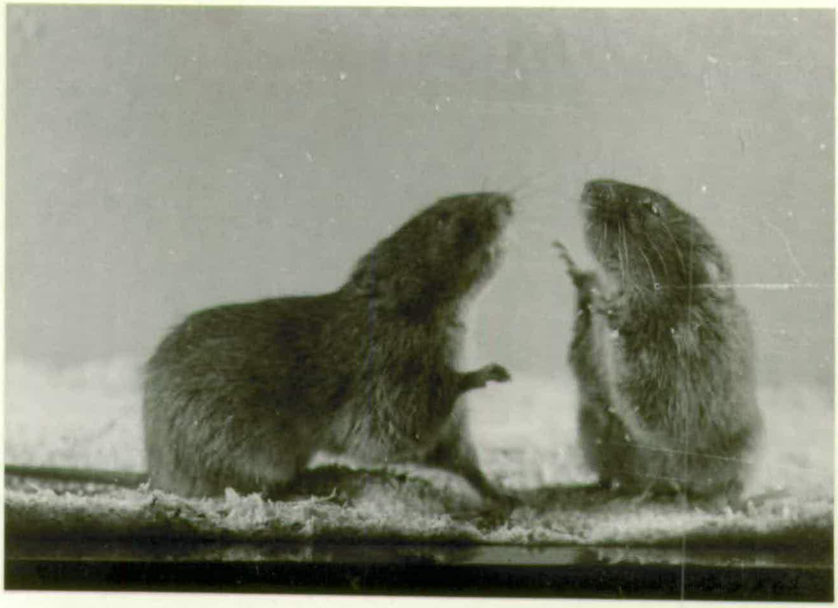
AGRESSIVE BEHAVIOUR 1. *erica* male resident; *alstoni* male visitor (i)

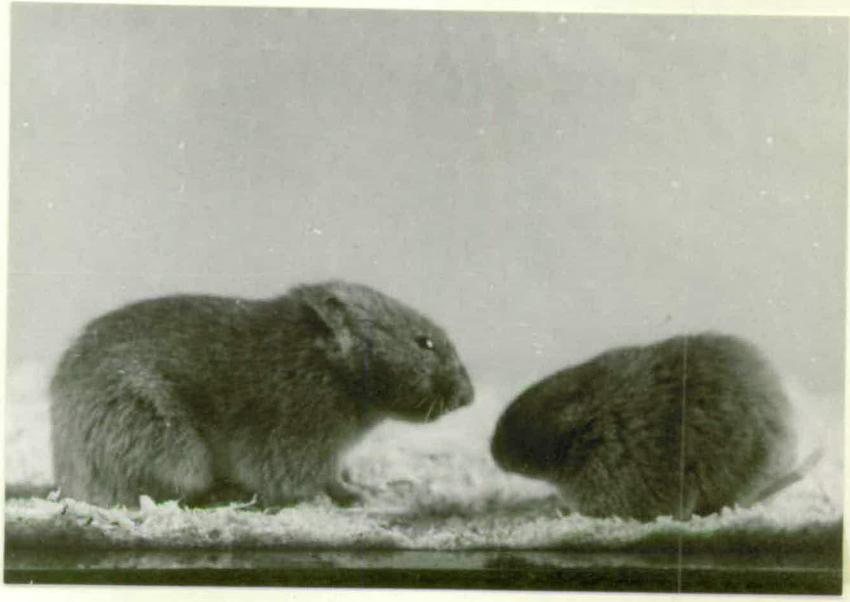
Plate 14	*erica* approaches *alstoni*
Plate 15	and sniffs him
Plate 16	*erica* in the prelunge position, *alstoni* defensive





AGRESSIVE BEHAVIOUR 1.	*erica* male resident; *alstoni* male visitor (ii)
Plate 17	*erica* in the pre-lunge position, *alstoni* boxing
Plate 18	*erica* and *alstoni* brawl
Plate 19	*alstoni* in the hunched submission posture.





AGRESSIVE BEHAVIOUR 2. *britannicus* male "A" resident;
britannicus male "B" visitor (i)

Plate 20	"A" and "B" boxing
Plate 21	"A" scuffling

AGGRESSIVE BEHAVIOUR 2 (ii)

Plate 22 britannicus male "B" in the rigid submission posture

AGGRESSIVE BEHAVIOUR 3

Plate 23 A resident alstoni male lunges at a visiting erica male.

