The relationship between population variables and male aggressive behaviour in communities of bank voles (Clethrionomys glareolus) in large field enclosures.

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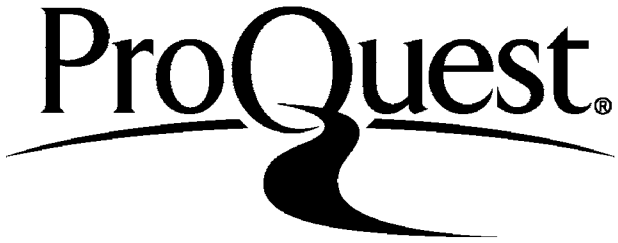

ABSTRACT

J.H.W. GIPPS : The relationship between population variables and male aggressive behaviour in communities of bank voles (Clethrionomys glareolus) in large field enclosures.

The relationship between male aggressive behaviour and population variables in the bank vole (Clethrionomys glareolus (Schreber, 1780)) was studied using two large(550m^2) field enclosures. Known populations were established in each of the enclosures, and followed by live trapping. In an attempt to manipulate the level of aggressive behaviour in one (the experimental) enclosure with respect to the other (the control) a majority of the founding males in the experimental enclosure were castrated.

Laboratory arena testing was used to study the behaviour of adult, castrated and immature male voles. It was demonstrated that both castrated and immature male voles were significantly less aggressive than adult males. Adult males were found to fight less with castrated and immature males than with other adults. Castrated males sometimes exhibited retaliatory behaviour when approached by either an adult or immature male, but overt aggressive behaviour rarely resulted. Immature males were very rarely aggressive.

Observation of behavioural interactions in the field (at a bait point) showed them to be qualitatively different to those observed in the laboratory arena; voles appeared very wary of each other, and many interactions observed were characterised by mutual avoidance or flight. Overtaggressive behaviour was rarely seen. It can be inferred that voles do fight in the field, because they commonly exhibit small wounds on rump, tail, and face; these could however, be sustained in the confinement of burrows, where escape and mutual avoidance are less possible than at a bait point, and which may be more closely paralleled by the laboratory arena. Significantly more adult males in the enclosures showed fresh wounds than did castrated or immature males, or adult or immature females.

The number of voles in the experimental enclosure increased significantly faster than did the number in the control enclosure; the density in both enclosures was also significantly higher than commonly encountered in the wild. The difference in numbers between the two enclosures was due to a difference in the number of immature animals entering the trappable population; mortality of marked animals in both enclosures was very slight but mortality of infants was significantly higher in the control enclosure than in the experimental. Reproductive inhibition of adult and immature animals of both sexes was observed in both enclosures. At the same time, extremely young animals trapped in the wild populations were found to be sexually mature. The differences in the use of space by different age and sex classes between the two enclosures were also investigated.

The study demonstrated that male aggressive behaviour had a significant effect on the population variables of bank voles at the high densities and at the high rates of population growth observed in large enclosures. The findings are discussed in the light of several hypotheses put forward to explain population regulation and cyclic changes in numbers of Microtine rodents.

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CHAPTER 1

INTRODUCTION

Population regulation in small mammals.

It is axiomatic that both extrinsic and intrinsic factors act to regulate the numbers of animals. Clearly, however, the relative importance of different factors in controlling numbers varies in time and space. Extrinsic, density independent factors are of greatest importance in marginal or only temporarily suitable habitat (for instance, in a population of house mice (Mus musculus) inhabiting a South Australian wheatfield, studied by Newsome, (1969), availability of home sites in cracks in the ground was controlled by rainfall, and this controlled the population density). Intrinsic, density related factors, on the other hand, clearly assume greatest importance with a population's independence from its environment (for example, mice in a granary are unlikely to die of starvation (Anderson, 1970)).

Watson and Moss (1970) point out that the traditional concept of limiting factors, borrowed from the physical sciences, does not necessarily apply to complex biological systems which can adjust their requirements to varying availability of resources; as a result, more than one factor can be limiting at any one time, and it is probable that many of the apparently conflicting number-controlling mechanisms can and do operate either together or separately depending upon the circumstances. Lidicker (1973, 1975) also argues for a 'community view of small mammal population dynamics'.

This introduction concentrates only upon the role of intrinsic factors, mediated by intraspecific social behaviour, in regulating the numbers of rodents. This is not to say that I believe all the other potential number-regulating processes to be unimportant, but that, because a totally experimental approach to the study of intrinsic factors in population regulation was adopted in the present inquiry, with all extrinsic factors as far as possible held constant, they are not reviewed here; full reviews of both extrinsic and intrinsic factors thought to affect rodent numbers are given by DeLong (1967), Krebs and Myers (1974) and Tapper (1976).

Clear evidence that social behaviour can have profound effects on demographic variables has been presented for many vertebrate species including rodents, and has been fully reviewed by, among others, Watson and Moss (1970), King (1973) and Wilson (1975); a

review of the literature on vertebrates other than rodents will not be repeated here.

Considerable uncertainty remains however, about the mechanisms by which social behaviour, in particular intraspecific aggression, affects rodent population dynamics; this uncertainty is largely the result of there being several strongly held and conflicting views about the relative importance, in natural populations, of each of the intrinsic mechanisms that have been demonstrated to regulate numbers under different experimental conditions.

The two rodent groups whose population dynamics have been most studied have been the family Muridae (particularly mice) and the sub-family Microtinae (voles and lemmings). Although mice and voles are superficially similar, their ecological and reproductive strategies are considerably different. Mice are commonly found living commensally in granaries and hay ricks where food is extremely plentiful; in these habitats they often reach very high densities. Voles, however, rarely live commensally, and are generally found at much lower population densities than mice, even under conditions where essential resources are in excess.

Being the most common laboratory animal, it is not surprising that the population ecology of the house mouse has been so intensively studied. The majority of these studies have been on enclosed groups of animals, ranging from 'populations' in small laboratory cages, through large laboratory and field enclosures, to granaries and hay ricks; relatively few studies of free-living populations have been carried out. This introduction will cover mechanisms of population regulation in all the above habitats.

Vole (and lemming) population dynamics have been much investigated for a different reason; the numbers of these animals appear to exhibit regular, as opposed to random, fluctuations, with a period of 3 - 5 years. The form of this population cycle, and in particular the phase of decline in numbers, has been shown to be rather variable, and is described in detail by Krebs and Myers (1974). Although the existence of regular cycles has been disputed,

Krebs and Myers (1974) point out (p.273) that no population of Microtine rodents that has been studied over a 3 - 4 year period or longer has failed to show cyclic changes in numbers; however, even if the fluctuations are not cyclic, their amplitude is still of interest to population biologists, since fluctuations of the magnitude exhibited by voles and lemmings do not appear to be exhibited by other rodent groups. A larger proportion of the vole studies (as opposed to those on mice) have been on free living populations; the studies of enclosed populations have tended to be on populations in relatively large field enclosures.

There are four processes that can affect population numbers:- 1. Births, 2. Deaths, 3. Immigration, and 4. Emigration

In unenclosed populations, (1) and (3) have often had to be combined under a blanket term such as 'recruitment', and (2) and (4) combined under a term such as 'losses', since births are not distinguishable from immigration, or deaths from emigration, when a population is being studied by live-trapping techniques alone; as a result, most of the studies of unenclosed populations have not been able to demonstrate the relative importance of each of these four fundamental processes in regulating population numbers. In enclosed populations however, immigration and emigration are eliminated, and population regulation can only occur in either or both of two ways:- 1. Depression of the birth rate, or 2. Elevation of the death rate.

Each of the major intrinsic mechanisms, by which it is hypothesised that the numbers of rodents are controlled, and the evidence for each, will now be reviewed under four main headings; these are:-

1.1 The relationship between social interactions and the endocrine and neural physiology of individuals, affecting (a) reproduction and (b) mortality.

1.2 The relationship between increased numbers of aggressive interactions, associated with increased population density, and mortality of different age and sex classes.

1.3 The relationship between social behaviour and dispersal.

1.4 The behavioural genetic hypothesis, particularly related to the regular cyclic variations of Microtine populations, in which different genotypes have selective advantage at different stages of the population cycle, dependant upon the frequency of aggressive interactions; this mechanism also makes allowance for dispersal as a major contributing factor to population regulation.

1.1(a). The relationship between social interactions, endocrine physiology, and reproduction.

Potential regulation of population numbers by depression of the birth rate can be the result of several distinct processes:-
(a) permanent or semi-permanent female anoestrus, either by regression of previously breeding females or by failure of young females to mature, leading to decreased length of the breeding season, increased time interval between pregnancies, or simply a reduction in the proportion of females that are in breeding condition at any one time.
(b) suppression of testicular ability to produce viable spermatozoa, again either by regression of previously breeding males, or by failure of young males to mature.
(c) conception failure.
(d) failure of all or some of the embryos to develop as a result of foetal resorption.

In general, these phenomena have been most often observed in enclosed freely-growing laboratory populations of house mice, where there has been little scope for a social system of any complexity, based upon territorial subdivision of the available space to develop. (e.g. Strecker and Emlen, 1953; Crowcroft and Rowe, 1957; Petrusewicz, 1957, 1963; Lidicker, 1965). This depression of reproduction has usually been observed to occur after a rapid initial increase in numbers due to breeding by the founder members, followed, as progressively more crowded conditions have led to a rise in the rate of aggressive interactions, by failure of both male and female animals to mature sexually, and by the sexual regression of adults which had previously been in breeding condition.

Reproductive stunting has also been observed in house mouse populations in larger, more complex enclosures, where spatial subdivision as a result of territorial behaviour has been possible; in these larger enclosures, it has usually acted together with other factors, rather than alone, to control numbers (Southwick, 1955(a); Christian, 1956; Lloyd, 1975; Lidicker, 1978).

That reproductive inhibition is the direct result of crowding has been demonstrated by Crowcroft and Rowe. As mentioned above, inhibition of reproduction of females was shown by them (1957) to have had the most significant effect on their populations of house mice in small laboratory enclosures. In a subsequent paper (Crowcroft and Rowe, 1958), they showed that non-fecund members of asymptotic populations in these small enclosures, either moved or allowed to move of their own accord into larger (130, 225, or 400ft^2) pens, rapidly became reproductively capable again, and population growth was renewed; animals just moved from one small pen to another remained reproductively inhibited.

Delayed maturation at high densities has also been observed in confined populations of voles (Clarke, 1955; Van Wijngaarden, 1960; Keller and Krebs, 1970). Similarly, in free living populations, reproductive stunting at high densities has been observed both in voles (Kalela, 1957; Koshkina, 1965; Zejda, 1964; Christian, 1971b) and house mice (DeLong, 1967). Bujalska (1970) has suggested that, in an island population of bank voles in Poland, studied extensively by herself and others (Gliwicz, 1975, lists the major references) territorial behaviour of adult breeding females prevents other females from coming into breeding condition, and so limits the number of young born; in effect, non-territorial females are reproductively inhibited by the social behaviour of females with territories.

A second physiological phenomenon that has been observed to be associated with increased density is foetal resorption. This has been shown to occur in crowded laboratory populations of mice (Christian, 1956; Lloyd and Christian, 1969), and percentage resorption was shown by Crowcroft and Rowe (1957) to be significantly higher in their crowded populations than in a previous study (Laurie, 1946) of free-living house mice. Foetal resorption has almost certainly been the cause of the observation that litter size is lower at high densities, both in mice (e.g. Southwick, 1958) and voles (Zejda, 1964; Keller

and Krebs, see also Krebs and Myers, 1974, pp291-3 for a review).

A further physiological consequence of crowding which has been demonstrated in both voles and mice is permanent stunting of young as a result of deficient lactation (Chitty, 1955; Christian and Lemunyan, 1958). Young physically stunted in this way would clearly be at a disadvantage in crowded conditions and less likely to breed than normal individuals.

The mechanism by which it is hypothesised that increased rates of social interaction affect the reproductive physiology of individual animals is one by which those interactions cause increases in the functioning of the pituitary-adrenocortical axis leading to increased levels of adrenal androgens and progesterone; these may in turn inhibit gonadotrophin secretion and hence maturation. Low artificial doses of some adrenal androgens have been shown to inhibit maturation of immature mice (Christian et al, 1965). Gonadotrophin secretion may also be inhibited by ACTH, possibly by the inhibition of the secretion of hypothalamic gonadotrophin-releasing hormones (Christian, 1975).

Studies of static groups of mice assembled in cages for relatively short periods, (as opposed to freely-growing populations), have demonstrated other effects that may well be important, at least in very crowded populations; these are relatively short-term physiological reproductive blocks, controlled by olfactory cues. For instance, the Lee-Boot effect causes pseudo-pregnancy when a few female mice are grouped together, but can cause anoestrus when large groups of females are assembled (Lee and Boot, 1956; Whitten, 1959). Similarly, the Bruce effect, (Bruce, 1960(a) and (b)) causes implantation to be blocked when a newly inseminated female is exposed to a strange male or his odour. This phenomenon has been observed in both house mice and several species of Microtus (Bruce, 1960; Clulow and Clarke, 1968; Bronson, 1971). The odour of

conspecifics has also been shown to be able to delay maturation in both male and female Peromyscus leucopus (Rogers and Beauchamp, 1976) and in female mice (Vandenbergh, 1973). The role, if any, of these phenomena in natural or freely growing enclosed populations of rodents is not known.

1.1(b). The relationship between social interactions, endocrine physiology, and mortality.

As set out in the previous section, it is postulated that this mechanism is based upon the activation of the pituitary-adrenal system by increased rates of social interaction at high density. It is hypothesised that increased adrenocortical activity leads to raised levels of corticoids, which inhibit antibody formation and inflammatory responses; as a result, there is an increase in susceptibility to disease and parasitism, and hence, indirectly, to mortality. This phenomenon has been much more rarely observed than inhibited reproduction at high densities, and its effect on natural populations of rodents is unknown (Christian et al, 1965).

1.2. The relationship between social interactions and mortality.

In this section, the direct effects of social interactions upon mortality are to be considered; in other words, death must be the direct result of conflict, or the result of increased disturbance and activity associated with high densities. It would seem reasonable to assume that nestlings are most vulnerable to general disturbance in crowded populations, and high mortality of infants has repeatedly been observed in studies of enclosed populations of both mice and voles (Brown, 1953; Southwick, 1955(b); Christian, 1956; Louch, 1956; Anderson, 1961; Reimer and Petras, 1967; Lloyd, 1975; Lidicker, 1965, 1976). This high neonatal mortality has been ascribed individually to abandonment of the young by their mother, cannibalism, trampling and nest disturbance, or to combinations of these; it has, in the main, been associated with populations enclosed in relatively complex laboratory or field enclosures, where it is possible for more extensive spatial sub-division to develop than in laboratory cages. House mice have been shown to be territorial in many studies of large captive colonies (Crowcroft, 1955; Crowcroft and Rowe, 1963; Anderson and Hill, 1965; Reimer and Petras, 1967 and Lidicker, 1976), and in field and commensal situations (Anderson and Hill, 1965; Reimer and Petras, 1968; Rowe and Redfern, 1969); it has also been shown that territories are not necessarily held by individuals, but may be held by social groups (Reimer and Petras, 1967; Selander, 1970; Lidicker, 1976). It would appear that in enclosed populations of mice at least, juvenile mortality, associated with increased population density, is the result of elevated levels of activity and aggressive behaviour within these discrete and relatively stable social groups, since territorial groups in the same habitat can exist at widely differing densities (Lidicker, 1976).

In the studies described above, the relationship between population density and infant mortality has been simply observed; in a few cases, an experimental approach has been attempted. Controlled disturbance (either by cage changing, or by the addition or removal of individuals for a limited period) of caged mouse populations by Petrusewicz (1957, 1963) elevated significantly both juvenile survival and the numbers born; controlled exploitation of mouse populations

of juvenile mortality or reproductive inhibition in regulating population numbers.

1.3. The relationship between social interactions and dispersal.

Many of the studies so far described have been on enclosed populations of house mice and voles, where emigration (and immigration) have been completely thwarted. However, it has long been observed that the densities reached in artificially enclosed populations of rodents commonly greatly exceed densities found in natural populations. The difference between free-living and enclosed populations is perhaps most striking when mice or voles are confined in large outdoor enclosures; in these conditions, where there is space for a complex social system to develop, it might be expected that social behaviour could act to control density at a level similar to free living populations. This has not, however, been found to be the case, and extremely high asymptotic densities of both mice and voles have repeatedly been observed in large enclosures (Clarke, 1955; Louch, 1956; Crowcroft and Rowe, 1957; Van Wijngaarden, 1960; Moulihan, 1963; Gentry, 1968; Krebs et al, 1969; Lidicker, 1976). In the majority of these cases, food and water were supplied in excess, thereby making it impossible to eliminate these as factors allowing the population to expand so dramatically. Firstly, however, provision of supplementary food to free-living populations of voles has not proved sufficient alone to produce a peak population, or to prevent a decline (Krebs and Delong, 1965) and secondly, voles in large enclosures without supplementary food have still exhibited very high initial rates of increase in density, with maxima far in excess of normal field densities, and with starvation and decimation of the forage only setting in later (Krebs et al, 1969). Thus it would appear that dispersal alone is an important factor in controlling the density of small mammal populations, and this case has been consistently argued by W.Z.Lidicker (see Lidicker, 1975). He argues for the existence of both pre- and post-saturation dispersal and suggests that the former occurs well before the numbers of animals approach carrying capacity, and is carried out by animals in good condition, of any age or sex or group (including pregnant females), with good chances of survival. Saturation dispersal, on the other hand, is the outward movement of surplus,

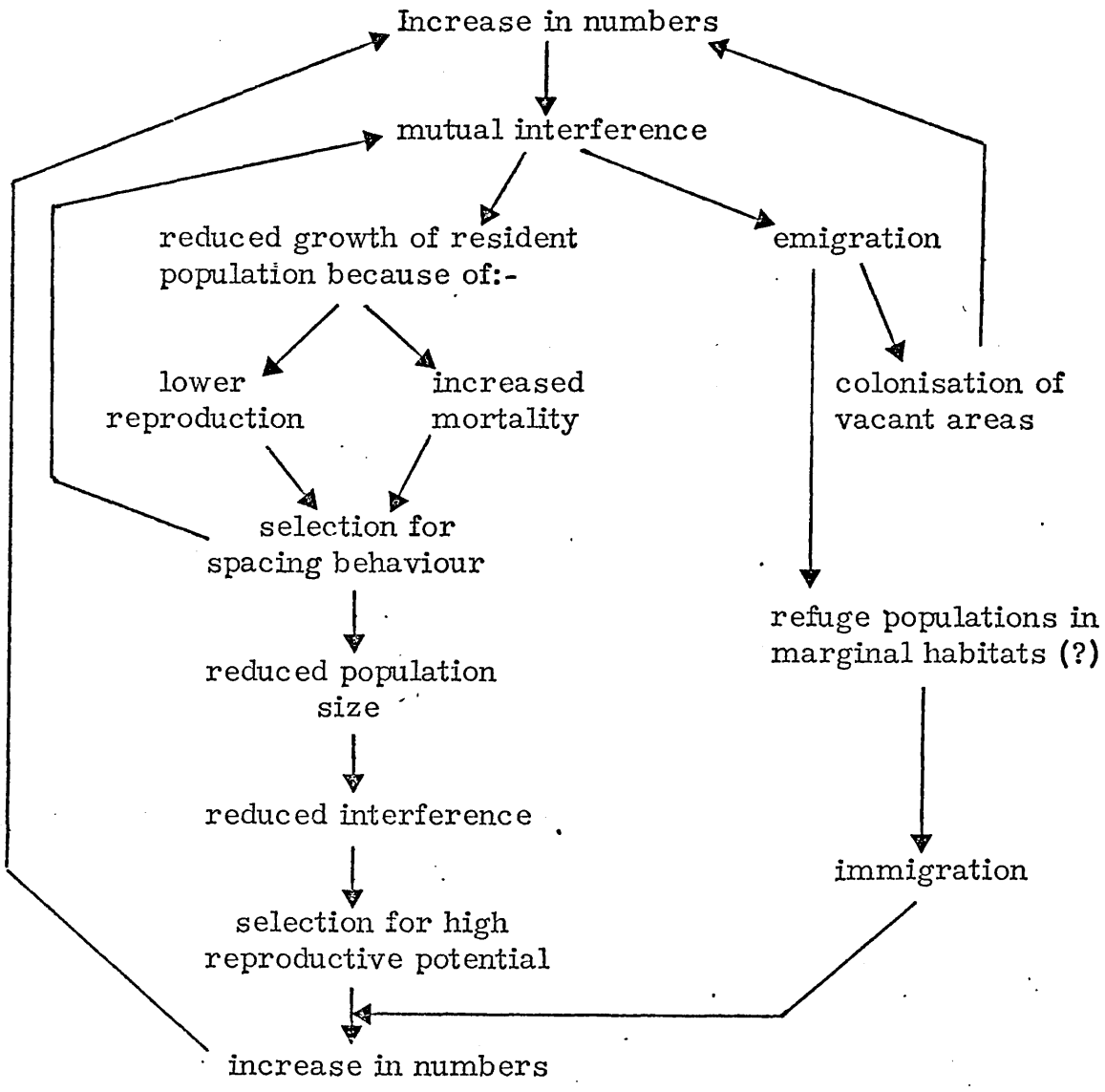
probably socially subordinate, juvenile or old individuals, forced to disperse as the population reaches the carrying capacity of its habitat, and with poor chance of survival. This latter is the traditional view of dispersal (Lidicker, 1975). The concept of pre-saturation dispersal is more contentious, but has been observed in house mice, bank voles and several species of Microtus, as well as in other rodent groups (see list in Lidicker, 1965, p.108; Hilborn and Krebs, 1976; Krebs et al, 1976). Both types, but particularly pre-saturation dispersal, are mediated by social behaviour, and both can obviously have profound demographic effects. Regulation of numbers can be achieved by saturation dispersal, where dispersal of individuals into marginal habitat probably causes widespread mortality. Pre-saturation dispersal,on the other hand, serves to prevent numbers from reaching carrying capacity, by colonising unused, perhaps only temporarily suitable, habitat.