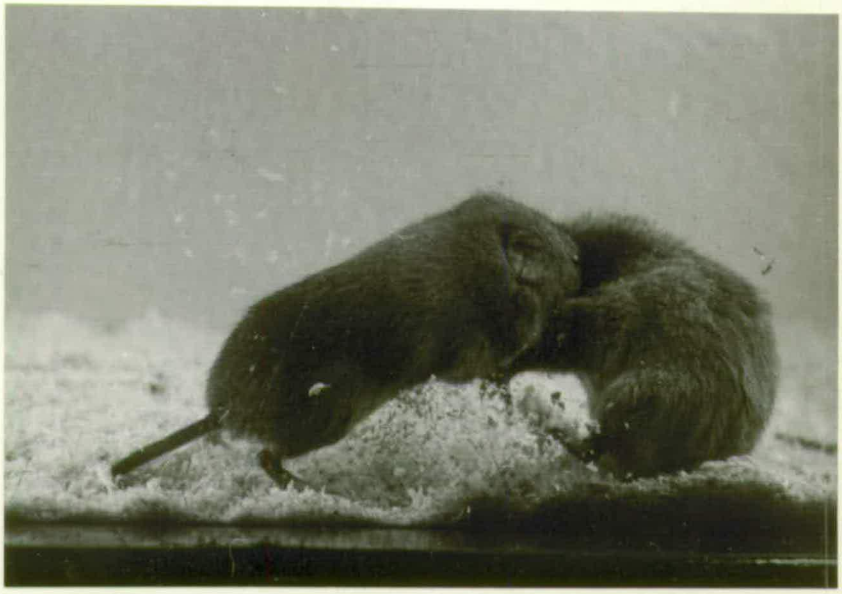
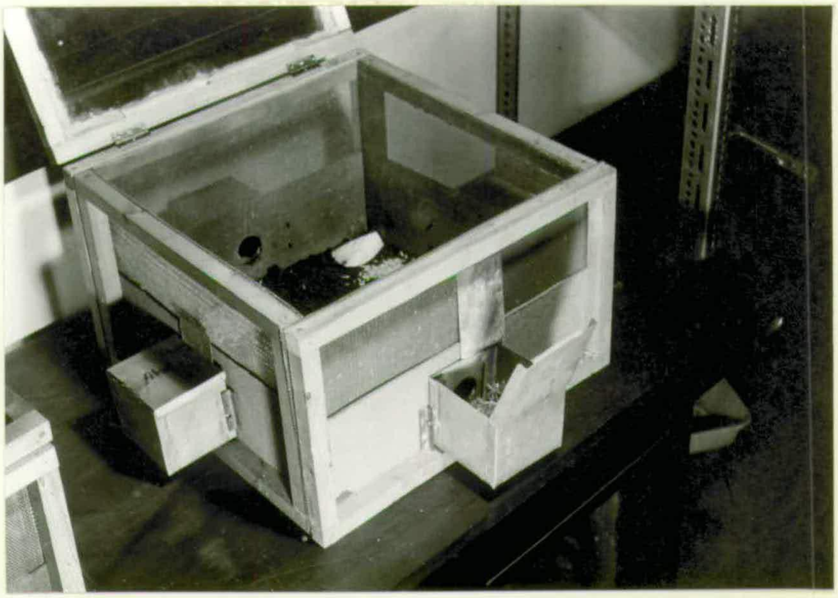


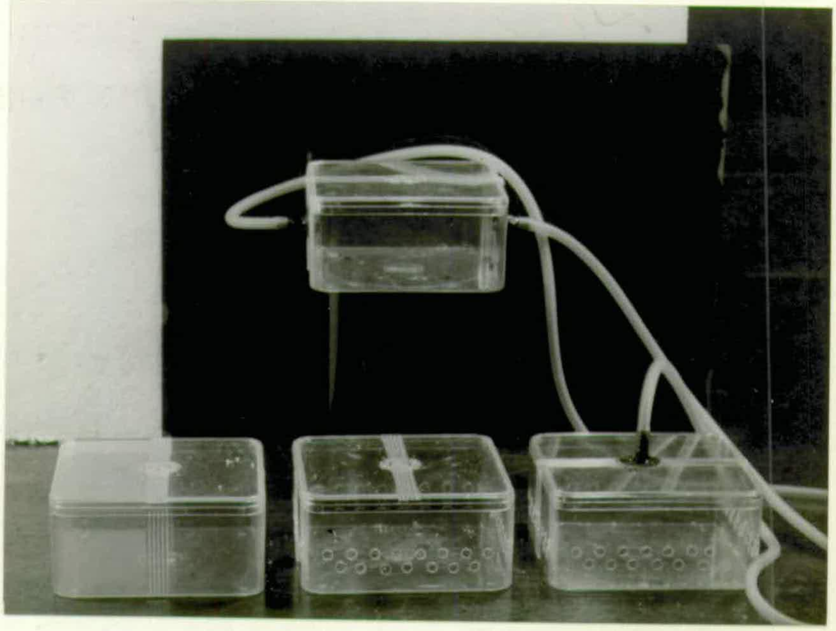
Plate 24 One of the cages used to house experimental communities of four bank voles. Each of the four nest boxes can be shut off from the cage, and opened for inspection, from outside the cage.

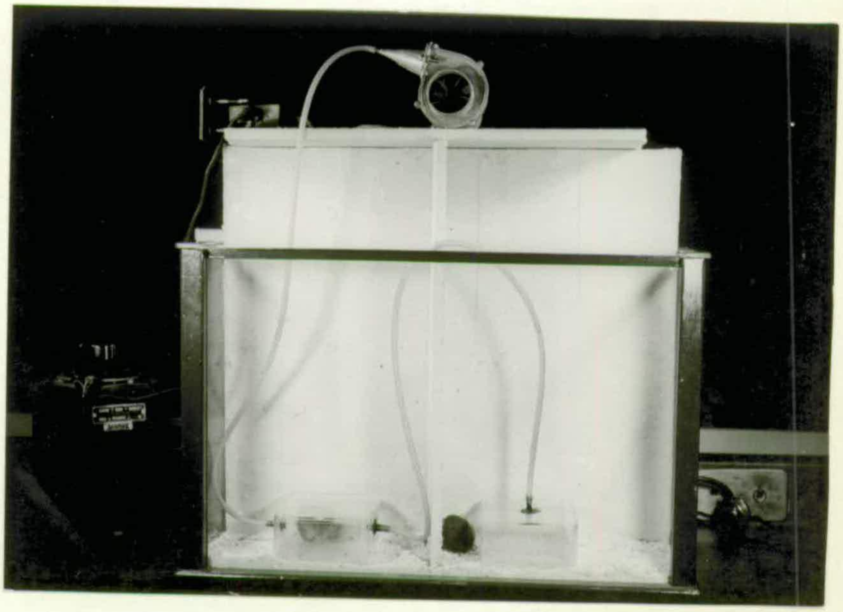


APPARATUS FOR INVESTIGATING THE IMPORTANCE OF OLFACTORY CUES IN THE RECOGNITION BY A MALE OF THE RACE OF A FEMALE.

Plate 25 The boxes used (see text)

Plate 26 The apparatus for an experiment of type D
(see Fig. 18).





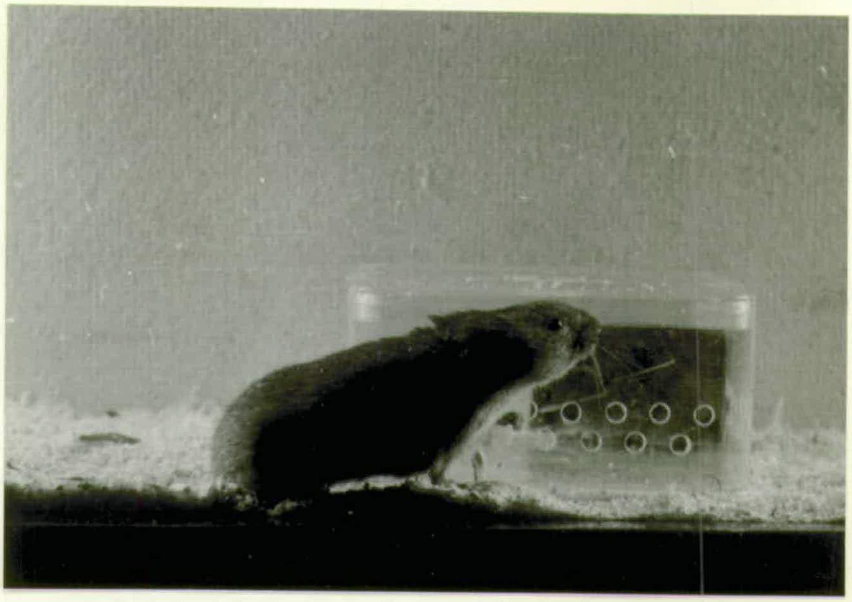
TEST FOR THE IMPORTANCE OF OLFACTORY CUES (TYPE B)

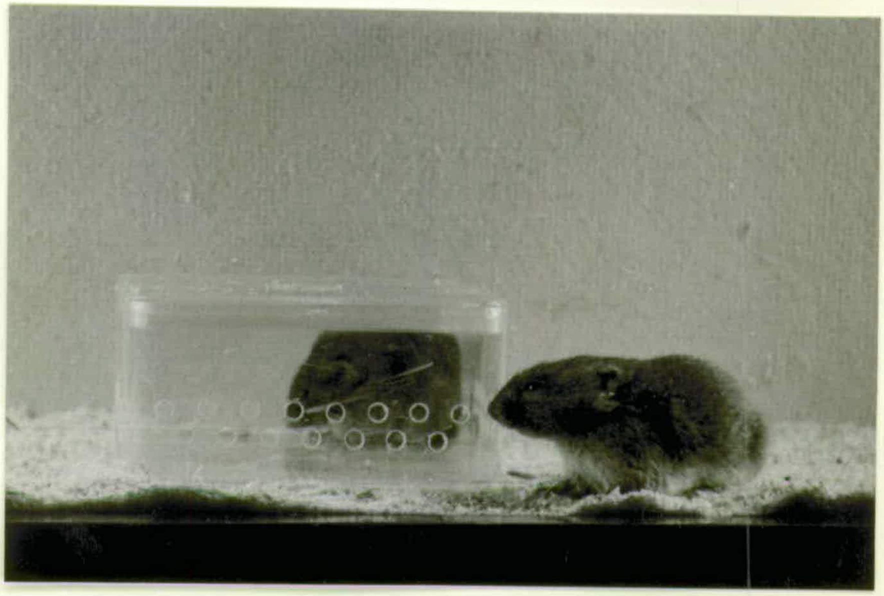
alstoni male and female (i)