1.4. The relationship between social behaviour, genetics and demography.

The final major mechanism by which it is suggested that social behaviour affects the population dynamics of rodents is rather more complex than the others, and is derived from the hypothesis originally proposed by Chitty (1958). The central feature of this hypothesis is that selection, acting through behavioural interactions, causes short-term genetic changes within the population, which affect the aggressiveness, breeding success and propensity for dispersal of individuals, and cause the regular cyclic changes observed in vole populations. It is best summarised in a diagram from Krebs and Myers, (1974, p.384) (Fig. 1.1.), and is reviewed fully by Krebs et al (1973) and Krebs and Myers (1974). The evidence for this mechanism being the driving force behind vole cycles is largely circumstantial. It has been shown that genetic changes (the frequency of polymorphic marker genes) correlate (either positively or negatively) with the cycle of numbers of several Microtus species (Semeonoff and Robertson, 1968; Tamarin and Krebs, 1969; Gaines and Krebs, 1971); aggressive behaviour, measured in neutral arena tests, has also been shown to be correlated with the phase of the cycle (Krebs, 1970). However, no relation between genotype and aggressive behaviour has been found, (Krebs, 1970) although propensity for dispersal, which presumably is behaviourally mediated, was found to be associated with the phase of the population cycle (Myers and Krebs, 1971; Hilborn, 1975; Hilborn and Krebs, 1976),and Hilborn (1975) showed that there were significant differences in tendency to disperse between sibling groups, although, as he pointed out, this result might have been due to maternal, rather than genetic influences. However, no differences in fitness were detected (Gaines, Myers and Krebs, 1971) between three genotypes of Microtus ochrogaster introduced into enclosures, and studied during the phase of initial population growth.

The major stumbling block to acceptance of this hypothesis is that none of the studies described above demonstrate whether the genetic changes are the driving force behind the population changes,

Fig. 1.1. Modified version of the Chitty behavioural-genetic hypothesis to explain Microtine cycles (from Krebs and Myers, 1974)).



or whether the demographic processes of mortality and natality are causing the changes in gene frequencies. Krebs and Myers (1974) argue for the former, but there is, as yet, no conclusive evidence.

The four possible intrinsic mechanisms of rodent population control reviewed above have a clear common factor, and that is that they all depend upon there being a relationship between social behaviour and population density. More specifically, they assume a positive relationship between either the quantity and/or quality of aggressive interactions and population density. It is not necessary to assume that this relationship is linear, and evidence that the frequency of interactions between individuals is not directly proportional to population density, at least in field populations of Microtus californicus (Pearson, 1960) and M.ochrogaster (Carroll and Getz, 1976) suggests that this assumption would be unwarranted.

The central aim of the present study was to determine experimentally if male aggressive behaviour was associated with population variables in communities of bank voles, Clethrionomys glareolus (Schreber, 1780) in large field enclosures; in particular, the aim was to modify overall levels of aggressive behaviour in the population in one enclosure (hereafter called 'the experimental enclosure') with respect to the levels of aggressive behaviour in the population in another enclosure (hereafter called 'the control enclosure'), and to determine the effects of this manipulation upon demographic variables. This was achieved by establishing in each of the enclosures similar populations of bank voles. In the experimental enclosure, the majority of the founding males were castrated; in the control enclosure, none of the males were castrated. Other variables (weight - structure of the introduced populations, enclosure areas, availability of food and water, etc.) were kept constant. This thesis is therefore divided into three major parts, each corresponding to a section of the study.

Firstly, it was necessary to determine the effects of castration on the aggressive behaviour of bank voles; this was done in a laboratory study of interactions, in a neutral arena, between pairs of voles drawn from laboratory-maintained groups of individually housed adult, immature and castrated male bank voles. This

study is described in Chapter 2, with a review of the literature on the factors that affect rodent aggressive behaviour.

Secondly, it was necessary to determine the degree to which the behavioural interactions observed between voles in the neutral arena were comparable to those occurring under field conditions; direct observations of behavioural interactions between voles at bait points in the enclosures and at a field study site were therefore carried out. This study is described in Chapter 3.

Finally, populations of voles were established in the enclosures as described above, and followed by live-trapping. This study is described in Chapter 4, which includes a review of the literature derived from previous research in which the demographic consequences of deliberate manipulation of rodent populations have been studied. Only one introduction of voles into the enclosures was followed for long enough to give useful results on population dynamics (experiment ENCL 4); at the end of this experiment, which ran for 10 months, the behaviour of some of the animals removed from the enclosures was tested using the same neutral arena technique mentioned above, and previously used in the main behaviour study to compare the behaviour of adult, castrated and immature male voles. The results of this supplementary study of behaviour are described in Chapter 2.

CHAPTER 2

Laboratory observation of male bank vole behaviour

2.1. INTRODUCTION

Many factors have been shown experimentally to affect the outcome of interactions between male rodents in the laboratory; any study of the aggressive behaviour of rodents in the laboratory must take these factors into account, and allow for, or eliminate them.

This introduction therefore reviews a large number of studies on various aspects of rodent agonistic behaviour, with particular reference to the intrinsic factors affecting it. The first full description of the behaviour of a microtine rodent in the laboratory was Clarke's (1956) study of the aggressive behaviour of the field vole, Microtus agrestis. He described qualitatively various acts and postures observed in interactions between both adult and adult, and adult and immature voles, and males and females. As well as describing adult male-adult male behaviour, he noted that adult males will attack males or females, and will, if successful in fights, become the dominant animal of the group to which they belong. Pregnant and nursing females were also observed to attack animals approaching their nest. Grant and Mackintosh (1963) described in detail the behaviour of four laboratory rodents, including Mus musculus and drew attention (p247) to the glaring inconsistancies between previous descriptions of the social behaviour of rats and mice. The names and descriptions of the majority of the behavioural components scored in the present study were derived either from Grant and Mackintosh (1963) or from Clarke (1956), and are described fully in section 2.2.2; most of the studies to be described below have also derived much of their nomenclature of behavioural components from these two papers. Getz (1962) described the aggressive behaviour of Microtus pennsylvanicus and Microtus ochrogaster but pooled results from male and female encounters, used each animal several times, and used small numbers of individuals. Allin and Banks (1968) described in detail the agonistic behaviour of sexually mature males of the collared lemming Dicrostonyx groenlandicus, and recorded the duration and frequency of eleven components of aggressive behaviour. However, only 21 encounters were observed with no attempt to match the animals of a pair for age, weight or experience. In one of a series of papers on the population biology of Microtus, Krebs (1970) compared changes in the aggressive behaviour of the male Microtus

pennsylvanicus and Microtus ochrogaster with changes in numbers over a population cycle; using Clarke's (1956) description of behavioural categories, he used Multiple discriminant analysis successfully to characterise the behaviour of males from different phases of the cycle. Colvin (1970) described the interspecific behaviour of five species of Microtus in 160 encounters between pairs of individuals of the different species, using the behavioural components described by Allin and Banks (1968). Turner and Iverson (1973) showed that aggressive behaviour of Microtus pennsylvanicus varied over the season by combining the weighted values of four aggressive acts into an Index of aggression and showing that this was significantly higher during the breeding season than outside it.

A few studies have been made on the agonistic behaviour of Clethrionomys species. Von Volker Johst (1967) compared the behaviour of four species of Clethrionomys (including Clethrionomys glareolus) and divided agonistic behaviours into 'Attack, defence, and escape syndromes'. Schleidt (1948) described the sounds made by Evotomys (Clethrionomys) glareolus. Perrin (1970) described and compared the behavioural elements of Microtus agrestis and Clethrionomys glareolus, using the terminology of Clarke (1956), and Ashworth (1973) studied the aggressive behaviour of two subspecies of Clethrionomys glareolus, the mainland and Skomer forms, and their hybrids. She noted that, in a small neutral arena, often no aggressive behaviour was observed during a five minute encounter. Transition matrices were used to analyse sequences of behavioural components and she demonstrated that the subspecies behaved significantly differently.

A very large volume of literature on the relationship between endocrines and aggressive behaviour in murid rodents, particularly mice, exists as a result of investigations into several distinct fields; these include the organisational effects of neonatal hormonal influences, the 'concurrent' (Mugford, 1974) effects of hormones on behaviour, the relationship between hormonal status and aggression - facilitating and - inhibiting cues (usually pheromones) and the effects of different naturally occurring and artificial androgens.

The developmental effects of androgens on neural organisation in both male and female neonatal mice are well known; castration and the administration of hormones to neonates has marked effects on the future development of behaviour (Bronson and Desjardins, 1968, 1971; Edwards, 1969; Peters et al, 1972; Whitsett et al, 1972). In particular, neonatal castration of male mice prevents adult aggressive responses from developing. A single injection of testosterone immediately after castration reverses the effect, but a single injection ten days after neonatal castration is much less effective in restoring adult aggressive behaviour (Edwards, 1969).

Many studies have shown that castration of both adult and immature male mice reduces aggression; the ability of artificially administered androgens to restore the aggressive behaviour of castrates is also well known (Uhrich, 1938; Beeman, 1947; Bevan et al, 1957; Suchowsky et al, 1969; Haug and Ropartz, 1970; Leshner and Moyer, 1975).

Uhrich (1938) castrated both adult and prepubertal male albino mice; he found that prepubertal castration greatly reduced fighting, whereas castration of adults was much less effective. In both groups, fighting continued in a few individuals for some time following castration, and one animal castrated as an adult fought for many months afterwards, demonstrating that simply drastically lowering levels of circulating androgens is not necessarily sufficient to suppress aggressive behaviour completely. Early castration was more effective in reducing aggressive behaviour than was castration in adulthood, but neither succeeded in abolishing fighting behaviour completely. In contrast, Beeman (1947) castrated laboratory mice (C57 black or Bagg albino) at 23 and 80 days old, and found very little aggressive behaviour in either group 25 days after castration. Subcutaneously implanted pellets of testosterone propionate restored aggression; removal of the implant resulted in a return to the non-aggressive castrate condition. Bevan et al (1957) found that both the frequency and intensity of aggressive acts was greater in intact male mice (C_3H agouti) than in males castrated as weanlings. They also showed that three androgens, including testosterone, restored fighting in castrated animals, at a

dose level of 150mg/day. In a second experiment, hormone levels of 300-600mg/day given to a different strain of mice (Swiss albino) appeared to suppress fighting behaviour. Suchowsky et al (1969) also demonstrated that the percentage of fighting incidence in male Swiss albino mice dropped considerably following castration. It was also stated that animals castrated at the beginning of their 30 day isolation and testing period did not become aggressive; the age of castration was not however stated. Leshner and Moyer (1975) showed that in standard opponent tests male CFW albino mice castrated at 42 days old fought significantly less than sham operated animals and less than castrates receiving 150mg/day of testosterone propionate; there was no significant difference between the shams and the castrates with testosterone. They were unable to show that these treatments had any effect on avoidance responses to agonistic stimuli.

In summary, studies described above have shown that castration of male mice both pre- and post-pubertally reduces aggression, but that pre-pubertal castration is probably the more effective.

The development of aggressive and mating behaviour, and of the testes and levels of circulating androgens, have been studied in the mouse by McKinney and Desjardins (1973). They showed that between 21-35 days of age, plasma androgen concentration in male mice increased by 300% and then dropped by around 50% at 100 days old. This increase in plasma androgen was associated with a marked increase in the Leydig cells in the testes; spermatozoa were detected in 40 day old mice. Intermale aggression was first observed in 35 day old, previously isolated animals, by which age 90% of males had exhibited aggressive behaviour. Intermale aggressive behaviour was more closely correlated with age than with the amounts of any particular androgen, but McKinney and Desjardinscame to the conclusion that the onset of aggressive behaviour coincided with general elevation of androgen secretion; they also suggested that the onsets of mating and fighting behaviour were independant of one another, and that the neural centres controlling aggression required

lower androgen levels for activation than did those activating sexual behaviour. Brain and Nowell (1969) also described changes in organ weights and histology, and fighting behaviour associated with maturation of TT mice. Fighting behaviour was associated with development of the testes in Microtus pennsylvanicus by Christian (1971a); he showed a correlation between scars received from fighting and seminal vesicle weight, assuming development of the latter to parallel testicular secretion of androgens. Levy and King (1953) found that a control group of male mice would not fight before 34 days of age, but that by subcutaneous injection of 0.5mg of testosterone propionate, they were able to make mice fight as early as 18 days old. Lagerspetz and Talo (1967) also showed that the age at which aggressive behaviour was observed could be lowered by administration of testosterone. Svare and Gandleman (1975) studied the intermale aggressive behaviour of male Rockland-Swiss mice between the ages of 21 and 50 days; they found that testosterone propionate administered in an oil vehicle to castrated male mice from day 21 of life to day 50 caused them to exhibit aggressive behaviour, whether or not they had been given testosterone propionate neonatally. Control animals given oil alone from days 21-50 exhibited no aggressive behaviour. It would clearly appear to be the case, therefore, that the onset of aggressive behaviour in male mice is directly associated with puberty, and in particular the onset of the secretion of testicular androgens.

The mode of action of androgens in mediating aggressive behaviour is not known; however, Owen, Peters and Bronson (1974) have shown, by stereotaxic implants of testosterone propionate into various parts of the brain of castrated male CFI mice, and subsequent testing for aggression, that the septal region of the forebrain is responsive to androgen. Slotnick and McMullen (1972) have found that septal lesions abolish aggressive behaviour in male CFI mice.

The role of the adrenal gland in aggressive behaviour has also been much investigated, (see Leshner, 1975; Leshner and Candland, 1973 for reviews). Adrenalectomy of male mice reduces aggressiveness, and corticosterone replacement therapy restores it in operated mice to the level of intact controls (Brain et al, 1971; Brain and Poole, 1974; Leshner, 1972; Leshner et al, 1973). In general, the effects are not so marked as the effects of castration and androgen replacement therapy. Since androgen therapy does not restore aggressive behaviour to adrenalectomised male mice, nor corticosterone restore it in castrated male mice, the two systems appear independant (Leshner, 1972). Leshner et al (1973) and Brain and Poole (1974) suggest that it may be the levels of circulating ACTH, rather than levels of corticosteroids or adrenal androgens that, presumably through neural action, actually affect aggressive behaviour. The complex nature of the structure and function of the adrenal glands in mice means that the relationship between pituitry - adrenocortical influences and behaviour in mice is not well understood (Brain, 1972); the marked variation of the gland between different groups of rodents also means that it is not really possible to generalise from the findings of laboratory mice.

In all the previous examples, it has been solely the effects of hormones on aggressive behaviour that have been investigated. Previous social experience has also been shown to have a marked effect on subsequent behaviour. The study of McKinney and Desjardins (1973) showed that previously isolated males, without fighting experience, could exhibit spontaneous aggressive behaviour, and in many of the studies described above, male mice were isolated as weanlings and therefore had no opportunity to fight before being tested for the first time. However, in competitive aggression tests, using male C57D1/10 mice, Bevan et al (1960) showed that pre-test experience was highly important in determining the winner. The fact that several authors have used trained fighters or losers as stimulus animals in neutral arena tests shows that experience must be an important factor (Sadleir, 1965; Healey, 1967; Lee and Brake, 1971,

1972; Drain and Poole, 1974). In the wild, few animals can reach adulthood in the behaviourally naive state of many of the animals used in laboratory behaviour tests (Leshner 1975). These studies may, at least in part, explain why castration of adults is less effective in reducing aggressive behaviour than prepubertal castration; circulating androgen levels may have been lowered or removed as a result of castration, but probably fighting experience alone is enough to make animals aggressive and allow fighting, even in the absence of hormonal influences. King and Gurney (1957) showed that male mice raised in isolation from the age of 20 days to around 110 days were less aggressive than males raised with either males or females from 20 to 45 days old, then isolated until around 110 days old.

The degree of familiarity between opponents in aggressive interactions has also been shown to affect the outcome, and, in rodents, the existence of species, subspecies and group odours have been demonstrated (see Stoddart, 1974 for a review).

Mackintosh and Grant (1966) showed that the urine of a strange male mouse rubbed on the fur of a pair of familiar mice enhanced aggressive behaviour, whereas the urine of a familiar male mouse reduced aggression between strangers. Ivankina (1974) and Healey (1967) also showed that strangers were more aggressive than mice familiar with each other. It is well known that the level of fighting in newly grouped animals decreases quite quickly with time, and a relatively stable system results (Crowcroft and Rowe, 1963; Nowak, 1971; Poole and Morgan, 1973; Terman, 1974). Crowcroft and Rowe (1963) observed a family of mice for a total of 300 hours, and saw no aggressive behaviour between members; all however displayed aggressive behaviour to strangers of either sex. Rowe and Redfern (1969) report similar results.

Most of the studies previously described used isolated, and therefore strange animals for neutral-arena aggression testing. Other studies have specifically used this phenomenon to elevate aggressive levels in encounters by introducing a strange mouse into the home cage of another animal (e.g.Mugford and Nowell, 1973).