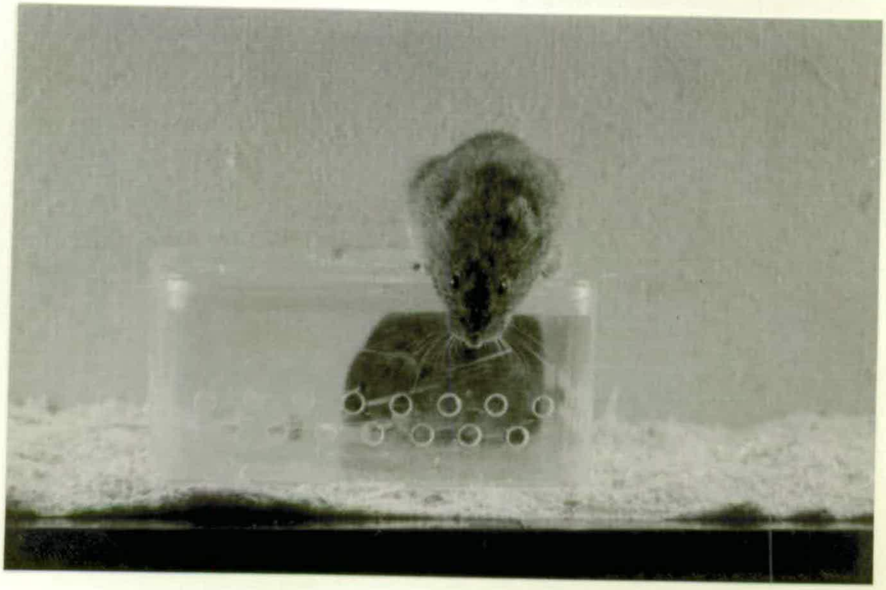
Plate 27 The male approaches, squeaking,

Plate 28 Sniffs at a hole in the box, the female not trying to escape,

Plate 29 and climbs on the box.





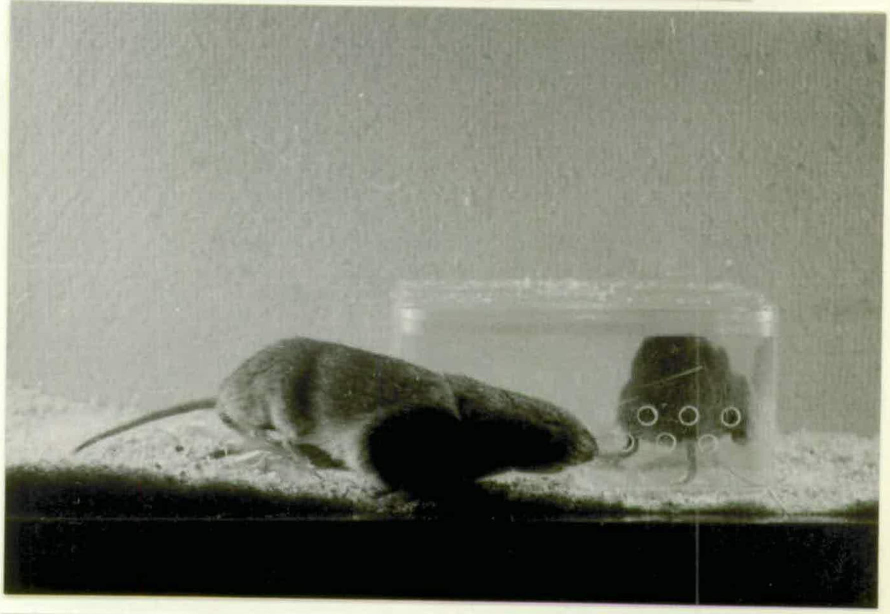


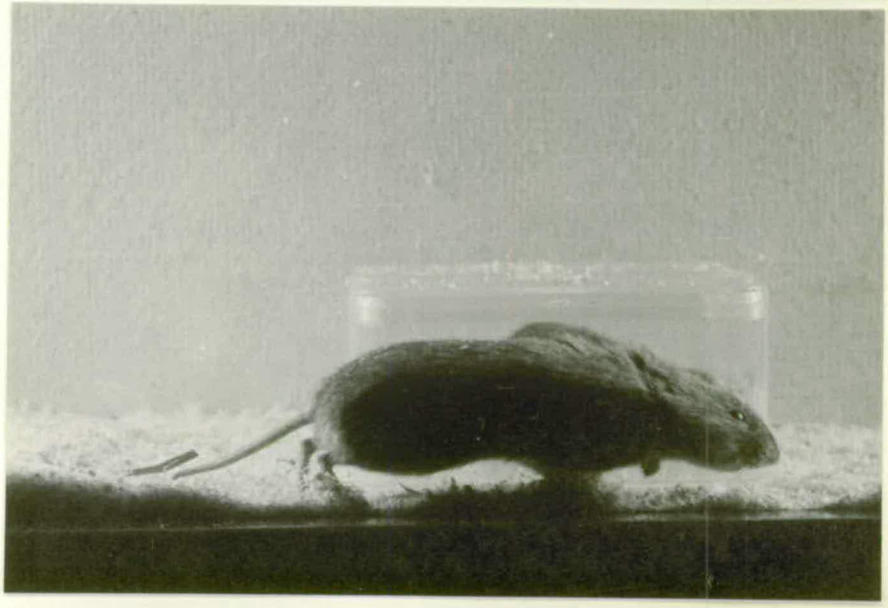
TEST FOR THE IMPORTANCE OF OLFACTORY CUES (TYPE B)

alstoni male and female (ii)

Plate 30 The male leaps.

Plate 31 and Plate 32 The male scuffles and the female attempts to escape.

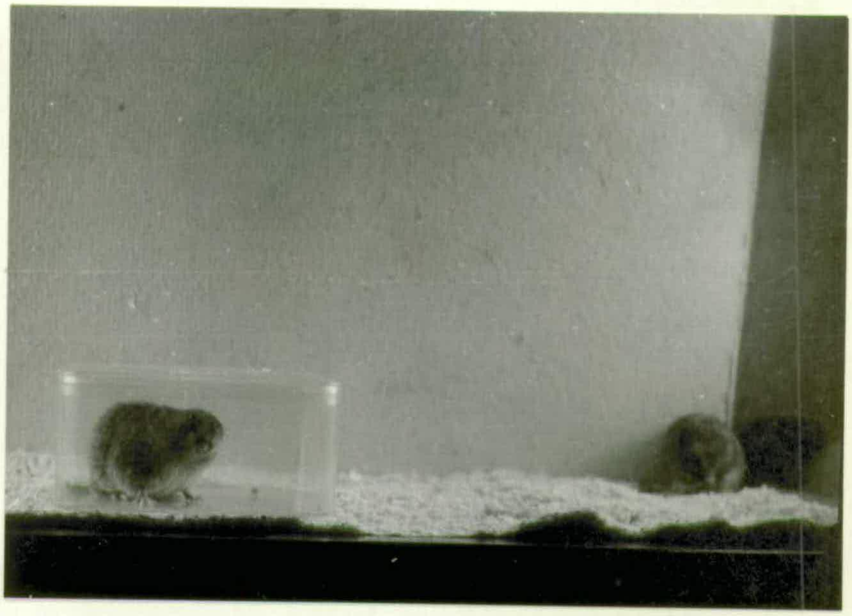


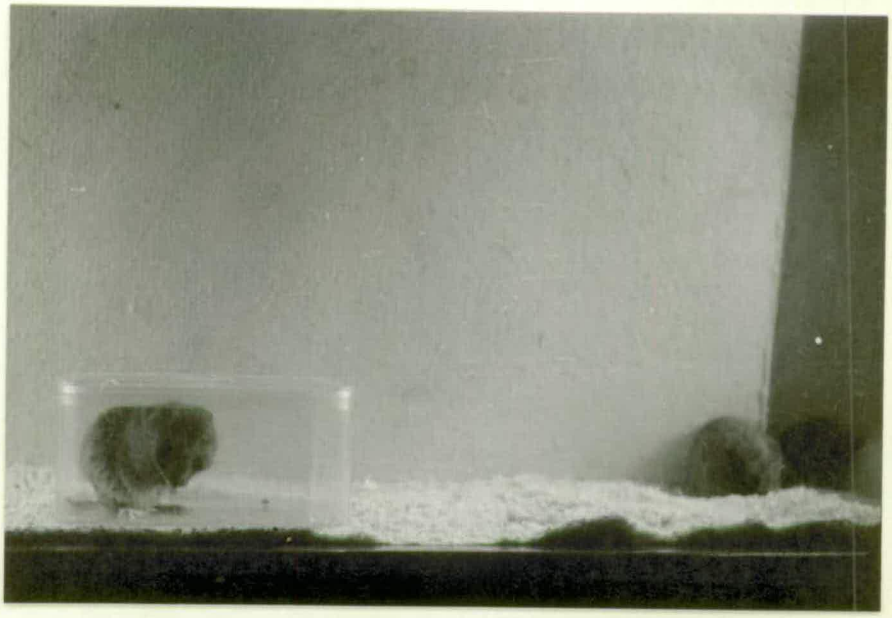


TEST FOR THE IMPORTANCE OF OLFACTORY CUES, (TYPE C)

erica male and female

Plate 33 and Plate 34	The male and female make no apparent response to one another.