A further factor known to affect aggressive behaviour is the inherent difference between individuals; many workers have noted the fact that individuals, without prior fighting experience, were very variable in their aggressive tendencies, even when other variables were held constant (e.g.Brain and Evans, 1974 a; Bevan et al, 1957 and Luttge and Hall, 1973). Lagerspetz (1964) found that she could select for aggressive and non-aggressive genotypes of male mice within two generations. Genetically controlled aggressive behaviour is the basis for Chitty's hypothesis on the regulation of numbers and the control of cycles in Microtine rodents (Summarised in Chapter 1).

The behaviour of an individual is not the only thing to be influenced by its hormonal state; the ways in which different hormonal states elicit different responses from opponents in behaviour tests has provided a large field of investigation, particularly in the ways in which this information is transmitted. In many studies it has been shown that olfactory cues transmitted by an individual have had a profound effect on the degree of aggression shown to that individual (see Bronson, 1971 for a review). For example, Lee and Brake (1971) have shown that female mice are less prone to attack by isolated fighter males than are other males. Mugford and Nowell (1970, 1971a), Dixon and Mackintosh (1971) and Svare and Gandleman (1975) have shown that a substance in female mouse urine inhibits inter-male fighting, and castrated male mice are less susceptible to attack by fighter mice than are intact males (Lee and Brake, 1971; Mugford and Nowell, 1970, 1971b). However, castrated male (A/J) mice were attacked by trained (DBA/2J) fighters if the castrates were treated with testosterone propionate (Lee and Brake, 1972); Mugford (1974) also showed that castrated male mice injected with testosterone propionate were attacked more by trained fighters than were oil injected controls, but that there was no difference between injected castrates and intact males in the amount of aggression elicited. Brain and Evans (1974a) showed that castrated T0 males given daily i.m. injections of 1mg of either androstenedione or dihydrotestosterone were attacked significantly more than were oil

injected controls. In a further experiment, Brain and Evans (1974,b) painted urine from intact or castrated male donors of three strains (TO, ASHXP and CFLP) onto the fur of castrated males, and distilled water into the fur of castrated and intact males; they found that trained TO fighters attacked intacts with distilled water significantly more than castrates with distilled water, castrates with the urine of intacts significantly more than castrates with distilled water, and castrates with intact urine significantly more than castrates with castrate urine. Slight strain differences were noted. Jones and Nowell (1973a)have shown that the urine of adult male mice, as well as containing an aggression promoting factor, also contains an aversive factor which causes other adults to avoid areas marked with it in an open field test.

These experiments have shown that, apart from the central motivational effect that androgens have on individual males, presumably acting upon neural tissue, androgens also exert effects through olfactory cues, some of which at least are present in the urine. Thus, adult male urine appears to possess an aggression releasing character, under androgenic control; castration extinguishes its effect, and androgen replacement therapy restores it.

If the aggression releasing factor of adult male urine is under androgenic control, then immature males should not possess it. Mackintosh (1970) noted that, in his enclosure experiments, juvenile mice were immune from the aggression of territorial males; Dixon (1973), however, found that painting the urine of juvenile males on the fur of adult males did not inhibit attacks on them by other adult males; similarly, juvenile male urine failed to evoke aggressive behaviour in pairs of familiar (and therefore non-aggressive) adult males. He therefore concluded that the relative protection of juveniles from attack was due to the absence of the urinary releaser of aggression which has been demonstrated to be present in the urine of adults, and which has already been shown to be under androgenic control; as a corollary of this, he concluded that the juveniles' immunity from attack was not due to the presence of an aggression-inhibiting factor in their urine.

The studies described above have demonstrated that there are

differences in the urine of adult, castrate and immature male mice. Jones and Nowell (1973b) have demonstrated that the urine of dominant and subordinate male TT mice is also qualitatively different. In an open field test, group housed males showed a marked preference for the half of an arena treated with water or the urine of a subordinate male rather than the half treated with the urine of dominant males. In a second experiment, they showed that the urine of dominant males, painted onto the fur of castrates, elicited significantly more aggression than the urine of subordinate males, or water; the difference in the reaction to animals painted with water or subordinate male urine was insignificant. They discussed the relationships between defeat, the pituitry-adrenocortical axis (Bronson and Eleftheriou, 1965a, b) and the ventral prostate gland which is sensitive to endogenous androgens (Brain and Nowell, 1970).

All the above experimental observations have been made on murid rodents, predominantly laboratory mice; as far as I know, the only experimental analysis of the relationship between androgenic hormones and the aggressive behaviour of male rodents of the sub-family Microtinae has been that of Perrin (1970). Apart from noting the differences in the behaviour of adults and juveniles, and males and females of both Microtus agrestis and Clethrionomys glareolus, he showed that castrated Microtus agrestis males explored a complex T-maze significantly more than did adults. Juvenile Clethrionomys glareolus exhibited more exploration of traps than did adults. In testing for aggression, juvenile Microtus agrestis males were less aggressive than adults, but approached adults more than they approached other castrates. The castrates showed more exploratory behaviour than adults. Testosterone phenylpropionate injections restored aggressive behaviour.

The present behavioural study was restricted completely to examining male bank vole aggressive behaviour, and the ecological study to be described in Chapter 4 is devoted to determining the role of that behaviour in population dynamics. However, female rodents can also exhibit aggressive behaviour, whose role in the population dynamics of voles and mice is not known; nevertheless, the enormous effort that has been devoted to the study of male mouse and vole aggressive behaviour has not been counterbalanced by an equal volume devoted to the same study of females; this has primarily been because it is difficult to make allowances for the oestrus cycle of females, with its associated hormonal fluctuations, and this renders interpretation of behavioural observations difficult. It is also well know that female rodents are much less aggressive than males (see Beach, 1948) (with exceptions, like the golden hamster, see, for instance, Payne and Swanson, 1972); they have therefore been considered less important in the control of socially mediated population processes and consequently have received less attention. Regrettably, the trend continues with the present study.

It was the purpose of the present study:-

(a) To demonstrate that castrated male bank voles were less aggressive than intact males.

(b) To demonstrate the differences between the ways in which intact, castrated and immature bank voles reacted to one another.

(c) To confirm that the animals used in the ecological studies in the enclosures (fully described in Chapter 4) did not differ significantly in their behaviour from the animals used in (a) above.

This introduction has reviewed many intrinsic factors that have been shown to affect the outcome of aggressive interactions between male rodents; these have included the effects of age and castration, the two variables concentrated upon in the present study. The effects of the remaining intrinsic factors, and all extrinsic factors known to affect rodent aggressive behaviour, have been eliminated as far as possible. The ways in which this has been attempted is described in the methods section (2.2) below.

2.2 METHODS

2.2.1 Animals used and procedure adopted for encounters

2.2.1(a) Animals used

This laboratory study of behaviour was made on two groups of animals:-

(i) The main behavioural study was carried out on animals caught in Longworth traps from several trapping sites within Crown Lands near Windsor, and in the grounds of Royal Holloway College.

(ii) A supplementary study was carried out on animals removed from the enclosures at the end of experiment ENCL 4 (see Chapter 4 for full details).

2.2.1(b) Procedure adopted for tests of behaviour

Encounters between unfamiliar pairs of male voles were carried out in a neutral arena.

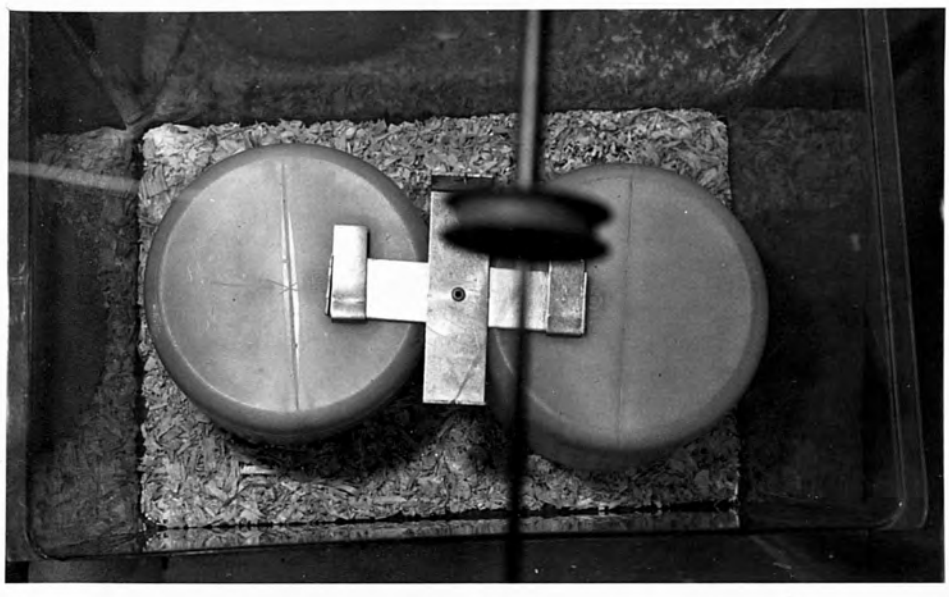
Before an encounter, the two animals to be tested were removed from their cages and each placed under a white opaque closed-top cylinder (diam. = 12cm, height = 12cm) in a perspex tank (H 20cm x W 20cm x L 45cm), in which a thin layer of fresh sawdust had been scattered. This tank was placed inside a sound-proofed box (H 60cm x W 45cm x L 45cm), with a glass observation panel in the front, and a glass lid. The tank was illuminated from above by 2 x 15W white light flourescent tubes. A string and pulley system enabled the two cylinders covering the animals to be raised from outside the sound-proofed box after it had been closed up (see Plates 2.2.1.(i), (ii),(iii)).

The animals were left under the cylinders for 600s before the encounter, which lasted 1,000s. Direct observation of the encounter was made through a sheet of one-way mirror and it was simultaneously recorded using an ITC VF 302 video camera linked to a Sony CV2 100 ACE video tape-recorder. A microphone inside the sound-proofed box, connected to an amplifier and headphones, enabled any vocalisations to be detected.

The following classes of animal were used:-

(a) Adult Intact Males: Body weight and size are not at all good measures of sexual maturity in rodents, since sexual maturation has

Plates 2.2.1. (i) - (ii)



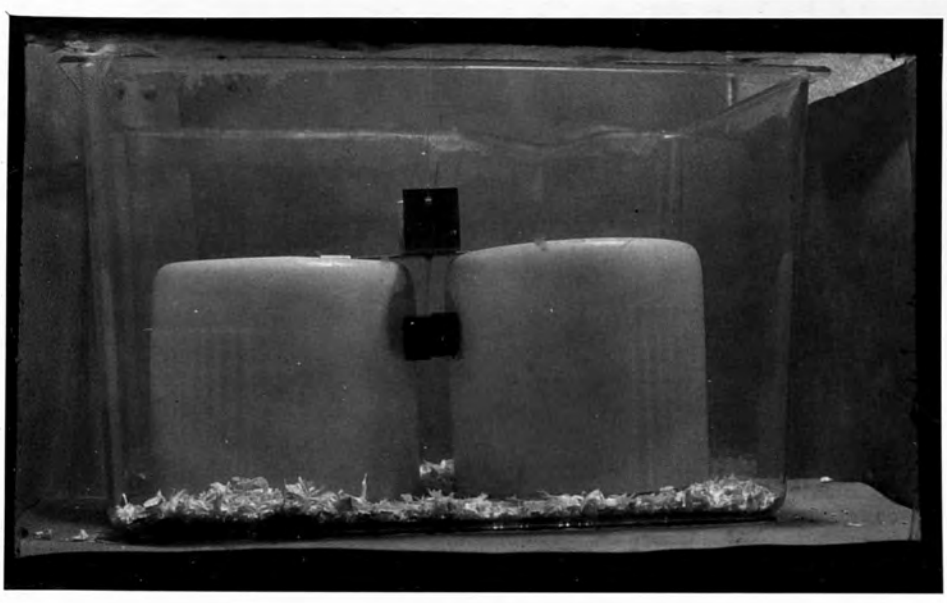
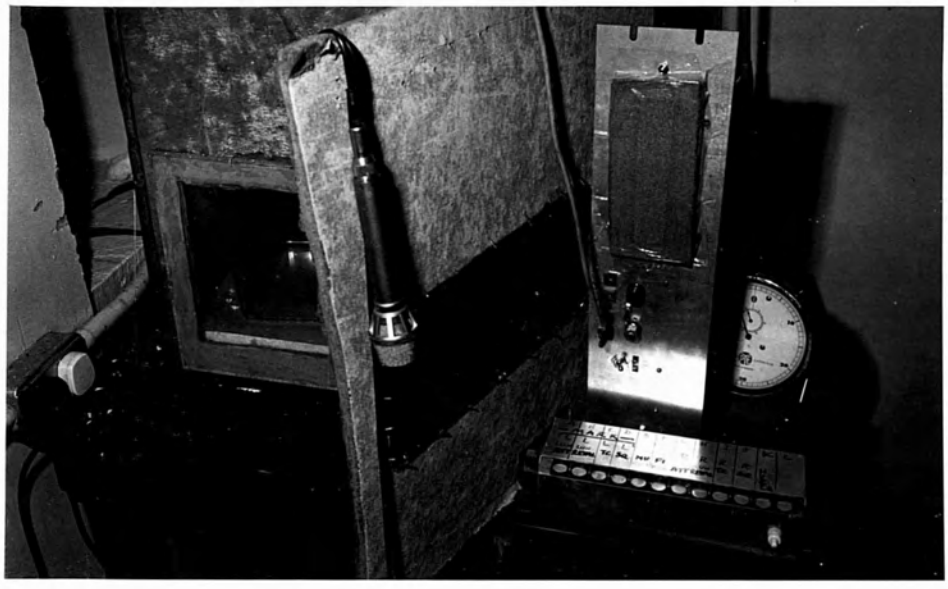


Plate 2.2.1(iii).



repeatedly been shown to be independant of body weight, but highly dependant on external factors (for instance, social environment, see Chapter 1 for a review). Rowlands (1936) showed that, in bank voles, 100mg was the critical weight (of one testis) above which spermatozoa were very rarely absent; since spermatogenesis in the seminiferous tubules and the active secretion of testosterone by the Leydig cells in the testes of rodents are closely associated (i.e. McKinney and Desjardins, 1973), it is reasonable to assume that the presence of spermatozoa is indicative of active androgen secretion. Thus an adult male was defined in the present study as one which had testes each greater than 100mg in weight. Since testis weight obviously cannot be determined in the field, the relationship between testis weight and some externally measurable characteristic had to be found.

Fig. 2.2(i) shows the relationship between weight and length of testes removed from 73 bank voles. The testes were fixed in Bouins fixative, then stored in 70% alcohol. After removal of all fat and connective tissue, excess fluid was dried off on filter paper and the length of each testis measured with dial calipers to the nearest 1/20th mm; each was then weighed on a torsion balance to the nearest milligram.

It can be seen that the weight per testis of 100mg corresponds to a length of approximately 0.8cm. In other words, animals with testes greater than 0.8cm in length are almost certainly fecund, with active androgen secretion. Because of the unreliability of estimating testis length by palpation through skin and fur, a 25% margin for error was introduced. Thus, adult animals were defined as those with the testes either in the scrotal sac or able to be pushed there with gentle pressure on the lower ventral abdomen, and whose testes were estimated by palpation to be around or above 1cm in length. Adult males when first brought in from the field were commonly found to be scarred on the tail, face and lower dorsal abdomen, and so clearly had had previous fighting experience in the wild.

(b) Immature Intact Males: Animals generally of light weight (up to around 15g) whose testes were abdominal and whose testes were estimated by palpation to be less than 0.5cm in length. It was hoped that these two criteria eliminated from the immature class all those whose testes were actively secreting androgens (see (a) above). Any

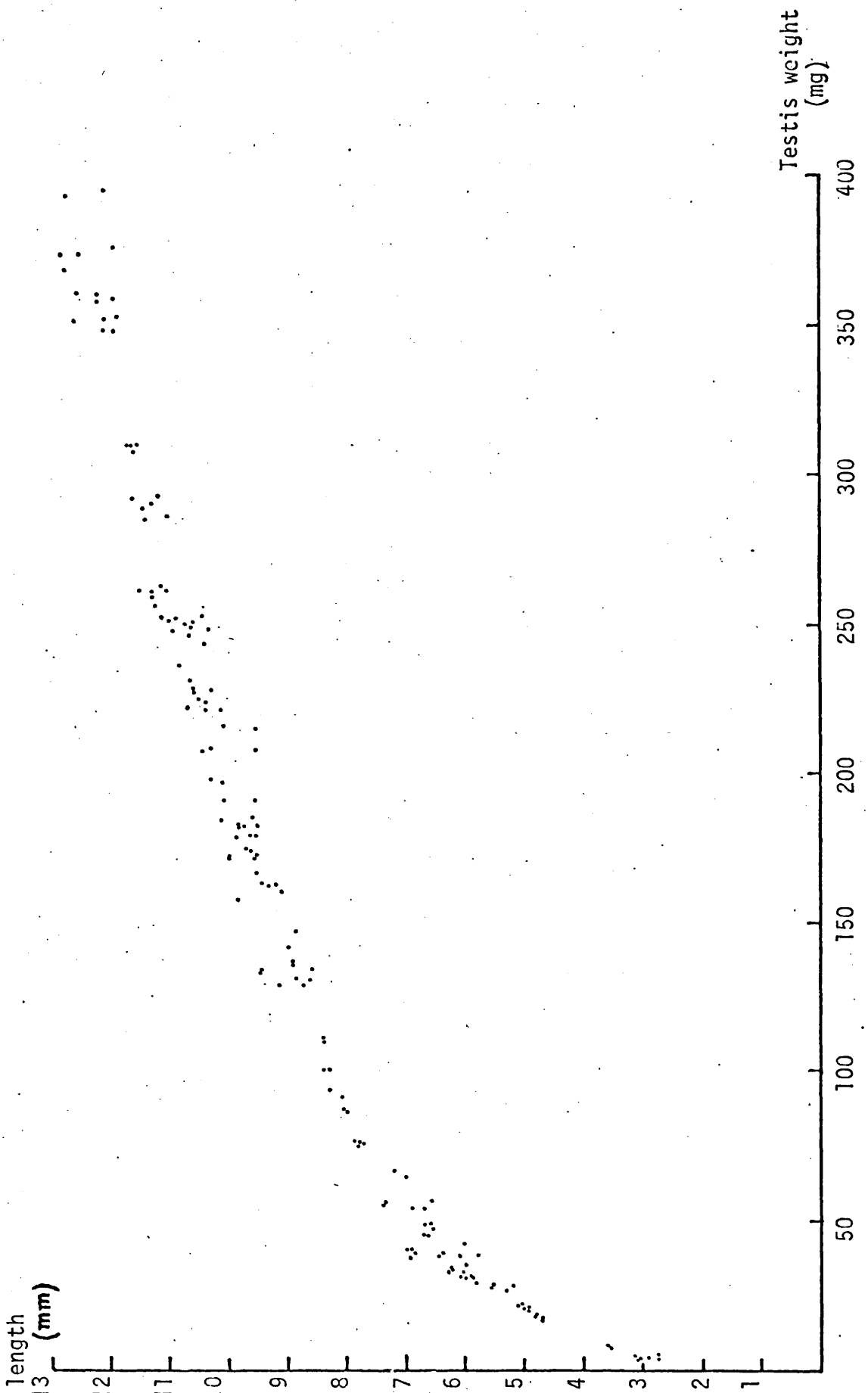


Fig. 2.2.(i) The relationship between testis weight and testis length of bank voles.

animals that had scars in this class were not used, with the intention of also eliminating all animals who had had any fighting experience in the wild.

(c) Castrated Males: Immature males with both testes removed. Bilateral castration was carried out under Vetalar anaesthetic (Parke-Davis brand of Ketamine hydrochloride) administered i.p. at a dose rate of 130mg/kg body weight. Under anaesthesia the lower ventral abdomen was shaved and washed in 70% alcohol. A ½cm midline incision was made anterior to the urinary papilla and each testis extracted. A chromic catgut ligature was then tied around the spermatic cord, artery and vein; these were then cut and the testis in its capsule removed. The incision was closed using two sutures of 2/0 monofilament nylon. Adult males all underwent a sham operation, to eliminate the possibility that the operative technique was affecting behaviour directly. This sham operation consisted of the same events as full castration, except that the testes were not extracted from the incision in the peritoneum.

The following measures were taken with the aim of standardising the encounters.

a) All encounters were done between May and November, that is within the normal breeding season of Clethrionomys glareolus. The only exception to this was the series of tests carried out on the animals removed, in November 1976, from the enclosures at the end of Experiment Encl 4, which were carried out between December 1976 and February 1977 (see Chapter 4 for full details).

b) All encounters were done between 08.30 and 11.00 to minimise the effect of circadian rhythms on the animals behaviour; this effect has been demonstrated for Clethrionomys glareolus by Saint-Girons (1960).

c) Animals were isolated in opaque white polypropylene cages (H 12cm x W 12cm x L 45cm) for a minimum of two and a maximum of five weeks prior to testing, with access to food (Dixons diet 86) and water ad lib.

d) The animal house where the animals were kept was kept between 18° and 22°C (Greenburg, (1972)has demonstrated the effects of temperature on the behaviour of mice) and under conditions of natural daylength.

e) The evening before an encounter, the animals to be used were moved in their cages from the animal house to the room in which the tests were to be carried out, which was maintained on the same lighting and temperature regime. A fan running continuously in this room effectively blanketed extraneous noises.

f) No animal was used more than twice; when an animal was used for a second time, it was always with a different opponent to that met in the first encounter, and always after a minimum of three weeks isolation following the first encounter.

g) Opponents in encounters were allocated using random numbers, with the added criterion that when two animals of the same class met (i.e. adult versus adult, castrate versus castrate or immature versus immature) their weights did not differ by more than 3grams. When an animal met another of a different class (i.e. adult versus castrate, adult versus immature, castrate versus immature) this criterion could obviously not be adhered to.

h) The encounters were all carried out in the standard perspex arena, within the sound-proofed box. A fan running continuously in the room used for encounters eliminated extraneous auditory distractions. The observer was invisible to the voles behind the one-way mirror, which was set at an angle so that they could not see their own reflections.

i) Both perspex tank and cylinders were thoroughly washed in hot water and detergent, hot rinsed and dried between each encounter.

2.2.2. Behavioural Components Observed

As already mentioned in the introduction above, the behavioural components observed and scored largely followed the scheme of Grant and Mackintosh (1963) in their description of the behaviour of Mus musculus. However, descriptions of particular postures or acts, and their names, were also drawn from Clarke's (1956) study of Microtus agrestis, Krebs' (1970) study of Microtus ochrogaster and Microtus pennsylvanicus, Turner and Iverson's (1973) study of Microtus pennsylvanicus, Colvin's (1973) study of Microtus montanus, Microtus longicaudus, Microtus californicus, Microtus ochrogaster and Microtus pennsylvanicus and Ashworth's (1973) study of Clethrionomys glareolus. Throughout the rest of this thesis, the following convention regarding the names of behavioural components will be observed:- Components observed and scored by myself, the descriptions of which follow, will be written in capitals, e.g. LOCOMOTION. Specifically defined components of other authors will be written as proper nouns, e.g. Nose. Certain of the names of behavioural components have been used by both myself and other authors, and may appear in either form, for instance APPROACH or Approach. When this occurs the description of each behavioural component given below will clarify whether my definition differs in any way from that of the previous author.

The following behaviours were observed.

1. LOCOMOTION. Any movement of the animal's whole body; movement of the head and front part of the body alone was not scored.

2. GROOM-SELF. Any cleaning action of the body surface. The degree to which this behaviour was displacement behaviour, as opposed to simple care of the body surface, was not possible to determine, since the two are not easily, if at all, visually distinguishable. Turner and Iverson (1973) noted that self-grooming often occurred when there appeared to be a 'conflict situation' and that displacement grooming was generally of longer duration than ordinary washing; they scored all Grs together. Clarke (1956) described Toilet in both

aggressive and non-aggressive situations, and Grant and Mackintosh (1963) also distinguished displacement and normal grooming activity, both suggesting however, that the displacement activity was considerably abbreviated with respect to the normal. Because of this conflict, all self-grooming was scored as GROOM-SELF in this study.

3. TEETH CHATTER. Low intensity noise (described by Clarke, 1956 as 'rather like a muffled pneumatic drill' in Microtus agrestis); the same description is apt for Clethrionomys glareolus, the noise was probably caused by gnashing the teeth. It was associated with vibration of the whiskers, which made it possible for the animal doing it to be identified easily. Teeth gnashing was included, with squealing, in Vocalisation by Turner and Iverson (1973). In the present study, it appeared to constitute a threat/deterrent behaviour; in some cases it appeared to serve to keep the animals separate, and hence not fighting, whereas in others it was the prelude to more aggressive behaviour. In many encounters, both overtly aggressive and not, it was not heard.

4. APPROACH. Movement by an individual to within approximately 15cm of an opponent. Grant and Mackintosh (1963) described Approach as any movement towards an opponent, without setting any arbitrary distance limit. Krebs (1970) scored Approach with 5-8cm of a stationary animal, with a second approach not being possible until the animals had separated by at least 15-20cm; no such condition was imposed in the present study. Turner and Iverson (1973) scored Time Together when the two animals were within 5cm of each other.

5. STRETCH-ATTEND. This is a posture in which the whole body, head and neck were extended towards the opponent, with ears and whiskers forward and tail stretched out straight behind; it was the exact equivalent of Grant and Mackintosh's (1963) Stretched Attention Posture, but was not described by Clarke (1956).

6. NOSE. The noses of the two opponents were within about $\frac{1}{2}$cm of each other with the whiskers touching. This behaviour was also described as Nose by Grant and Mackintosh (1963) and by Turner and Iverson (1973) as mutual Naso-Nasal.

7. SNIFF. The nose of the animal performing this behaviour was in contact with the fur on any part of the body of his opponent except the nose. This is a combination of Grant and Mackintosh's (1963) Sniff and Investigate.

8. RETREAT. This was any movement from a position within 15cm of an opponent to a position outside 15cm, the exact opposite of APPROACH. Not included in the category was FLEE (see below). Grant and Mackintosh (1963) described Retreat as any directed movement away from the opponent, as a complement to their Approach.

9. HUDDLE. The two animals were stationary together with bodies touching. The only other behaviour that could occur simultaneously was GROOM-SELF; the start of any other behaviour caused HUDDLE to stop.

10. LUNGE-ATTACK. An animal which had just made an approach lunged at his opponent with both fore-feet raised, as if trying to push him away. This act could be accompanied by movement of the whole body. It was equivalent to the offensive upright of Grant and Mackintosh (1963), and the Attack of Clarke (1956) and was included as pouncing within the Attack of Krebs (1970). Ashworth (1973) included Lunge, wrestling and chasing within her Attack.

11. LUNGE-RETALIATE. Exactly equivalent to LUNGE-ATTACK, except that it was performed by an animal which had been approached by his opponent. Grant and Mackintosh (1963) and Ashworth (1973) called this Defensive Upright, although Ashworth included it, with Sideways Defence, in her Ambivalent Posture. Clarke (1956) described the Lunging and Squatting type of retaliation as preliminaries to the rare complete Counter-attack by a subordinate; in this study, these two acts were combined. Krebs (1970) described Retaliation as 'the stationary vole responding to the approaching male by pouncing at him and sometimes retaliating'.

12. SQUEAL. An audible high-pitched sound of short duration, which was commonly associated with LUNGE-RETALIATE. It was also sometimes made during MUTUAL UPRIGHT (see 13 below) as well as by highly subordinate animals after aggressive interactions, when the

dominant animal, after retreat, made any sudden movement. Krebs (1970) described his Threat as 'upright stance or normal stance accompanied by baring of the teeth and squealing vocalisations'. He noted that this behaviour graded into his Retaliation and was distinguished by lack of physical contact. Turner and Iverson (1973) did not score Squeal and Teeth chatter separately.

13. MUTUAL UPRIGHT. This occurred when both animals were facing each other, resting on their hind legs and tails, and pushing at each other with their fore-feet. This corresponded to Grant and Mackintosh's (1963) Upright, Ashworth's (1973), Colvin's (1973) and Clarke's (1956) Box, and was a component of Kreb's (1970) Attack.

14. WRESTLE. The two animals were locked together, tumbling over each other. Grant and Mackintosh (1963) did not describe Wrestle as such, but divided the highest levels of aggressive behaviour into Attack, Bite and the Offensive and Defensive Upright and Sideways postures. In the present study WRESTLE was scored separately because of the extreme ferocity and speed with which it occurred. It was described as Wrestling by Clarke (1956), Colvin (1973) and Ashworth (1973), and was included as Wrestling within Krebs' (1970) Attack, along with Pouncing, Boxing and Chasing.

15. GROOM OTHER. This was when one animal carried out active grooming movements in the fur of the opponent. Grant and Mackintosh (1963) called this Aggressive Groom and it was generally associated with a dominant animal grooming a subordinate; in the present study it not infrequently led to LUNGE-RETALIATE by the groomee and sometimes to WRESTLE; on some occasions however, (particularly between two immature or two castrated animals) this behaviour did not appear to be part of a lead-up to more aggressive behaviour. Krebs (1970) described Mutual Grooming in connection with his Follow, but did not score it.

16. CROUCH. A common response to GROOM OTHER, but not necessarily always occurring with it; the animal crouching pressed both head and body against the floor, and remained motionless. When associated with GROOM OTHER, the groomer usually groomed the dorsal surface of the neck, the back of the head, or the back of the

groomee. Clarke (1956) described this posture as Freeze, and it is shown by Grant and Mackintosh in their fig.4. Their Elevated Crouch was not observed in this study.

17. CHASE. A vigorous pursuit of one animal by the other, both running, and representing, in the arena at least, very high levels of aggressive activity. This was described as Chase by Grant and Mackintosh (1963) and Clarke (1956), and included within Attack by Krebs (1970). Turner and Iverson (1970) distinguished Chase from Follow (not scored in the present study) but discontinued scoring Chase because it was so infrequently seen. It was similarly very rarely seen in the present study.

18. FLEE. The complement to CHASE, without which it could not occur. Grant and Mackintosh described Flee as a high intensity form of Retreat, associated with 'undirected bouncing movements'. Krebs (1970) scored Retreat and Flee together as Avoidance.

19. DOMINATE. The two animals were motionless, the dominant above his opponent, commonly with his fore-feet resting on the supine body of his opponent. This equalled the Aggressive posture of Grant and Mackintosh (1963) and was included within Krebs' (1970) Attack.

20. SUBMIT. The complement to DOMINATE; the submissive animal usually lay supine or propped up in a corner of the arena, with his flank or belly exposed. This posture was equivalent to Krebs' (1970) Submission, and Grant and Mackintosh's (1963) Submissive Posture. Clarke's (1956) 'Supine' (his fig.6) represented an extreme form of SUBMIT.

21. MW CD. Of the 20 behavioural components described above, four represented the highest levels of aggressive behaviour observed. These were MUTUAL UPRIGHT, WRESTLE, CHASE and DOMINATE. They were therefore combined into a composite 'aggressive behaviour' component, MW CD, and analysed in the same way as all the other individual components.

Most of the behaviours were obviously mutually exclusive. Apart

from those behaviours that commonly occurred together (e.g SQUEAL and LUNGE-RETALIATE) others did so by definition; thus LUNGE-ATTACK, LUNGE-RETALIATE, APPROACH, RETREAT, CHASE and FLEE were all included in, and were scored simultaneously with, LOCOMOTION. Similarly DOMINATE and SUBMIT, and CHASE and FLEE, were always scored together, one for each animal. NOSE and SNIFF commonly but not always occurred in association with STRETCH-ATTEND; CROUCH was commonly associated with GROOM OTHER but the two were not mutually dependant.

During the encounter, the following seven behaviours of both animals were recorded directly:- LUNGE-ATTACK, LUNGE-RETALIATE, TEETH CHATTER, SQUEAL, MUTUAL UPRIGHT, WRESTLE, and HUDDLE.

The video recording of the encounter, played back twice, enabled the other 13 behavioural components to be scored for each animal:- LOCOMOTION, GROOM-SELF, APPROACH, STRETCH-ATTEND, NOSE, SNIFF, RETREAT, CROUCH, CHASE, DOMINATE, FLEE, SUBMIT, GROOM OTHER.

2.2.3. Behavioural variables measured.

The following variables for each behavioural component observed were determined:-

Latency: The time interval in seconds from the start of the encounter to the first occurrence of a behaviour.

Occurrence: The number of times a behaviour occurred during the encounter.

Duration: The total accumulated time in seconds spent performing a behaviour.

2.2.4. Apparatus

The apparatus used to record the three measures of the 20 behaviours was as follows:- In front of the observer was a 12-button keyboard, each button activating, when pressed, two microswitches mounted side by side. (see plate 2.2.1(iii) above). The first of these switches, when closed, completed a circuit containing a 27 volt DC supply, a standard GPO solenoid five digit counter, and two further microswitches, each being activated alternately by a 20-toothed wheel, driven by a Venner synchronous motor rotating at a constant six revolutions/minute. Thus, when the push-button microswitch was closed, the GPO counter added one digit every quarter of a second. The second of the microswitches underneath each button, when closed, completed a circuit containing a 10 volt DC supply and one pen of an FC Robinson & Co. 10 pen event recorder, with a chart speed of .08 cm/s (see plate 2.2.1(iv)). Each push-button, activating the two microswitches, was pressed only when a particular behaviour occurred. Thus, at the end of an encounter, the number on the GPO counter equalled the accumulated time spent in a particular behaviour in seconds/4 (duration). From the paper output from the event recorder latency and occurrence were determined; Latency was determined to the nearest 10 seconds, and the minimum detectable gap between two marks on the event recorder output represented one second.

Plate 2.2.1(iv)

2.2.5. Statistical Analysis

The total number of encounters between individuals of different groups in the main behaviour study is given in Table 2.2.5(i)

Table 2.2.5(i) Main behaviour study, total numbers of encounters.

	Ad	C	I
I	17	8	19
C	20	19	
Ad	47		

Key:

Ad = Adult males
C = Castrated males
I = Immature males

The numbers of records obtained from these encounters is given in Table 2.2.5(ii)

Table 2.2.5(ii) Main behaviour study, numbers of records, all encounters.

Class of animals whose behaviour was being recorded.	Class of animals being used as opponents.	No. of records
Ad	Ad	94
Ad	C	20
Ad	I	17
C	Ad	20
C	C	38
C	I	8
I	Ad	17
I	C	8
I	I	38

Key as for Table 2.2.5(i)

In addition, animals removed from the enclosures at the end of experiment ENCL 4 in November 1973 (see Chapter 4) were also tested, and the total numbers of encounters are given in Table 2.2.5(iii)

Table 2.2.5(iii) Supplementary behaviour study, total numbers of encounters

	AdL4	CR4	IL4	IR4
IR4	-	-	-	16
IL4	-	-	16	
CR4	-	8		
AdL4	8			

Key: Ad4 = Adult males
I4 = Immature males
C4 = Castrated males
R = Right enclosure
L = Left enclosure
) Animals removed from enclosures following experiment ENCL 4

The records obtained from these encounters is given in Table 2.2.5(iv)

Table 2.2.5(iv) Supplementary behaviour study, numbers of records, all encounters.

Class of animals whose behaviour was being recorded	Class of animals being used as opponents	No. of records
AdL4	AdL4	16
CR4	CR4	16
IL4	IL4	32
IR4	IR4	32

Key: As for Table 2.2.5(iii)

Because the encounters were of a finite length, inevitably there were many occasions when a particular behaviour was not observed; the result of this was many scores of 1000 seconds for latency and zero for occurrence and duration, which still had to be included in the analysis. Clearly the results obtained were rarely, if ever, normally distributed, and any parametric statistical analysis would have been inappropriate. Comparison was therefore made for each of the measures for each of the behaviours observed between each class of animal and certain other classes using the Mann - Whitney test (Mann and Whitney, 1947; Siegel, 1956); details of which classes were compared with which are given in Table 2.2.5(v)

Comparisons of duration of LUNGE-ATTACK, LUNGE-RETALIATE, APPROACH, RETREAT and SOCIAL were omitted, since all these behavioural acts were essentially instantaneous, and therefore had no finite length; consideration of their duration was therefore meaningless.

The Latency, Occurrence and Duration of MUTUAL UPRIGHT, WRESTLE, CHASE and DOMINATE combined (MUCD), (being the four behavioural components observed in the arena which appeared to be exhibited at the highest levels of aggression) were also compared.

Table 2.2.5(v): Details of comparisons made between animals in different types of encounter. (Key on the next page.)

Group (1)	Group (2)	Group (1): Class of animal whose behaviour was being monitored — Group (2): Class of animal used as opponents													
		Ad	Ad	Ad	C	C	C	I	I	I	AdL4	CR4	IL4	IR4	I(L&R)4
		Ad	C *	I	Ad	C	I	Ad	C	I	AdL4	CR4	IL4	IR4	I(L&R)4
Ad	Ad		2.3.2 (a)(ii)	2.3.2 (b)(iii)		2.3.1 (iv)				2.3.1 (v)	2.3.4. (iv)				
Ad	C			2.3.2 (a)(iv)											
Ad	I														
C	Ad					2.3.2 (b)(ii)	2.3.2 (b)(iv)								
C	C						2.3.2 (b)(iii)			2.3.1 (vi)		2.3.4 (v)			
C	I														
I	Ad								2.3.2 (c)(iv)	2.3.2 (c)(ii)					
I	C									2.3.2 (c)(iii)					
I	I														2.3.4 (vi)
AdL4	AdL4											2.3.3 (i)	2.3.3 (vi)		
CR4	CR4													2.3.3 (vii)	
IL4	IL4													2.3.3 (v)	
IR4	IR4														
I(L+R)4	I(L+R)4														

Ad = Adult males
C = Castrated males
I = Immature males
Ad4) Animals removed from
C4) enclosures following
I4) experiment ENCL 4
R = Right enclosure
L = Left enclosure

Key to table 2.2.5(v).

Each unshaded cell in the table above corresponds to a comparison between two particular kinds of encounter (a row and a column). The number in the cell is the number of the table in the Results Section (3.3.) which contains values of U and p of the Mann-Whitney test associated with that comparison.

Thus, for example, cell* shows that Table 3.3.2(a)(ii) in the Results contains details of Mann-Whitney comparisons of three measures of 20 behavioural components of adults which had been confronted with other adults with the behavioural components of adults confronted with castrates.

Group (1) was the class of animal whose behaviour was being monitored.

Group (2) was the class of animal that was being used as opponents.