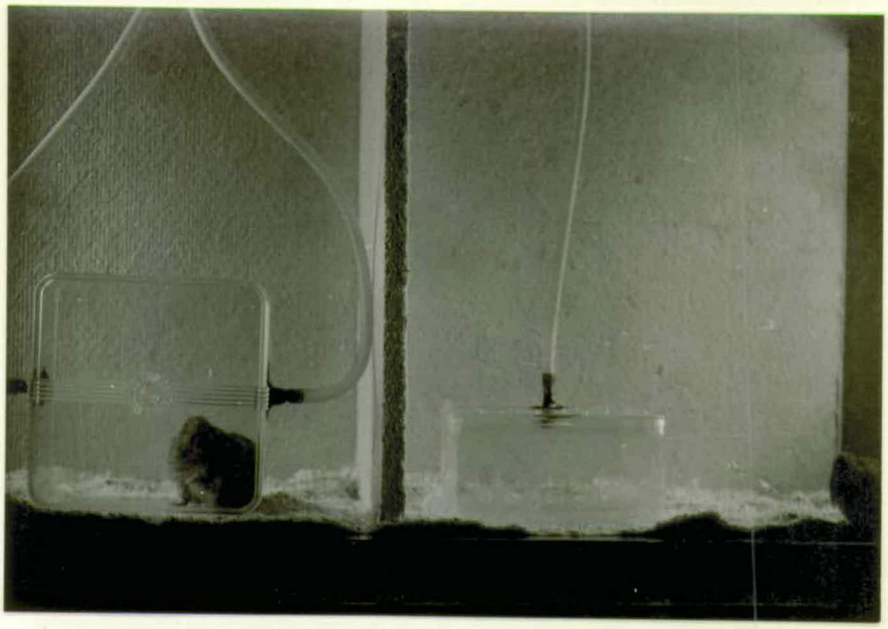
TEST FOR THE IMPORTANCE OF OLFACTORY CUES (TYPE D)

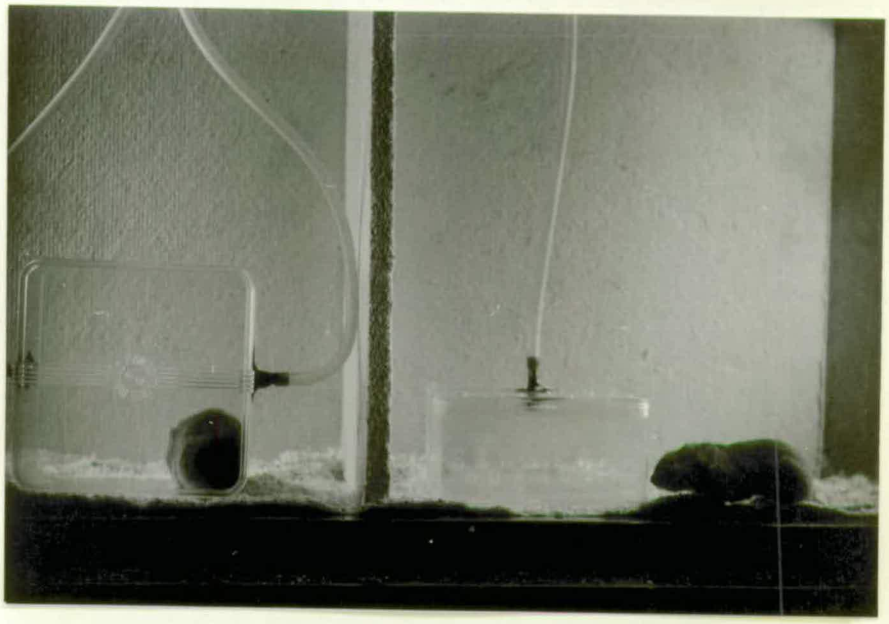
alstoni male and female

Plate 35 The male sits in a corner of the cage.

Plate 36 The male approaches the box, sniffs at it, squeaking

Plate 37 and climbs onto it.