The entire analysis was then repeated for all those encounters in which APPROACH occurred (i.e.omitting all these encounters in which no close-contact behaviour occurred). The number of these encounters are given in Tables 2.2.5(vi) and 2.2.5(vii).

Table 2.2.5(vi). Main behaviour study, numbers of encounters observed, only encounters with APPROACH.

	Ad	C	I
I	16	8	18
C	17	13	
Ad	31		

Key: Ad = Adult males
C = Castrated males
I = Immature males

Table 2.2.5(vi). Supplementary behaviour study, numbers of encounters observed, only encounters with APPROACH

	AdL4	CR4	IL4	IR4
IR4	-	-	-	14
IL4	-	-	14	
CR4	-	8		
AdL4	31			

Key:

Ad4) Animals removed from
C4) = enclosures following
I4) experiment ENCL 4

R = Right enclosure
L = Left enclosure

The numbers of records thereby obtained are given in Tables 2.2.5(vii) and (ix).

Table 2.2.5(viii). Main behaviour study, numbers of records, only encounters with APPROACH.

Class of animals whose behaviour was being recorded	Class of animals being used as opponents	No. of records
Ad	Ad	62
Ad	C	17
Ad	I	16
C	Ad	17
C	C	26
C	I	8
I	Ad	16
I	C	8
I	I	36

Key: Ad = Adult males
C = Castrated males
I = Immature males

Table 2.2.5(ix). Supplementary behaviour study, numbers of records, only encounters with APPROACH.

Class of animals whose behaviour was being recorded	Class of animals being used as opponents	No. of records
AdL4	AdL4	8
CR4	CR4	16
IL4	IL4	28
IR4	IR4	28

Key:

Ad4)
C4) = Animals removed from enclosures following experiment ENCL4
I4)

R = Right enclosure

L = Left enclosure

2.3 RESULTS

The results of the following comparisons are given in this section:-

2.3.1. A comparison of the behaviour of adults confronted with other adults, castrates confronted with other castrates and immatures confronted with other immatures (Main behaviour study).

2.3.2. Comparisons of the ways in which the behaviour of a particular class of animal varied when confronted with different sorts of opponent (Main behaviour study).

i.e. (a) The differences between the behaviour of adults confronted castrates, immatures or other adults.

(b) The differences between the behaviour of castrates confronted with adults, immatures or other castrates.

(c) The differences between the behaviour of immatures confronted with adults, castrates or other immatures.

2.3.3. A comparison of the behaviour exhibited in adult-adult, castrate-castrate and immature-immature encounters by animals removed from left and right enclosures at the end of experiment ENCL 4 (Supplementary behaviour study)

2.3.4. A comparison of the behaviour of the adult,castrated and immature male voles removed from experiment ENCL 4, described in section 2.3.3, (Supplementary behaviour study), with that of the adults, castrates and immatures used in the main behaviour study, described in Sections 2.3.1 and 2.3.2.

2.3.1. RESULTS.

Table 2.3.1(i) shows that the number of adult-adult encounters with APPROACH was not significantly different to the number of castrate-castrate encounters with APPROACH ($\chi^2 = 0.03$, df = 1, n.s.). However, Table 2.3.1(ii) shows that high levels of aggressive behaviour (MW CD) occurred in significantly more of the adult-adult encounters than in the castrate-castrate encounters. ($\chi^2 = 6.93$, df = 1, $p < 0.01$). Combining the two tables above, Table 2.3.1(iii) shows that if only those encounters in which APPROACH occurred are considered, the differences in the incidence of MW CD becomes more highly significant. ($\chi^2 = 10.09$, df = 1, $p < 0.001$).

Table 2.3.1(i) The number of encounters in which APPROACH did or not occur.

Type of encounter	Total no.	APPROACH	
		Yes	No
Ad vs Ad	47	31	13
C vs C	19	13	6
I vs I	19	18	1

$\chi^2 = 0.03$, df = 1, n.s.

$\chi^2 = 4.38$, df = 1, $p < 0.05$

$\chi^2 = 5.88$, df = 1, $p < 0.02$

Key: Ad = Adult males
C = Castrated males
I = Immature males

Table 2.3.1(ii)

The number of encounters in which high levels of aggressive behaviour (MWCD) did or did not occur - all encounters considered.

Type of encounter	Total No.	MWCD Yes	MWCD No
Ad vs Ad	47	21	26
C vs C	19	2	17
I vs I	19	2	17

$\chi^2 = 6.90$, df = 1, $p < 0.01$

$\chi^2 = 0$, df = 1, n.s

$\chi^2 = 6.90$, df = 1, $p < 0.01$

Key : As for Table 2.3.1.(i)

Table 2.3.1(iii)

The number of encounters in which MWCD did or did not occur - only encounters with APPROACH considered.

Type of encounter	Total No.	MWCD Yes	MWCD No
Ad vs Ad	31	21	10
C vs C	13	2	11
I vs I	18	2	16

$\chi^2 = 10.09$, df = 1, $p < 0.001$

$\chi^2 = 0.11$, df = 1, n.s.

$\chi^2 = 14.46$, df = 1, $p < 0.001$

Key: As for Table 2.3.1(i)

Table 2.3.1(iv) shows that adult males fought significantly more and sooner than did castrated males (MM CD, $p<0.001$). It can also be seen that the social and investigative behaviours (APPROACH, STRETCH-ATTEND, NOSE, SNIFF) were not significantly different between the two classes of male. Consideration of only those encounters in which APPROACH occurred shows that the differences in WRESTLE and MUTUAL UPRIGHT are significant ($p<0.001$), and that the adults also exhibit LUNGE-ATTACK more ($p<0.05$). In Table 2.3.1(iv), it can be seen that TLETH-CHATTER was more common and lasted longer in adults than castrates, but that the latencies were not significantly different. In encounters with APPROACH, the castrates huddled with each other significantly sooner and more often than the adults ($p<0.05$). As has already been shown, APPROACH did not occur in significantly more of the castrate-castrate encounters than in adult-adult encounters (Table 2.3.1(i), $\chi^2 = 0.03$, df = 1, n.s.); in other words, it appeared that castrates were as wary of other castrates as were adults of other adults. When APPROACH had occurred, there was no significant difference in the amount of social and investigative behaviours exhibited, but adults fought significantly more than the castrates.

In contrast to the comparison of adult-adult and castrate-castrate encounters, Table 2.3.1(i) shows that APPROACH occurred in significantly more of the immature-immature encounters than in the adult-adult encounters ($\chi^2 = 5.88$, df = 1, $p<0.02$). Table 2.3.1(ii) shows that aggressive behaviour (MM CD) occurred in significantly more of the adult-adult encounters than in the immature-immature encounters. ($\chi^2 = 8.00$, df = 1, $p<0.01$). Again, combining the two tables above gives Table 2.3.1(iii); considering only those encounters in which APPROACH occurred, the difference in the incidence of MM CD becomes more highly significant ($\chi^2 = 12.40$, df = 1, $p<0.001$).

Table 2.3.1(iv). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : Ad
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : C
Class of animals used as opponents: C

BEHAVIOURS	All encounters: Number of records, Group 1:94 Number of records, Group 2:38									Encounters with approach: Number of records, Group 1: 62 Number of records, Group 2: 26								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	1513			1508			-			629			623	3	(1)	-		
LUNGE-RETALIATE	1600			1572			-			693.5			665.5			-		
TEETH CHATTER	1506.5			691.5	1	(1)	706.5	1	(1)	768			286	1	(1)	302	1	(1)
SQUEAL	1588.5			1574.5			-			679.5			665.5			-		
MUTUAL UPRIGHT	1166	1	(2)	1192	2	(1)	1201	2	(1)	377	1	(2)	403	1	(1)	391	1	(1)
WRESTLE	1387	3	(2)	1387	3	(1)	1406	3	(1)	546	2	(2)	546	2	(1)	546	1	(1)
HUDDLE	1537.5			1509			1474			623	3	(1)	610	3	(2)	598	3	(2)
LOCOMOTION	1714			1726			1682.5			660			667			782		
GROOM-SELF	1600			1681			1663.5			729			743.5			761.5		
APPROACH	1689.5			1756			-			723.5			790			-		
STRETCH-ATTEND	1627.5			1626.5			1652			706			705.5			704		
NOSE	1763			1737			1700.5			759			734.5			712.5		
SNIFF	1755			1719			1696			767			731			732		
CROUCH	1699.5			1701			1672.5			736			737.5			730.5		
RETREAT	1631			1681			-			677			733.5			-		
CHASE	1729			1729			1748			780			780			780		
DOMINATE	1634			1634			1653			715			715			715		
FLEE	1729			1729			1748			780			780			780		
SUBMIT	1634			1634			1653			715			715			715		
GROOM-OTHER	1625			1634.5			1607.5			684			693.5			689.5		
MWCD	1132	1	(2)	1147	1	(1)	1155	1	(1)	355	1	(2)	370	1	(1)	357	1	(1)

Key to tables 2.3.1(iv), (v) and (vi)
2.3.2(a)(ii), (iii) and (iv)
2.3.2(b)(ii), (iii) and (iv)
2.3.2(c)(ii), (iii) and (iv)
2.3.3(i), (v), (vi) and (vii)
2.3.4(iv), (v) and (vi)

1. Each table shows the values of the statistic U and associated probability p obtained from Mann-Whitney tests comparing each measure of each behavioural component of the two groups of animals (Groups 1 and 2, shown above the main body of the table). The left-hand half of the table shows the results when all encounters in each group are compared, the right-hand half when only those encounters with APPROACH are compared.

2. Significancelevels are shown as follows:

$p<0.001 = 1$, $p<0.01 = 2$, $p<0.05 = 3$.

3. The figure in brackets shows which group of animals (1 or 2) had the higher values of each measure of each behavioural component.

Ad = Adult male
C = Castrated male
I = Immature male
R = Right (experimental) enclosure
L = Left (control) enclosure

Ad4, C4, I4 = Animals removed from the enclosures at the end of experiment ENCL 4

(see Chapter 4 for full details)

Table 2.3.1(v) shows further the differences between the behaviour of adults confronting adults and immatures confronting immatures. It can be seen that immatures fought significantly less with each other than did adults, particularly once an APPROACH had been made, (MWCD, $p<0.001$). The difference is still significant, though less so, for latency and duration of MWCD when all encounters are included ($p<0.01$). In the encounters with APPROACH, adults exhibited LUNGE-ATTACK more often and sooner ($p<0.05$) than did immatures. Table 2.3.1(v) also shows that STRETCH-ATTEND occurred sooner ($p<0.05$) more often ($p<0.01$) and lasted longer ($p<0.01$) in immature-immature encounters than in adult-adult encounters when only those encounters with APPROACH were considered, but that there is no significant difference when all encounters are considered. Although APPROACH occurred in significantly more of the immature-immature encounters than it did in the adult-adult encounters, (Table 2.3.1(i) $\chi^2 = 5.38$, df = 1, $p<0.02$) once it had occurred, then social and investigative behaviours were not more common, except in the case of STRETCH-ATTEND. In other words, social and investigative behaviours tended to lead to overt aggression in adult-adult encounters but not in immature-immature encounters. Adults exhibited TEETH-CHATTER sooner ($p<0.05$), more often ($p<0.001$) and longer ($p<0.001$) than did immatures when only the encounters with APPROACH are considered, and only the difference in latencies is non-significant in all encounters. TEETH-CHATTER appeared as a deterrent to further aggression in adult-adult encounters in many cases, sometimes apparently actively inhibiting APPROACH, but in other encounters it was seen to lead on to highly aggressive interactions. It can be seen that GROOM-SELF was seen more and for longer in immature-immature encounters than in adult-adult encounters, when all encounters are considered, and for longer in encounters with APPROACH. The equivocal nature of GROOM-SELF described in section 2.2.2 means that it was not really possible to interpret these differences.

Table 2.3.1(v). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : Ad
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : I
Class of animals used as opponents: I

	All encounters: Number of records, Group 1: 94; Number of records, Group 2: 38									Encounters with approach: Number of records, Group 1: 62; Number of records, Group 2: 36								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	1478.5			1480.5			-			830	3	(2)	832	3	(1)	-		
LUNGE-RETALIATE	1710			1684.5			-			972.5			947			-		
TEETH CHATTER	1576.5			1126.5	1	(1)	1141	1	(1)	811.5	3	(2)	501	1	(1)	531.5	1	(1)
SQUEAL	1647.5			1613			-			938			903.5			-		
MUTUAL UPRIGHT	1152	1	(2)	1098	1	(1)	1112	1	(1)	509	1	(2)	455	1	(1)	449	1	(1)
WRESTLE	1484			1488			1508			822	3	(2)	826	3	(1)	826	3	(1)
HUDDLE	1590			1590			1568			990			990			990		
LOCOMOTION	1644.5			1768			1322.5	2	(2)	1066.5			825	3	(2)	1004.5		
GROOM-SELF	1764.5			1500.5			1249.5	2	(2)	988			1025.5			850	3	(2)
APPROACH	1357.5	3	(1)	1495.5			-			999.5			1094.5			-		
STRETCH-ATTEND	1726			1662.5			1693.5			828.5	3	(2)	765	2	(1)	765	2	(1)
NOSE	1688			1632			1652.5			987			1042			1005.5		
SNIFF	1737			1694			1684.5			1037.5			1080.5			1065.5		
CROUCH	1611			1613			1586.5			1023.5			1025.5			1021.5		
RETREAT	1472.5			1573			-			1070			1060.5			-		
CHASE	1729			1729			1748			1080			1080			1080		
DOMINATE	1683			1680			1701.5			1023.5			1020.5			1022.5		
FLEE	1729			1729			1748			1080			1080			1080		
SUBMIT	1683			1680.5			1701.5			1023.5			1021			1022.5		
GROOM-OTHER	1639			1643			1607.5			1063			1067			1054.5		
MWCD	1215	2	(2)	1152.5	1	(1)	1175.5	2	(1)	541	1	(2)	480.5	1	(1)	482.5	1	(1)

Table 2.3.1(vi) shows the differences between the behaviour of castrates confronted with castrates, and that of immatures confronted with immatures. In spite of the large sample sizes, it can be seen that there were no significant differences between the social and investigative and aggressive behaviours of the two groups. When all encounters are considered, it can be seen that immatures spent longer($p<0.05$) in GROOM-SELF than castrates; again, the biological reason for this is difficult to interpret. Significantly more (Table 2.3.1(i), $\chi^2 = 4.33$, df = 1, $p<0.05$) immature-immature encounters involved an APPROACH than did the castrate-castrate encounters, but there is no significant difference in the numbers of encounters in which high levels of aggressive behaviour (ATTACK) occurred (Tables 2.3.1(ii) and 2.3.1(iii)).

2.3.1. Summary.

Consideration of the adult-adult, castrate-castrate and immature-immature encounters has shown that, in the arena test used in the present study, adults fought significantly more amongst themselves than did castrates or immatures, and that there were no important differences between the recorded behavioural components of castrates and immatures. However, immatures appeared less reluctant to approach each other than did either adults or castrates; in both of the latter groups, several encounters had no APPROACH at all. Once an APPROACH had been made, there was no real difference in the amount of social and investigative behaviours exhibited by the three groups; in the adult-adult encounters, the initial social behaviour escalated to aggressive behaviour, in the castrates and immatures it did not.

Table 2.3.1(vi). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page)

Group 1
Class of animals under test : I
Class of animals used as opponents: I

compared with:-

Group 2
Class of animals under test : C
Class of animals used as opponents: C

	All encounters: Number of records, Group 1: 38; Number of records, Group 2: 38									Encounters with approach: Number of records, Group 1: 36; Number of records, Group 2: 26								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	704			704			-			446			446			-		
LUNGE-RETALIATE	684			678.5			-			467			461.5			-		
TEETH CHATTER	693			584			601.5			366			450			438		
SQUEAL	700			703			-			464			461			-		
MUTUAL UPRIGHT	688			682			684			426			420			422		
WRESTLE	684			684			684			442			442			442		
HUDDLE	704			688			708			421			406			426		
LOCOMOTION	633.5			696.5			591			364.5			445.5			436		
GROOM-SELF	661.5			619			516.5	3	(1)	458.5			445.5			409.5		
APPROACH	587			610.5			-			459			453.5			-		
STRETCH-ATTEND	684.5			692			698.5			407.5			400			393.5		
NOSE	685			702.5			716.5			413			395.5			381.5		
SNIFF	717.5			720			717			416.5			410			407		
CROUCH	686			692.5			693.5			467			460.5			459.5		
RETREAT	656			677.5			-			426			404.5			-		
CHASE	722			722			722			468			468			468		
DOMINATE	703			703			703			455			455			455		
FLEE	722			722			722			468			468			468		
SUBMIT	703			703			703			455			455			455		
GROOM-OTHER	716			716.5			720			422			422.5			426		
MWCD	714			721			718			456			449			450		

2.8.2. Results (cont.)

2.3.2(a) Comparison of the ways in which the behaviour of adults varied when confronted with castrates, immatures or other adults.

Table 2.3.2(a)(i) shows that significantly more approaches were made in the adult-immature encounters than in the adult-adult encounters, but that other comparisons were non-significant.

Table 2.3.2(a)(i). The number of encounters in which APPROACH did or did not occur.

Type of encounter	Total No.	APPROACH			
		Yes	No		
Ad vs Ad	47	31	16	χ^2=2.57 df= 1, n.s.	χ^2= 5.05 df= 1 p<0.05
Ad vs C	20	17	3		
Ad vs I	17	16	1	χ^2=0.73 df = 1n.s.	

Key: Ad = Adult males
C = Castrated males
I = Immature males

Table 2.3.2(a)(ii) shows the comparison of adult-adult encounters with adult-castrate encounters. It can be seen that adults confronted with adults fought sooner, more often and for longer than did adults confronted with castrates (MWCD, p< 0.001). LUNGE-ATTACK and LUNGE-RETALIATE were also exhibited sooner and more often by adults in adult-adult encounters than by adults in adult-castrate encounters. In general, the amount of social and investigative behaviour was not different although, in all encounters, adults confronting castrates exhibited STRETCH-ATTEND more (p<0.05) and in the encounters with APPROACH, adults confronting adults exhibited SNIFF more (p<0.05). Once APPROACH had occurred, adults were more prone to SQUEAL when with other adults than when with castrates. This was because SQUEAL was commonly observed in association with high levels of aggressive behaviour (LUNGE-ATTACK, and LUNGE-RETALIATE as well as MUTUAL UPRIGHT

Table 2.3.2(a)(ii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : Ad
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : Ad
Class of animals used as opponents: C

BEHAVIOURS	All encounters: Number of records, Group 1: 94; Number of records, Group 2: 20									Encounters with approach: Number of records, Group 1: 62; Number of records, Group 2: 17								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	750			750			-			374	3	(2)	374	3	(1)	-		
LUNGE-RETALIATE	764			748.5			-			378.5	3	(2)	363	3	(1)	-		
TEETH CHATTER	720			884.5			835.5			405.5			471.5			443		
SQUEAL	740			740			-			365.5	3	(2)	365.5	3	(1)	-		
MUTUAL UPRIGHT	540	2	(2)	540	2	(1)	550	2	(1)	195.5	1	(2)	195.5	1	(1)	195.5	1	(1)
WRESTLE	730			730			740			357	3	(2)	357	3	(1)	357	3	(1)
HUDDLE	890			890			900			493			493			493		
LOCOMOTION	926			730.5			698			483.5			432			425		
GROOM-SELF	930.5			808.5			775.5	3	(2)	493			473			448.5		
APPROACH	878			814			-			474.5			515.5			-		
STRETCH-ATTEND	763.5			706	3	(2)	650.5	3	(2)	501			443.5			405.5		
NOSE	932			937.5			917.5			450			438.5			410.5		
SNIFF	733.5			731.5			741			351	3	(2)	349	3	(1)	348	3	(1)
CROUCH	860			860			870			467.5			467.5			467.5		
RETREAT	857			781.5			-			492.5			487.5			-		
CHASE	910			910			920			510			510			510		
DOMINATE	860			860			870			467.5			467.5			467.5		
FLEE	910			910			920			510			510			510		
SUBMIT	909			908.5			914.5			510			500.5			496		
GROOM-OTHER	820			820			830			433.5			433.5			433.5		
MWCD	520	1	(2)	520	1	(1)	530	1	(1)	178.5	1	(2)	178.5	1	(1)	178.5	1	(1)

and WRESTLE).