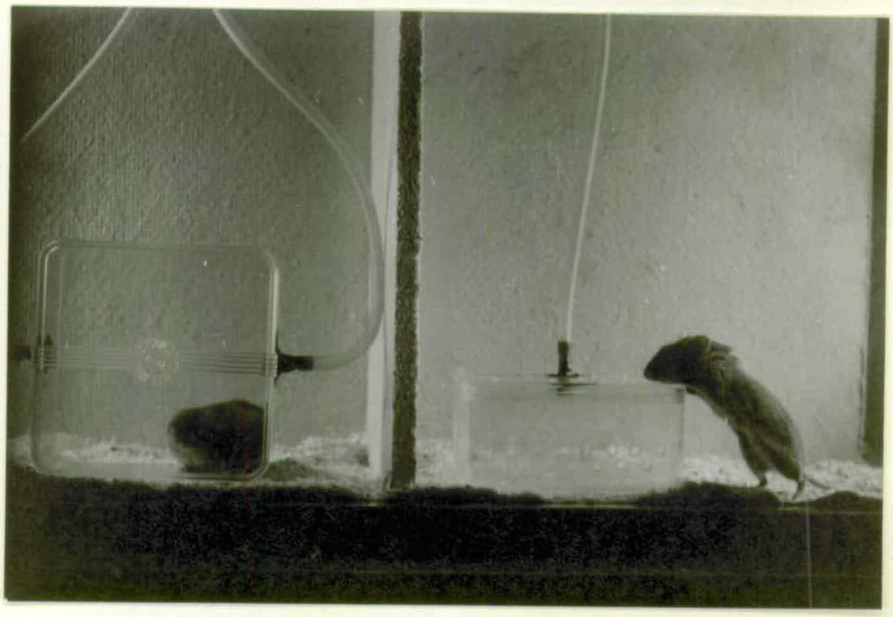
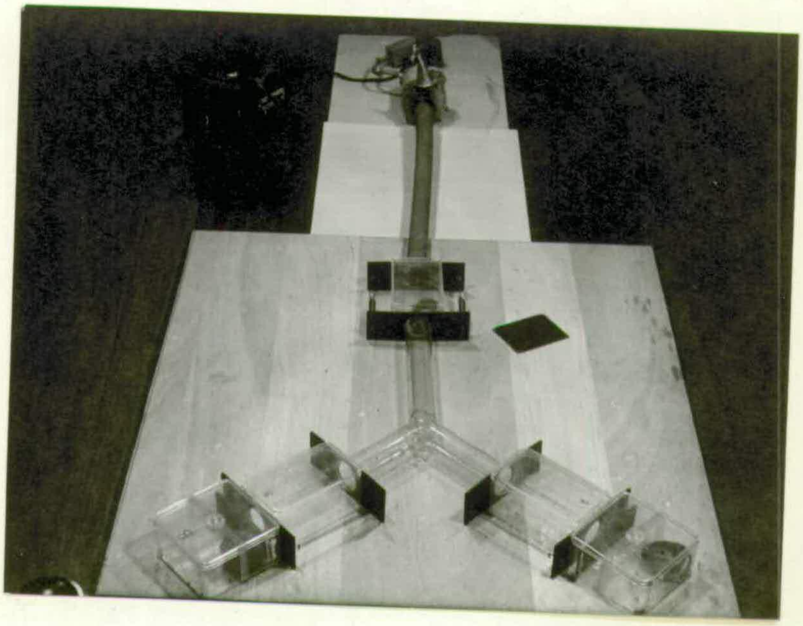
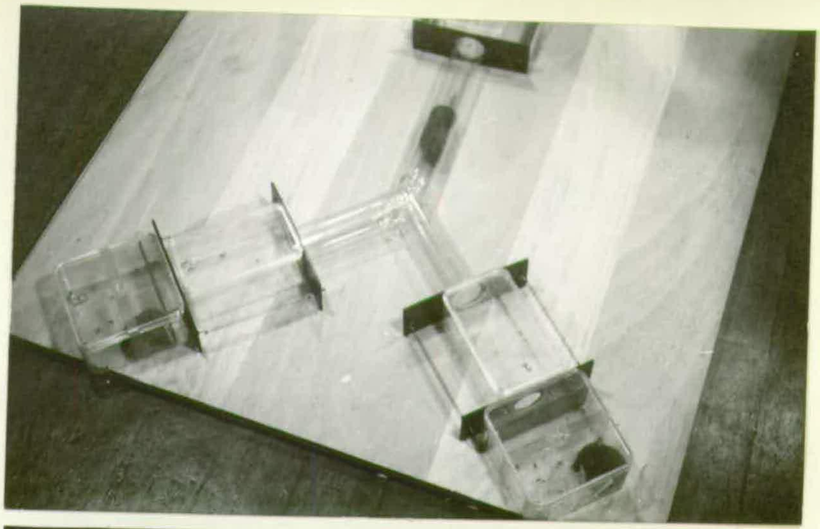


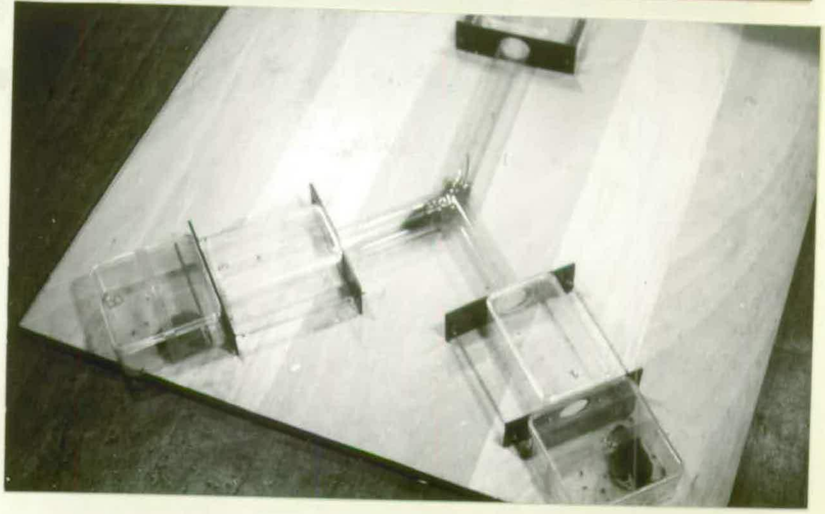
Plate 38 The Y-tube apparatus used in studying the ability of male Clethrionomys to distinguish between the odours of a female of his own, and a female of another, race.

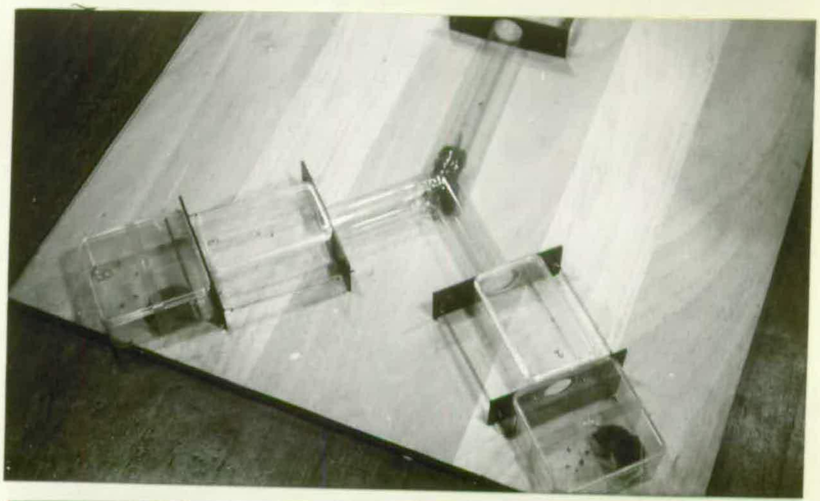


Plates 39 to 42

(i) the male leaves his box
(ii) and (iii) pauses at the Y-junction
moving his head from side to side
and (iv) moves towards the female on
his left.







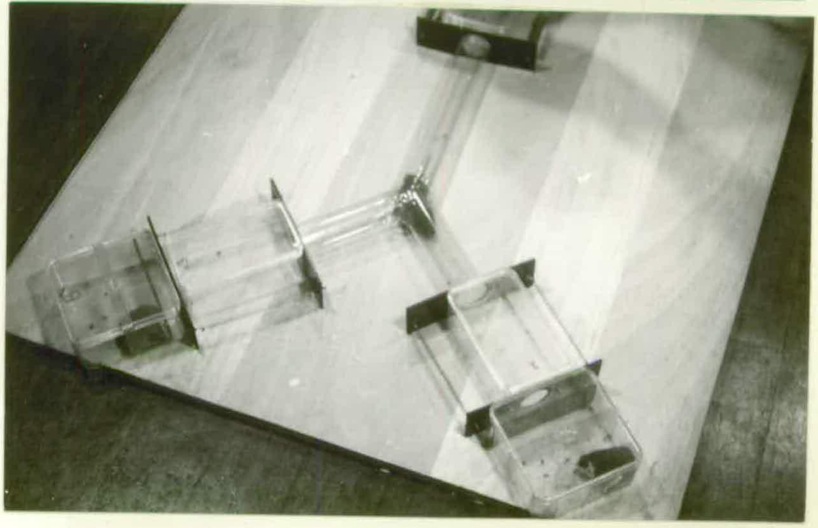


Plate 43 The habitat in which *Clethrionomys* were caught most readily. Morton Hall, Edinburgh

Plate 44 A vole run among grass. Traps were set near such runs if they were present.

SKOMER

Plate 45 An area with little ground cover where Apodemus, but not skomerensis, was common.

Plate 46 View looking S.E. along the Eastern trap line, showing heath; bracken; and marsh habitats.

Plate 47 Part of the battery of 24 cages in which the *Clethrionomys* breeding colony was kept out of doors at the Zoology Department, Edinburgh University.