Table 2.3.2(a)(iii) shows the comparison between the behaviour of adults confronted with adults and the behaviour of adults confronted with immatures; the results are very similar to those described in the previous section. Adults in adult-adult encounters indulged in significantly more aggressive behaviour than did adults confronted with immatures (MWCD, $p<0.01$ for all encounters, $p<0.001$ for encounters with APPROACH; MUTUAL UPRIGHT, $p<0.01$ for all encounters, $p<0.001$ for encounters with APPROACH; LUNGE-ATTACK and WRESTLE, $p<0.05$ for encounters with APPROACH). It can also be seen that adults in adult-adult encounters exhibited TEETH-CHATTER sooner, more often and for longer than adults confronted with immatures (TEETH-CHATTER, $p<0.05$ for duration in all encounters, and for latency and occurrence in encounters with APPROACH, $p<0.01$ for duration in encounters with APPROACH).

Table 2.3.2(a)(iv) shows that there was very little difference between the behaviour of adults confronted with castrates and that of adults confronted with immatures; the former group exhibited TEETH-CHATTER sooner ($p<0.05$, all encounters, $p<0.01$ in encounters with APPROACH, and longer ($p<0.05$, in encounters with APPROACH) than do the latter. Also, in the encounters with APPROACH, adults exhibited STRETCH -ATTEND more to castrates than to immatures ($p<0.05$). These slight differences have no obvious explanation.

2.3.3(a). Summary.

As expected, adults fought more with other adults than they did with either castrates or immatures. The response of adults to the presence of castrates is similar to their response to immatures, with little or no aggressive behaviour, and with similar amounts of social and investigative behaviour being exhibited.

Table 2.3.2(a)(iii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page)

Group 1
Class of animals under test : Ad
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : Ad
Class of animals used as opponents: I

BEHAVIOURS	All encounters: Number of records, Group 1:94 Number of records, Group 2:17									Encounters with approach: Number of records, Group 1: 62 Number of records, Group 2: 16								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	637.5			637.5			-			352	3	(2)	352	3	(1)	-		
LUNGE-RETALIATE	760			776.5			-			477			460.5			-		
TEETH CHATTER	634			631			553.5	3	(1)	310.5	3	(2)	337	3	(1)	301.5	2	(1)
SQUEAL	629			629			-			344	3	(2)	344	3	(1)	-		
MUTUAL UPRIGHT	459	2	(2)	459	2	(1)	467.5	2	(1)	184	1	(2)	184	1	(1)	184	1	(1)
WRESTLE	620.5			620.5			629			336	3	(2)	336	3	(1)	336	3	(1)
HUDDLE	756.5			756.5			765			464			464			464		
LOCOMOTION	728.5			739.5			788.5			413.5			440			391		
GROOM-SELF	785.5			742.5			729			464			480.5			475		
APPROACH	703			741.5			-			481.5			443			-		
STRETCH-ATTEND	772.5			787.5			776.5			378			393			369.5		
NOSE	786			786			790.5			383			409.5			398.5		
SNIFF	643.5			640.5			654			345.5	3	(2)	342.5	3	(1)	347	3	(1)
CROUCH	731			731			739.5			440			440			440		
RETREAT	722.5			752			-			476.5			446.5			-		
CHASE	773.5			773.5			782			480			480			480		
DOMINATE	731			731			739.5			440			440			440		
FLEE	773.5			773.5			782			480			480			480		
SUBMIT	731			731			739.5			440			440			440		
GROOM-OTHER	747			742.5			752			442.5			438			438.5		
MWCD	442	2	(2)	442	2	(1)	450.5	2	(1)	168	1	(2)	168	1	(1)	168	1	(1)

Table 2.3.2(a)(iv). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page)

Group 1
Class of animals under test : Ad
Class of animals used as opponents: C

compared with:-

Group 2
Class of animals under test : Ad
Class of animals used as opponents: I

	All encounters: Number of records, Group 1: 20; Number of records, Group 2: 17									Encounters with approach: Number of records, Group 1: 17; Number of records, Group 2: 16								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	170			170			-			136			136			-		
LUNGE-RETALIATE	129			127			-			102			100			-		
TEETH CHATTER	96.5	3	(2)	143			127			54	2	(2)	102.5			90	3	(1)
SQUEAL	170			170			-			136			136			-		
MUTUAL UPRIGHT	170			170			170			136			136			136		
WRESTLE	170			170			170			136			136			136		
HUDDLE	170			170			170			136			136			136		
LOCOMOTION	155			144.5			134.5			129			100			91		
GROOM-SELF	169.5			147			150			134.5			113			110.5		
APPROACH	155.5			158			-			129			116.5			-		
STRETCH-ATTEND	133			125			120			94.5			86.5	3	(1)	81.5	3	(1)
NOSE	164			166			162.5			123			133			135.5		
SNIFF	168			168			168			135			135			135		
CROUCH	170			170			170			136			136			136		
RETREAT	160			152			-			132			112			-		
CHASE	170			170			170			136			136			136		
DOMINATE	170			170			170			136			136			136		
FLEE	170			170			170			136			136			136		
SUBMIT	161.5			161.5			161.5			128			128			128		
GROOM-OTHER	160			160			160			127.5			127.5			127.5		
MWCD	170			170			170			136			136			136		

2.3.2(b) Comparison of the ways in which the behaviour of castrates varied when confronted with adults, immatures or other castrates.

Table 2.3.2(b)(i) shows that, in encounters with castrates, there were no significant differences in the numbers of encounters containing APPROACH between the different groups.

Table 2.3.2(b)(i). The number of encounters in which APPROACH did or did not occur.

Type of encounter	Total No.	APPROACH Yes	APPROACH No		
C vs Ad	20	17	3	$\chi^2 = 1.49$, df = 1, n.s.	$\chi^2 = 1.45$, df = 1, n.s.
C vs C	19	13	6	$\chi^2 = 3.31$, df = 1, n.s.	
C vs I	8	8	0		

Table 2.3.2(b)(ii) gives the differences between the behaviour of castrates confronted with other castrates and that of castrates confronted with adults. It can be seen that when all the encounters are considered, castrates exhibited APPROACH with adults significantly sooner ($p<0.05$) and more often ($p<0.05$) than they did with other castrates. Similarly, castrates exhibited STRETCH-ATTEND to adults significantly more ($p<0.05$) than they did to other castrates. It has already been noted that APPROACH only occurred at all in 13 out of the 19 castrate-castrate encounters, and this is reflected by the fact that these significant differences are not repeated when only those encounters with APPROACH are considered. It can also be seen that castrates exhibited TEETH-CHATTER significantly more often and for longer at adults than they did at other castrates ($p<0.001$). LUNGE-RETALIATE also has lower latency ($p<0.05$) and higher occurrence ($p<0.01$) for the castrates in the castrate-adult encounters than in the castrate-castrate encounters, as does SQUEAL (Latency and Occurrence, $p<0.05$). LUNGE-RETALIATE by a castrate usually quickly deterred further approaches by an adult. On the other hand,

Table 2.3.2(b)(ii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : C
Class of animals used as opponents: C

compared with:-

Group 2
Class of animals under test : C
Class of animals used as opponents: Ad

	All encounters: Number of records, Group 1:38; Number of records, Group 2:20									Encounters with approach: Number of records, Group 1: 26; Number of records, Group 2: 17								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	300.5			302			-			168.5			170			-		
LUNGE-RETALIATE	246	3	(1)	231.5	2	(2)	-			139.5	3	(1)	125	2	(2)	-		
TEETH CHATTER	256.5	3	(1)	143	1	(2)	154.5	1	(2)	167.5			74	1	(2)	84.5	1	(2)
SQUEAL	240	3	(1)	239.5	3	(2)	-			129	3	(1)	128.5	3	(2)	-		
MUTUAL UPRIGHT	340			340			340			187			187			187		
WRESTLE	380			380			380			221			221			221		
HUDDLE	310			300			300			161.5			153	3	(1)	153	3	(1)
LOCOMOTION	302.5			287.5			357			162.5			143.5	3	(2)	205		
GROOM-SELF	260	3	(1)	245.5	3	(2)	264	3	(2)	159.5			168			179		
APPROACH	273.5	3	(1)	263	3	(2)	-			177.5			167			-		
STRETCH-ATTEND	254.5	3	(1)	271.5	3	(2)	276.5	3	(2)	161.5			178.5			183.5		
NOSE	351.5			370			363.5			213.5			175			168.5		
SNIFF	341.5			327.5			327			179.5			165.5			165		
CROUCH	330			330			330			178.5			178.5			178.5		
RETREAT	298			287			-			196			185.5			-		
CHASE	380			380			380			221			221			221		
DOMINATE	361			361			361			208			208			208		
FLEE	380			380			380			221			221			221		
SUBMIT	380			380			380			221			221			221		
GROOM-OTHER	300			300			300			153	3	(2)	153	3	(1)	153	3	(1)
MWCD	361			361			359			202			202			200		

the Latency of GROOM-OTHER is significantly lower ($p<0.05$) and the occurrence and duration of both GROOM-OTHER and HUDDLE are significantly higher ($p<0.05$) for castrates confronting castrates than for castrates confronting adults. Thus, close contact was more likely in castrate-adult encounters than in castrate-castrate encounters; however, LUNGE-RETALIATE, SQUEAL and TEETH-CHATTER were most often the result in castrate-adult encounters, whereas HUDDLE and GROOM-OTHER predominated in castrate-castrate encounters.

Table 2.3.2(b)(iii) compares the behaviours of castrates confronted with other castrates with that of castrates confronted with immatures. When all encounters are considered, it can be seen that LOCOMOTION occurred more often ($p<0.001$) and for longer ($p<0.01$) in the castrates in castrate-immature encounters than in the castrates in castrate-castrate encounters. In those encounters in which an APPROACH occurred, LOCOMOTION occurred sooner ($p<0.05$), more often ($p<0.01$) and for longer ($p<0.05$) in the encounters when castrates were confronted with immatures than when castrates were confronted with other castrates. It can also be seen from Tables 2.3.2(b)(iii) that the castrates tended to exhibit to APPROACH, STRETCH-ATTEND, NOSE and RETREAT more with immatures than they did with other castrates; even when only those encounters with an APPROACH are considered, these social and investigative behaviours were more common in castrates with immatures than in castrates with other castrates. Similarly TEETH-CHATTER occurred more often and for longer ($p<0.001$ for all encounters) in castrates with immatures than in castrates with other castrates, as did LUNGE-RETALIATE ($p<0.001$ for all three measures in all encounters and for occurrence and duration in encounters with APPROACH). In neither sort of encounter, however, was there an appreciable amount of overt aggression.

Table 2.3.2(b)(iv) compares the behaviour of castrates in castrate-adult and castrate-immature encounters. It has been shown that in both these two sorts of encounter, castrates tended to exhibit more social and investigative behaviours than they did to other castrates; it has also been shown that castrates exhibited TEETH-CHATTER and LUNGE-RETALIATE

Table 2.3.2(b)(iii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : C
Class of animals used as opponents: C

compared with:-

Group 2
Class of animals under test : C
Class of animals used as opponents: I

BEHAVIOURS	All encounters: Number of records, Group 1: 38; Number of records, Group 2: 8									Encounters with approach: Number of records, Group 1: 26; Number of records, Group 2: 8								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	144			144			-			96			96			-		
LUNGE-RETALIATE	65.5	2	(1)	51.5	2	(2)	-			53.5	3	(1)	39.5	2	(2)	-		
TEETH CHATTER	151			41	1	(2)	45.5	1	(2)	77.5			32.5	2	(2)	37	2	(2)
SQUEAL	115			108.5			-			85			78.5			-		
MUTUAL UPRIGHT	151			150			149			99			100			101		
WRESTLE	152			152			152			104			104			104		
HUDDLE	126.5			129			135			96.5			99			103		
LOCOMOTION	100			23.5	1	(2)	59	2	(2)	60	3	(1)	23.5	1	(2)	57	3	(2)
GROOM-SELF	108.5			83.5	3	(2)	99			85.5			80			91		
APPROACH	99.5			42.5	1	(2)	-			97.5			42.5	2	(2)	-		
STRETCH-ATTEND	87.5	3	(1)	38.5	1	(2)	39	1	(2)	87.5			38.5	2	(2)	39	2	(2)
NOSE	102			69.5	2	(2)	76	3	(2)	102			69.5			76		
SNIFF	111			109.5			108			93			91.5			90		
CROUCH	134			135			133			98			99			97		
RETREAT	94.5	3	(1)	40	1	(2)	-			94.5			40	2	(2)	-		
CHASE	152			152			152			104			104			104		
DOMINATE	152			152			152			104			104			104		
FLEE	152			152			152			104			104			104		
SUBMIT	114			114			114			78			78			78		
GROOM-OTHER	133			124			126			103			94			96		
MWCD	151			150			149			99			100			101		

Table 2.3.2(b)(iv). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : C
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : C
Class of animals used as opponents: I

BEHAVIOURS	All encounters: Number of records, Group 1: 20; Number of records, Group 2: 8									Encounters with approach: Number of records, Group 1: 17; Number of records, Group 2: 8								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	60			60			-			48			48			-		
LUNGE-RETALIATE	69			59.5			-			66			56.5			-		
TEETH CHATTER	46.5	3	(2)	53.5			51			31.5	3	(2)	46.5			43		
SQUEAL	64.5			69			-			48			52.5			-		
MUTUAL UPRIGHT	70			70			70			49.5			59.5			59.5		
WRESTLE	80			80			80			68			68			68		
HUDDLE	50			50			50			42.5			42.5			42.5		
LOCOMOTION	68			34.5	3	(2)	43	3	(2)	56			34.5	3	(2)	43		
GROOM-SELF	56			74.5			78			46			65.5			62		
APPROACH	76.5			37	3	(2)	-			59.5			37	3	(2)	-		
STRETCH-ATTEND	74			33	2	(2)	39	3	(2)	62			33	3	(2)	39	3	(2)
NOSE	53			24.5	2	(2)	20	2	(2)	53			24.5	2	(2)	20	2	(2)
SNIFF	46.5	3	(1)	39.5	3	(2)	40	3	(2)	42			35	3	(2)	35.5	3	(2)
CROUCH	60			60			60			51			51			51		
RETREAT	72.5			32.5	2	(2)	-			63.5			32.5	3	(2)	-		
CHASE	80			80			80			68			68			68		
DOMINATE	76			76			76			64			64			64		
FLEE	80			80			80			68			68			68		
SUBMIT	60			60			60			51			51			51		
GROOM-OTHER	50			50			50			42.5			42.5			42.5		
MWCD	74.5			74.5			74.5			64			64			63		

more to adults and immatures than they did to other castrates. Table 2.3.2(b)(iv) shows that in both all encounters, and in encounters with APPROACH, castrates indulged in social and investigative behaviours significantly more with immatures than with adults. There are no significant differences in those behaviours which were shown to be exhibited more by castrates to adults and immatures than to other castrates such as TEETH-CHATTER and LUNGE-RETALIATE.

2.3.2(b). Summary

Fewer castrate-castrate encounters contain APPROACH than do castrate-adult and castrate-immature encounters. In encounters with APPROACH castrate-castrate encounters are characterised by HUDDLE and GROOM-OTHER, whereas castrates commonly LUNGE-RETALIATE, TEETH-CHATTER and SQUEAL in castrate-adult encounters, and LUNGE-RETALIATE and TEETH-CHATTER in castrate-immature encounters. LUNGE-RETALIATE and TEETH-CHATTER appeared to have a deterrent effect to the advances of adults or immatures but were not common in castrate-castrate encounters.

2.3.2(c). Comparison of the ways in which the behaviour of immatures varied when confronted with adults, castrates or other immatures.

Table 2.3.2(c)(i) shows that very few encounters with immatures did not contain APPROACH, and there are no significant differences between the groups.

Table 2.3.2(c)(i). The number of encounters in which APPROACH did or did not occur.

Type of encounter	Total No.	APPROACH Yes	APPROACH No		
I vs Ad	17	16	1	$\chi^2=0.45$ df= 1, n.s.	$\chi^2=0.02$ df=1 n.s.
I vs C	8	8	0	$\chi^2=0.34$ df=1, n.s	
I vs I	19	18	1		

Table 2.3.2(c)(ii) shows that the only significant differences between the behaviour of immatures in immature-immature encounters and in immature-adult encounters was more LOCOMOTION and STRETCH-ATTEND in the latter. No immature-adult encounters contained any high levels of aggressive behaviour (MWCD), and only two immature-immature encounters contained any MWCD.

Table 2.3.2(c)(iii) compares the behaviour of immatures confronted with castrates with that of immatures confronted with other immatures. It can be seen that both occurrence and duration of LOCOMOTION are significantly greater in the former than in the latter ($p<0.001$ and $p<0.01$ respectively) and that in general immatures confronted with castrates exhibited significantly more APPROACH, STRETCH-ATTEND, NOSE, SNIFF and RETREAT. The reason for this is that in immature-immature encounters approaches were few, and after a bout of investigative behaviour, the two animals tended to settle down. TEETH-CHATTER was more common in immature-

Table 2.3.2(c)(ii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : I
Class of animals used as opponents: I

compared with:-

Group 2
Class of animals under test : I
Class of animals used as opponents: Ad

	All encounters: Number of records, Group 1:38; Number of records, Group 2:17									Encounters with approach: Number of records, Group 1: 36; Number of records, Group 2: 16								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	314.5			314.5			-			280			280			-		
LUNGE-RETALIATE	311.5			299			-			277			264.5			-		
TEETH CHATTER	318			269			287			287			214			230.5		
SQUEAL	291.5			282.5			-			258			249			-		
MUTUAL UPRIGHT	306			306			306			272			272			272		
WRESTLE	306			306			306			272			272			272		
HUDDLE	272			272			272			240			240			240		
LOCOMOTION	245.5			177.5	2	(2)	294			206			138.5	2	(2)	254		
GROOM-SELF	273.5			301			287			260			256.5			266		
APPROACH	294.5			271.5			-			259.5			236.5			-		
STRETCH-ATTEND	289.5			234			212	3	(2)	256			200.5	3	(2)	178.5	3	(2)
NOSE	284.5			294			293			251.5			261			260		
SNIFF	284			284			284			251.5			251			251.5		
CROUCH	284			280			283			251.5			247			250.5		
RETREAT	317			251.5			-			283.5			218			-		
CHASE	323			323			323			288			288			288		
DOMINATE	314.5			314.5			314.5			280			280			280		
FLEE	323			323			323			288			288			288		
SUBMIT	314.5			314.5			314.5			280			280			280		
GROOM-OTHER	255			255			255			224			224			224		
MWCD	289			289			289			256			256			256		

Table 2.3.2(c)(iii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : I
Class of animals used as opponents: I

compared with:-

Group 2
Class of animals under test : I
Class of animals used as opponents: C

BEHAVIOURS	All encounters: Number of records, Group 1: 38; Number of records, Group 2: 8									Encounters with approach: Number of records, Group 1: 36; Number of records, Group 2: 8								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	137.5			137.5			-			130.5			130.5			-		
LUNGE-RETALIATE	149			148			-			143			142			-		
TEETH CHATTER	148.5			103			105.5			139.5			87	3	(2)	89.5	3	(2)
SQUEAL	149.5			151.5			-			140.5			143.5			-		
MUTUAL UPRIGHT	142			141			140			135			134			133		
WRESTLE	144			144			144			136			136			136		
HUDDLE	122			123			128			117			118			123		
LOCOMOTION	148			22	1	(2)	87	3	(2)	138			22	1	(2)	86	3	(2)
GROOM-SELF	152			144			117			140			139.5			112		
APPROACH	118			64.5	2	(2)	-			118			64.5	2	(2)	-		
STRETCH-ATTEND	116.5			72.5	3	(2)	76	3	(2)	111.5			71.5	3	(2)	75	3	(2)
NOSE	112.5			69.5	2	(2)	70	2	(2)	112.5			69.5	3	(2)	70	3	(2)
SNIFF	91	3	(1)	81.5	3	(2)	69	2	(2)	89	3	(1)	79.5	3	(2)	67	2	(2)
CROUCH	127.5			118.5			121.5			122.5			113.5			116.5		
RETREAT	111.5			54.5	2	(2)	-			111.5			54.5	2	(2)	-		
CHASE	152			152			152			144			144			144		
DOMINATE	119			119			119			113			113			113		
FLEE	152			152			152			144			144			144		
SUBMIT	148			148			148			140			140			140		
GROOM-OTHER	129.5			127.5			124			124.5			122.5			119		
MWCD	133			130.5			131			127			124.5			125		

castrate encounters, and APPROACH by an immature was commonly countered by LUNGE-RETALIATE by the castrate; the immature then retreated but often the cycle of APPROACH - STRETCH-ATTEND - NOSE - LUNGE-RETALIATE (by the castrate) - RETREAT was repeated several times.

Table 2.3.2(c)(iv) shows the differences between the behaviour of immatures confronted with adults and that of immatures confronted with castrates. It can be seen that immatures exhibited LOCOMOTION, APPROACH, NOSE, SNIFF and RETREAT significantly more with castrates than with adults. It has already been shown that, in comparison with immature-immature encounters, immatures confronted with castrates exhibited more LOCOMOTION, APPROACH and social and investigative behaviours as a result of the castrates tendency to LUNGE-RETALIATE; the same appears to be the case when immature-castrate and immature-adult encounters are compared.

Table 2.3.2(c)(iv). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : I
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : I
Class of animals used as opponents: C

BEHAVIOURS	All encounters: Number of records, Group 1: 17; Number of records, Group 2: 8									Encounters with approach: Number of records, Group 1: 16; Number of records, Group 2: 8								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	59.5			59.5			-			56			56			-		
LUNGE-RETALIATE	66			66			-			61			61			-		
TEETH CHATTER	67			65			55			59			63.5			54		
SQUEAL	59.5			58.5			-			55			54			-		
MUTUAL UPRIGHT	59.5			59.5			59.5			56			56			56		
WRESTLE	68			68			68			64			64			64		
HUDDLE	42.5			42.5			42.5			40			40			40		
LOCOMOTION	53.5			26	2	(2)	47			48.5			26	2	(2)	47		
GROOM-SELF	56.5			55			52			56.5			48			44.5		
APPROACH	51.5			39	3	(2)	-			51.5			39			-		
STRETCH-ATTEND	66.5			49.5			60.5			62			49			60		
NOSE	32.5	3	(1)	24	2	(2)	22	2	(2)	32.5	3	(1)	24	2	(2)	22	2	(2)
SNIFF	33	3	(1)	25	2	(2)	25	2	(2)	32	3	(1)	24	2	(2)	24	2	(2)
CROUCH	48			45			45			45.5			42.5			42.5		
RETREAT	55			37.5	3	(2)	-			55			37.5			-		
CHASE	68			68			68			64			64			64		
DOMINATE	51			51			51			48			48			48		
FLEE	68			68			68			64			64			64		
SUBMIT	68			68			68			64			64			64		
GROOM-OTHER	42.5			42.5			42.5			40			40			40		
MWCD	51			51			51			48			48			48		

2.3.2(c). Summary

Immatures confronted with any opponent rarely exhibit overt aggressive behaviour. The degree of LOCOMOTION and investigative behaviour exhibited by immatures appears to be greatest in immature-castrate encounters and least in immature-immature encounters, with immature-adult encounters falling between these two. This is due to the fact that immatures settled down with each other, whereas castrates tended to exhibit retaliatory behaviour, thus elevating levels of activity amongst their immature opponents.

2.3.3. and 2.3.4. Results (cont.)

It has been the object in the main behaviour study, the results of which have been presented in sections 2.3.1 and 2.3.2, to demonstrate the differences between the behaviour of adult, castrated and immature male bank voles, by comparing encounters of adults with adults, castrates with castrates and immatures with immatures, and by comparing their reactions to different opponents. The aim of this behavioural study was to validate the premises upon which the experimental ecological study described in Chapter 4 was based.

Following experiment ENCL 4, the actual animals used (see section 2.2.5 for details), upon whose behaviour the experiment depended, were tested, firstly to demonstrate the behavioural differences between the various classes of male removed from the enclosures, and secondly to demonstrate that their behaviour was comparable to that of the animals used in the main behaviour study. These results are described in Section 2.3.3 and 2.3.4 respectively which follow.

2.3.3. Results (cont.) - Supplementary behaviour study, animals from Experiment ENCL 4.

The section that follows gives the results of the following comparisons:-

2.3.3(a) : between the behaviour of adults from the left (control) enclosure and that of castrates from the right (experimental) enclosure.

2.3.3(b) : between the behaviour of adults from the left (control) enclosure and that of immatures also from the left.

2.3.3(c) : between the behaviour of castrates from the right (experimental) enclosure and that of immatures also from the right.

2.3.3(d) : between the behaviour of immatures from the left (control) enclosure and that of immatures from the right (experimental) enclosure.

2.3.3(a). Comparison of the behaviour of adults from the left (control) enclosure with that of castrates from the right (experimental) enclosure.

Table 2.3.3(i) shows the differences between the behaviours of the castrates and adults removed from the enclosures at the end of experiment ENCL 4. It can be seen that adults exhibited high levels of aggressive behaviour significantly sooner and more often that did the castrates (MWCD, $p<0.01$ for all encounters, $p<0.001$ for encounters with APPROACH). Tables 2.3.3(ii) and (iii) and (iv) show that out of a total of eight adult-adult encounters, four contained APPROACH, and of these four, all four contained MWCD. Among the castrates, all eight encounters contained APPROACH, but none of these contained MWCD. Thus it can be seen that the adults removed from the left enclosure, once APPROACH had occurred, were clearly much more aggressive than the castrates from the right enclosure.

Table 2.3.3(i) shows that general social and investigative behaviours occurred, as one would expect, sooner, more often and for longer in the castrate-castrate encounters than in the adult-adult encounters. The highest level of amicable behaviour, HUDDLE, occurred significantly more between castrates than between adults, both when all and when only encounters with APPROACH are considered. TEETH-CHATTER which it has already been noted appeared to be a behaviour with threat properties, occurred significantly more often between adults than between castrates ($p<0.05$ for all encounters, $p<0.01$ for encounters with APPROACH. The castrates also exhibited LOCOMOTION significantly more than the adults; because of its association with fighting in the adult-adult encounters, the significance is markedly less in the encounters with APPROACH than when all encounters are considered.

In general therefore, this comparison paralelled that between the behaviour of castrates and adults in the main behaviour study (Results given above in section 2.3.1). Adults fought significantly more than castrates; following APPROACH, castrates exhibited more social and amicable behaviour.

Table 2.3.3(i). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : CR4
Class of animals used as opponents: CR4
] compared with:- [
Group 2
Class of animals under test : AdL4
Class of animals used as opponents: AdL4

	All encounters: Number of records, Group 1:16; Number of records, Group 2:16									Encounters with approach: Number of records, Group 1:16; Number of records, Group 2: 8								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	120			120			-			56			56			-		
LUNGE-RETALIATE	120.5			120			-			44.5			44			-		
TEETH CHATTER	118			69	3	(2)	74.5	3	(2)	44			17	2	(2)	20.5	2	(2)
SQUEAL	112			112			-			48			48			-		
MUTUAL UPRIGHT	64	2	(1)	64	2	(2)	64	2	(2)	0	1	(1)	0	1	(2)	0	1	(2)
WRESTLE	96			96			96			32	3	(1)	32	3	(2)	32	3	(2)
HUDDLE	40	1	(2)	38	1	(1)	44	1	(1)	24	2	(2)	22	2	(1)	28	3	(2)
LOCOMOTION	116.5			32	1	(1)	22	1	(1)	36	3	(1)	24	2	(1)	19	2	(1)
GROOM-SELF	113.5			127.5			125			37.5			49			49		
APPROACH	49	2	(2)	40	1	(1)	-			41			32	3	(1)	-		
STRETCH-ATTEND	48.5	2	(2)	35	1	(1)	31	1	(1)	40.5			27	3	(1)	23	2	(1)
NOSE	48.5	2	(2)	39.5	1	(1)	32	1	(1)	40.5			31.5	3	(1)	24	2	(1)
SNIFF	36	1	(2)	35	1	(1)	35	1	(1)	28	3	(2)	27	3	(1)	27	3	(1)
CROUCH	58	2	(2)	55	2	(1)	54	2	(1)	34	3	(2)	31	3	(1)	30	3	(1)
RETREAT	52	2	(2)	43.5	1	(1)	-			44			35.5	3	(1)	-		
CHASE	128			128			128			64			64			64		
DOMINATE	120			120			120			56			56			56		
FLEE	128			128			128			64			64			64		
SUBMIT	120			120			120			56			56			56		
GROOM-OTHER	69	3	(1)	74	3	(2)	72	3	(2)	45			50			48		
MWCD	64	2	(1)	64	2	(2)	64	2	(2)	0	1	(1)	0	1	(2)	0	1	(2)

Table 2.3.3(ii). The number of encounters in which APPROACH did or did not occur in behaviour tests of animals from Experiment ENCL 4.

Type of encounter	Total No.	APPROACH Yes	APPROACH No			
AdL4 vs AdL4	8	4	4	$\chi^2 = 5.33$, df = 1, $p<0.05$	$\chi^2 = 4.00$, df = 1, $p<0.05$	$\chi^2 = 1.08$, df = 1, n.s.
CR4 vs CR4	8	8	0			
IL4 vs IL4	16	14	2	$\chi^2 = 0$, df = 1, n.s		
IR4 vs IR4	16	14	2			

Key: Ad4 = Adult males) removed from enclosures at end of experiment ENCL 4
C4 = Castrated males)
I4 = Immature males)
L = Left enclosure
R = Right enclosure

Table 2.3.3(iii). The number of encounters in which high levels of aggressive behaviour (MWCD) did or did not occur - all encounters considered.

Type of encounter	Total No.	MWCD Yes	MWCD No			
AdL4 vs AdL4	8	4	4	$\chi^2 = 5.33$, df = 1, $p<0.05$	$\chi^2 = 9.64$, df = 1, $p<0.01$	$\chi^2 = 0$, df = 1, n.s.
CR3 vs CR4	8	0	8			
IL4 vs IL4	16	0	16	$\chi^2 = 0$, df = 1, n.s.		
IR4 vs IR4	16	0	16			

Key: As for Table 2.3.3(ii)

Table 2.3.3(iv). The number of encounters in which MWCD did or did not occur - only encounters with APPROACH considered.

Type of encounter	Total No.	MWCD	
		Yes	No
AdL4 vs AdL4	4	4	0
CR4 vs CR4	8	0	8
IL4 vs IL4	14	0	14
IR4 vs IR4	14	0	14

$\chi^2 = 12.04$, df = 1, $p < 0.001$

$\chi^2 = 0$, df = 1, n.s.

$\chi^2 = 17.98$, df = 1, $p < 0.001$

$\chi^2 = 0$, df = 1, n.s.

Key: As for Table 2.3.3(ii)

2.3.3(b). Comparison of the behaviour of immatures from the left (control) enclosure with that of immatures from the right (experimental) enclosure.

Table 2.3.3(v) shows that the only difference between the behaviour of immatures from left (control) and right (experimental) enclosures was that for immatures from the left, the occurrence of GROOM-SELF was significantly higher than for immatures from the right ($p<0.01$ for all encounters, p 0.05 for encounters with APPROACH). Immatures from left and right enclosures had lived all their lives in different social environments - those in the left in the presence of adult intact males only, those in the right in the presence of the same number of adult males, the majority of which were castrated (see Chapter 4 for full details). It was therefore highly likely that there were differences in the learnt behaviour of these two groups; the method of arena testing used in the present study was clearly not sensitive enough to give any clear indications of these differences. It is interesting to note, however, that the only other behaviour where the difference between the groups approached significance was TEETH-CHATTER ($p<0.10$ for latency, occurrence and duration for all encounters, immatures from the right enclosure exhibiting it sooner, more often and for longer than those from the left). Perhaps the fact that both these behaviours are sometimes part of low level and or conflict aggressive situations indicates that the immatures from the control enclosure were more acquainted with aggression than were the immatures from the experimental enclosure.

Table 2.3.3(v). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : IL4
Class of animals used as opponents: IL4

compared with:-

Group 2
Class of animals under test : IR4
Class of animals used as opponents: IR4

BEHAVIOURS	All encounters: Number of records, Group 1:32; Number of records, Group 2:32									Encounters with approach: Number of records, Group 1: 28; Number of records, Group 2: 28								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	512			512			-			392			392			-		
LUNGE-RETALIATE	507.5			510.5			-			387.5			390.5			-		
TEETH CHATTER	396.5			396			399			356.5			362.5			363		
SQUEAL	512			512			-			392			392			-		
MUTUAL UPRIGHT	512			512			512			392			392			392		
WRESTLE	512			512			512			392			392			392		
HUDDLE	474			480			476			358			364			360		
LOCOMOTION	472.5			456			458			379			359.5			360		
GROOM-SELF	399.5			334	2	(1)	443.5			313			271	3	(1)	371.5		
APPROACH	475.5			510			-			353.5			388			-		
STRETCH-ATTEND	437.5			443.5			457.5			319.5			325.5			339.5		
NOSE	492			493			470			376			369			346		
SNIFF	475			463			441.5			361			349			327.5		
CROUCH	453			465.5			467			339			351.5			353		
RETREAT	476			503.5			-			354			385.5			-		
CHASE	512			512			512			392			392			392		
DOMINATE	512			512			512			392			392			392		
FLEE	512			512			512			392			392			392		
SUBMIT	512			512			512			392			392			392		
GROOM-OTHER	438.5			453.5			464			324.5			329.5			350		
MWCD	512			512			512			392			392			392		

2.3.3(c). Comparison of the behaviour of adults from the left (control) enclosure with that of immatures also from the left enclosure.

As with the comparison of adult-adult and immature-immature encounters in the main behaviour study, the results of which are given in section 2.3.1., Table 2.3.3(vi) shows that the adults from the left (control) enclosure fought significantly more than did the immatures also from the left enclosure (MW CD, $p<0.01$ for all encounters, $p<0.001$ for encounters with APPROACH). The same result is demonstrated in Table 2.3.3(iii) where it can be seen that the number of encounters between adults containing MW CD was significantly higher than the number of encounters between immatures containing MW CD ($\chi^2 = 9.64$, df = 1, $p<0.01$). When all encounters are considered, the immatures exhibited APPROACH more and sooner than the adults (latency $p<0.05$, occurrence $p<0.01$). They also exhibited significantly higher levels of social and investigative behaviours. These differences are not significant, however, when only these encounters containing APPROACH are considered. This is primarily because four out of the eight adult-adult encounters contained no APPROACH. Even so, immatures exhibited LOCOMOTION sooner and for longer than the adults in the encounters with APPROACH ($p<0.05$ for both). Adults exhibited TEETH-CHATTER more than the immatures in all encounters ($p<0.05$) and when only encounters containing APPROACH are considered ($p<0.01$). Not surprisingly, the comparison between the behaviour of immatures from the left enclosure and that of the adults from the left enclosure is very similar to the comparison made between immature-immature and adult-adult encounters in section 2.3.1. There appeared to be less inhibition of movement and APPROACH when two immatures confronted each other than when two adults confronted each other, and as a result more acts of APPROACH were made. In those encounters where this inhibition was overcome, social and investigative behaviour tended to lead on to aggression between adults and on to amicable behaviour between immatures.

Table 2.3.3(vi). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : IL4
Class of animals used as opponents: IL4
] compared with:- [
Group 2
Class of animals under test : AdL4
Class of animals used as opponents: AdL4

BEHAVIOURS	All encounters: Number of records, Group 1:32 Number of records, Group 2:16									Encounters with approach: Number of records, Group 1: 28 Number of records, Group 2: 8								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	240			240			-			98			98			-		
LUNGE-RETALIATE	219.5			216			-			71.5			68	3	(2)	-		
TEETH CHATTER	170	3	(1)	153	3	(2)	156	3	(2)	36	2	(1)	33.5	2	(2)	32.5	2	(2)
SQUEAL	224			224			-			84			84			-		
MUTUAL UPRIGHT	128	2	(1)	128	2	(2)	128	2	(2)	0	1	(1)	0	1	(2)	0	1	(2)
WRESTLE	192			192			192			56	3	(1)	56	3	(2)	56	3	(2)
HUDDLE	162	3	(2)	162	3	(1)	162	3	(1)	70			70			70		
LOCOMOTION	221.5			162.5	3	(1)	116.5	2	(1)	64	3	(1)	78.5			58	3	(1)
GROOM-SELF	248			214			201			94			103			108		
APPROACH	154.5	3	(2)	144.5	2	(1)	-			86.5			76.5			-		
STRETCH-ATTEND	155.5	3	(2)	153	3	(1)	140.5	2	(1)	89.5			87			74.5		
NOSE	186			171.5	3	(1)	171.5	3	(1)	108			93.5			93.5		
SNIFF	155.5	3	(2)	165	3	(1)	159	3	(1)	75.5			85			79		
CROUCH	184.5			185.5			184.5			82.5			83.5			82.5		
RETREAT	150	3	(2)	146	2	(1)	-			82			78			-		
CHASE	256			256			256			112			112			112		
DOMINATE	240			240			240			98			98			98		
FLEE	256			256			256			112			112			112		
SUBMIT	240			240			240			98			98			98		
GROOM-OTHER	200			204			204			100			104			104		
MWCD	128	2	(1)	128	2	(1)	128	2	(2)	0	1	(1)	0	1	(2)	0	1	(2)

2.3.3(d). Comparison of the behaviour of castrates from the right (experimental) enclosure with that of the immatures also from the right enclosure.

Table 2.3.3(iii) shows that there was no fighting either between the castrates or the immatures from the right (experimental) enclosure, and Table 2.3.3(ii) shows that there was no significant difference in the number of encounters that contained APPROACH. Table 2.3.3(vii) however, shows that the castrates from the right enclosure were markedly more active than the immatures. LOCOMOTION occurred significantly more often and lasted longer in castrate-castrate than in immature-immature encounters, both when all encounters are considered, and when only encounters with APPROACH are considered ($p<0.05$). In general, the social and investigative behaviours also occurred significantly sooner, more often and for longer when castrates encountered one another than when immatures encountered immatures. These elevated levels of LOCOMOTION and investigative behaviours exhibited by the castrates were associated with high levels of TEETH-CHATTER, HUDDLE, GROOM-OTHER and CROUCH, all of which were significantly higher than in the immature-immature encounters (TEETH-CHATTER, $p<0.001$ for latency, occurrence and duration when all encounters are considered, $p<0.001$ for latency occurrence and duration in encounters with APPROACH, HUDDLE, $p<0.05$ for latency and occurrence both when all encounters and only encounters with APPROACH are considered. GROOM-OTHER and CROUCH, $p<0.05$ for all three measures for all and for encounters with APPROACH).

These results are in marked contrast to the comparison of castrate-castrate and immature-immature in encounters in the main behaviour study (section 2.3.1) where there were practically no differences in behaviour between the two groups. The reasons for this contrast are that the castrates removed from the right (experimental) enclosure were much more active than the castrates previously studied and hence indulged in more investigatory behaviours. A direct comparison between castrates removed from the right enclosure at the end of experiment ENCL 4 and castrates from the main behaviour study is given in section 2.3.4(b).

Table 2.3.3(vii). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66.)

Group 1
Class of animals under test : IR4
Class of animals used as opponents: IR4
compared with:-
Group 2
Class of animals under test : CR4
Class of animals used as opponents: CR4

BEHAVIOURS	All encounters: Number of records, Group 1: 32; Number of records, Group 2: 16									Encounters with approach: Number of records, Group 1: 28; Number of records, Group 2: 16								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	256			256			-			224			224			-		
LUNGE-RETALIATE	230			230.5			-			204.5			204.5			-		
TEETH CHATTER	77.5	1	(1)	96	1	(2)	97	1	(2)	75.5	1	(1)	94	1	(2)	95	1	(2)
SQUEAL	256			256			-			224			224			-		
MUTUAL UPRIGHT	256			256			256			224			224			224		
WRESTLE	256			256			256			224			224			224		
HUDDLE	152	3	(1)	156	3	(2)	196			144	3	(1)	148	3	(2)	188		
LOCOMOTION	222.5			144.5	2	(2)	150.5	3	(2)	211			144.5	3	(2)	149.5	3	(2)
GROOM-SELF	245			198.5			245.5			221			181			199.5		
APPROACH	175	3	(1)	178.5	3	(2)	-			171			174.5			-		
STRETCH-ATTEND	157	3	(1)	110.5	1	(2)	101	1	(2)	153	3	(1)	106.5	2	(2)	97	1	(2)
NOSE	157	3	(1)	169	3	(2)	176	3	(2)	153	3	(1)	165			172		
SNIFF	158	3	(1)	129	2	(2)	129	2	(2)	154	3	(1)	125	2	(2)	125	2	(2)
CROUCH	154	3	(1)	145	3	(2)	146	3	(2)	142	3	(1)	133	3	(2)	134	3	(2)
RETREAT	206			199			-			202			195			-		
CHASE	256			256			256			224			224			224		
DOMINATE	256			256			256			224			224			224		
FLEE	256			256			256			224			224			224		
SUBMIT	256			256			256			224			224			224		
GROOM-OTHER	164.5	3	(1)	149	3	(2)	151	3	(2)	152.5	3	(1)	137	3	(2)	139	3	(2)
MWCD	256			256			256			224			224			224		

2.3.3. Summary.

Adults from the left (control) enclosure were significantly more aggressive in laboratory arena tests than the castrates from the right. This fact is the foundation stone upon which the entire study of the populations within the enclosures rested; calculated manipulation of the levels of aggression in one enclosure with respect to the other, whilst as far as possible keeping other differences minimal, was an integral part of the experimental design. Adults from the left enclosure were less inclined to exhibit APPROACH with each other than were castrates from the right; as expected however, following APPROACH, castrates exhibited more amicable behaviour, adults exhibited more aggressive behaviour. Immatures from different enclosures showed no marked differences in behaviour.

Adults from the left enclosure, as expected, fought more than immatures from the same enclosure; following APPROACH, adults fought, immatures were amicable. Neither castrates or immatures from the right enclosure fought; however, the castrates were significantly more active and social than the immatures, something that was not observed in the main behaviour study (see 2.3.1.). The reasons for this difference are discussed below (2.4).

2.3.4. Results (cont.)

Sections 2.3.3(a) - (d) have clearly demonstrated the differences between the behaviour of the adult, castrated and immature males removed from left and right enclosures of Experiment ENCL 4. Chapter 4 describes the results that this difference in overall levels of aggression between the two enclosures had on population variables. Section 2.3.4, which follows, compares the results of the adult-adult, castrate-castrate and immature-immature encounters between animals from Experiment ENCL 4 with equivalent encounters previously described in the main behaviour study (section 2.3.1. above).

2.3.4(a). Comparison of the behaviour seen in adult-adult encounters from the main behaviour study with the behaviour seen in encounters between adults removed from the left enclosure at the end of experiment ENCL 4.

Table 2.3.4(i) shows that there was no significant difference in the number of encounters with APPROACH between the adults from the left enclosure and those previously studied, nor was there any significant difference in the number of encounters with high levels of aggressive behaviour (MWCD), (Tables 2.3.4(ii) and (iii)).

Table 2.3.4(iv) shows that there were only slight differences between the behaviour of the two groups; in particular, the adults from the main study exhibited MUTUAL UPRIGHT and hence MWCD sooner ($p<0.05$) than did the adults removed from the left enclosure, when only those encounters with APPROACH are considered. In all encounters, adults from the main study exhibited TEETH-CHATTER more often and for longer than adults from the left enclosure ($p<0.05$). These differences are lost when only those encounters with APPROACH are considered. Conversely, adults from the left enclosure exhibited GROOM-SELF more and for longer, both when all encounters are considered, and when only encounters with APPROACH are considered ($p<0.05$). The uncertain nature of GROOM-SELF either as a displacement behaviour, or as simple body care, mean that the differences shown are difficult to interpret.

Table 2.3.4(i) The number of encounters in which APPROACH did or did not occur - comparison of results of main behaviour study with those of supplementary behaviour study.

Type of encounter	Total No.	APPROACH		
		Yes	No	
Ad vs Ad	47	31	16	$\chi^2 = 0.77$, df = 1, n.s.
Ad L4 vs AdL4	8	4	4	
C vs C	19	13	6	$\chi^2 = 3.25$, df = 1, n.s.
CR4 vs CR4	8	8	0	
I vs I	19	18	1	$\chi^2 = 0.77$, df = 1, n.s.
IL4 vs IL4 and IR4 vs IR4 (encounters from both enclosures combined)	32	28	4	

Key: Ad = Adult males)
C = Castrated males) from main behaviour study
I = Immature males)

Ad4 = Adult males)
C4 = Castrated males) removed from enclosures at end of experiment ENCL 4
I4 = Immature males)

L = Left enclosure
R = Right enclosure

Table 2.3.4(ii). The number of encounters in which MWCD did or did not occur - all encounters considered; comparison of results of main behaviour study with those of supplementary behaviour study.

Type of encounter	Total No.	MWCD		
		Yes	No	
Ad vs Ad	47	21	26	$\chi^2 = 0.10$ df = 1 n.s.
AdL4 vs AdL4	8	4	4	
C vs C	19	2	17	$\chi^2 = 0.93$ df = 1 n.s.
CR4 vs CR4	8	0	8	
I vs I	19	2	17	$\chi^2 = 3.47$ df = 1 n.s.
IL4 vs IL4 and IR4 vs IR4 (encounters from both enclosures combined)	32	0	32	

Key: As for table 2.3.4(i)

Table 2.3.4(iii). The number of encounters in which MWCD did or did not occur - only those encounters with APPROACH considered; comparison of results of main behaviour study with those of supplementary study.

Type of encounter	Total No.	MWCD		
		Yes	No	
Ad vs Ad	31	21	10	$\chi^2 = 2.93$ df = 1 n.s.
AdL4 vs AdL4	4	4	0	
C vs C	13	2	11	$\chi^2 = 1.47$ df = 1 n.s.
CR4 vs CR4	8	0	8	
I vs I	18	2	16	$\chi^2 = 3.13$ df = 1 n.s.
IL4 vs IL4 and IR4 vs IR4 (encounters from both enclosures combined)	28	0	28	

Key: As for Table 2.3.4(i)

Table 2.3.4(iv). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : Ad
Class of animals used as opponents: Ad

compared with:-

Group 2
Class of animals under test : Ad L4
Class of animals used as opponents: Ad L4

	All encounters: Number of records, Group 1:94 Number of records, Group 2:16									Encounters with approach: Number of records, Group 1: 62 Number of records, Group 2: 8								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	640.5			654.5			-			201			215			-		
LUNGE-RETALIATE	749.5			733.5			-			211.5			232.5			-		
TEETH CHATTER	691			519	3	(1)	487	3	(1)	202			181			169.5		
SQUEAL	674.5			682			-			223.5			231			-		
MUTUAL UPRIGHT	694			747			746			150	3	(1)	203			226		
WRESTLE	746			730			708			216			200			188		
HUDDLE	703			703			690			206			206			202		
LOCOMOTION	735			665.5			583			184			174			150		
GROOM-SELF	592			517.5	3	(2)	513	3	(2)	166			135	3	(2)	146.5	3	(2)
APPROACH	620.5			580			-			226.5			186			-		
STRETCH-ATTEND	583.5			566.5			587			202			185			195.5		
NOSE	704			726.5			751.5			227			203.5			183.5		
SNIFF	720			750			743			238			204			207		
CROUCH	735			735			744.5			244.5			244.5			243.5		
RETREAT	635.5			610			-			233.5			204			-		
CHASE	728			728			736			240			240			240		
DOMINATE	736			737.5			744			243.5			242			243.5		
FLEE	728			728			736			240			240			240		
SUBMIT	736			737.5			744.5			243.5			242			243.5		
GROOM-OTHER	748			745			735			223			220			219		
MWCD	691			737			704			139	3	(1)	185			164		

2.3.4(b). Comparison of the behaviour seen in castrate-castrate encounters from the main behaviour study with the behaviour seen in encounters between castrates removed from enclosures at end of experiment ENCL 4.

Tables 2.3.4(i), (ii) and (iii) show that there are no significant differences in the number of encounters containing APPROACH and MW CD between the two groups of castrates being compared. APPROACH occurred in eight out of eight encounters between castrates from the right enclosure, and MW CD in none of them. Table 2.3.4(v) shows however, that there were considerable differences in the locomotory and social and investigative behaviours between the two groups, particularly when all encounters are considered. In general, it is the castrates from the right enclosure which exhibited significantly more LOCOMOTION, STRETCH-ATTEND, NOSE, SNIFF, HUDDLE, GROOM-OTHER and CROUCH than the castrates from the main study. Castrates from the right enclosure were particularly active and non-aggressive. As in the main part of the study, LUNGE-RETALIATE was occasionally observed, and, along with TEETH-CHATTER, it appeared to prevent any higher levels of aggression being exhibited; however, there were no significant differences in these two behaviours between the two groups.

Table 2.3.4(v) Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test : C
Class of animals used as opponents: C

compared with:-

Group 2
Class of animals under test : CR4
Class of animals used as opponents: CR4

BEHAVIOURS	All encounters: Number of records, Group 1:38 Number of records, Group 2:16									Encounters with approach: Number of records, Group 1: 26 Number of records, Group 2: 16								
	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	288			288			-			192			192			-		
LUNGE-RETALIATE	287.5			290			-			206.5			204			-		
TEETH CHATTER	227.5			260			263.5			293.5			183.5			181		
SQUEAL	272			272			-			176			176			-		
MUTUAL UPRIGHT	272			272			272			176			176			176		
WRESTLE	304			304			304			208			208			208		
HUDDLE	142	2	(1)	122	1	(2)	140	1	(2)	118	2	(1)	98	2	(2)	116	2	(2)
LOCOMOTION	280.5			133.5	1	(2)	167	2	(2)	206.5			118	2	(2)	149		
GROOM-SELF	246			206	3	(2)	188.5	3	(2)	187.5			191.5			175		
APPROACH	174	2	(1)	178.5	2	(2)	-			162			166.5			-		
STRETCH-ATTEND	158	2	(1)	144	2	(2)	95	1	(2)	146			132	3	(2)	83	1	(2)
NOSE	150	2	(1)	160.5	2	(2)	194	3	(2)	138	3	(1)	148.5			182		
SNIFF	132	1	(1)	132	1	(2)	126	1	(2)	120	3	(1)	120	3	(2)	114	2	(2)
CROUCH	164	2	(1)	158	2	(2)	154	2	(2)	128	3	(1)	122	3	(2)	118	2	(2)
RETREAT	202	3	(1)	194.5	3	(2)	-			190			182.5			-		
CHASE	304			304			304			208			208			208		
DOMINATE	304			304			304			208			208			208		
FLEE	304			304			304			208			208			208		
SUBMIT	304			304			304			208			208			208		
GROOM-OTHER	189.5	3	(1)	175.5	2	(2)	170	2	(2)	153.5			139.5	3	(2)	134	3	(2)
MWCD	272			272			272			176			176			176		

2.3.4(c). Comparison of the behaviour seen in immature-immature encounters in the main behaviour study with the behaviour seen in encounters between immatures removed from left and right enclosures at the end of experiment ENCL 4.

For this comparison, the results of encounters between immatures from the right enclosure have been considered jointly with the results of encounters between immatures from the left enclosure; it has been already shown that the behaviour of these two groups was not significantly different in any important points.

Tables 2.3.4(i), (ii) and (iii) show that there were no significant differences between the number of encounters with APPROACH and MWCD between the two groups. Table 2.3.4(vi) shows however, that there were quite considerable differences in the amounts of various behavioural components. The most striking was that, both when all encounters are considered and when only those encounters with APPROACH are considered, TEETH-CHATTER was exhibited sooner, more often and for longer by the animals from the main study than by the animals from the enclosures ($p<0.001$). In contrast to this, social and investigative behaviours were, in general, exhibited more by the immatures from the enclosures, particularly when only encounters with APPROACH are considered (HUDDLE, $p<0.01$, for latency, occurrence and duration, STRETCH-ATTEND, $p<0.05$ for latency and occurrence, $p<0.01$ for duration, NOSE, $p<0.05$ for occurrence, $p<0.01$ for duration, SNIFF, $p<0.05$ for latency and occurrence, $p<0.01$ for duration).

Table 2.3.4(vi). Values of Mann-Whitney U and probability p associated with differences in three measures of twenty behavioural components in laboratory tests of behaviour between adult, castrated and immature male voles. (For key see page 66)

Group 1
Class of animals under test :I(L+R)4
Class of animals used as opponents: I(L+R)4
compared with:-
Group 2
Class of animals under test : I
Class of animals used as opponents: I

	All encounters: Number of records, Group 1:64 Number of records, Group 2:38									Encounters with approach: Number of records, Group 1: 56 Number of records, Group 2: 36								
BEHAVIOURS	Latency			Occurrence			Duration			Latency			Occurrence			Duration		
	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)	U	p	(g)
LUNGE-ATTACK	1184			1184			-			980			980			-		
LUNGE-RETALIATE	1108			1090			-			922			904			-		
TEETH CHATTER	723	1	(1)	729.5	1	(2)	743	1	(2)	596.5	1	(1)	597.5	1	(2)	610	1	(2)
SQUEAL	1056			1056			-			868			868			-		
MUTUAL UPRIGHT	1152			1152			1152			952			952			952		
WRESTLE	1152			1152			1152			952			952			952		
HUDDLE	912	3	(2)	906	3	(1)	916	3	(1)	706	2	(2)	700	2	(1)	710	2	(1)
LOCOMOTION	874.5	2	(1)	1028.5			1075			745	3	(1)	771.5	3	(2)	923.5		
GROOM-SELF	1064.5			1133			1112			850			924			908		
APPROACH	1200.5			1215			-			970.5			956			-		
STRETCH-ATTEND	1036			1017.5			944.5	3	(1)	795	3	(2)	776.5	3	(1)	703.5	2	(1)
NOSE	1061			1000			936	3	(1)	823			762	3	(1)	698	2	(1)
SNIFF	947	3	(2)	937.5	3	(1)	898	3	(1)	728	3	(2)	718.5	3	(1)	679	2	(1)
CROUCH	1081			1076.5			1070.5			864			859.5			853.5		
RETREAT	1108			1117.5			-			859			868.5			-		
CHASE	1216			1216			1216			1008			1008			1008		
DOMINATE	1184			1184			1184			980			980			980		
FLEE	1216			1216			1216			1008			1008			1008		
SUBMIT	1184			1184			1184			980			980			980		
GROOM-OTHER	1071			1066.5			1071.5			852			847.5			852.5		
MWCD	1088			1088			1088			896			896			896		

2.3.4. Summary.

The behaviour of adults from experiment ENCL 4 differed only very slightly from the behaviour of adults in the main behaviour study. The behaviour of castrates from the right enclosure of experiment ENCL 4 and the behaviour of immatures from both enclosures of ENCL 4 combined, however, differed markedly from the behaviour of castrates and immatures from the main behaviour study. In both cases, there was no difference in the amount of aggressive behaviour observed, but the animals from the enclosures exhibited significantly more locomotory, social and investigative behaviours such as LOCOMOTION, APPROACH, STRETCH-ATTEND, NOSE and SNIFF.

2.4. DISCUSSION

The studies described in the introduction to this chapter have shown that many factors are capable of influencing the form that encounters between male rodents in the laboratory can take. Section 2.2.1. describes the precautions taken to standardise the testing procedure used in the present study, aimed at eliminating as far as possible all factors except the condition of the individuals being tested. Most of the studies described in 2.1. used animals from carefully selected strains of mice, whose lineage for many generations was known; in this study the males used were standardised only with respect to age, weight and treatment. Notwithstanding this, the results obtained have largely corresponded to those of previous reports.

Each section of the results of the laboratory study of behaviour (2.3 above) will now be discussed in turn.

Section 2.4.1. Discussion of section 2.3.1. - Comparison of the behaviour of adults confronted with other adults, castrates confronted with other castrates, and immatures confronted with other immatures.

Pre-pubertally castrated male bank voles fought significantly less with each other than did sham-operated adults. This is in agreement with all the previous studies of the direct effects of pre-pubertal castration of rodents (Uhrich, 1938; Beeman, 1947; Suchowsky et al., 1969; Leshner and Moyer, 1970 among others), where testicular androgens are assumed to control directly, through neural influence, an animal's tendency to aggressive behaviour.

Also as expected from previous studies of other rodents, immature male voles fought significantly less with each other than did adults. Rowlands (1939) has shown that at around a weight of 100mg, the testes of Clethrionomys glareolus start to contain spermatozoa, and, as described in the introduction (2.1), several studies have demonstrated that the onset of aggressive behaviour coincides with puberty and the general elevation of circulating androgens associated with it (Levy and King, 1953; Lagerspetz and Talo, 1967; Brain and Nowell, 1969; Christian, 1971; and McKinney and Desjardins, 1973).

Because wild caught animals were used in the present study, immaturity had to be defined in physiological (testis size, body weight, etc) rather than chronological terms, as is possible with laboratory born animals. An immature was defined, therefore, as an animal weighing less than 15gm, whose testes were estimated by palpation to be less than 0.5cm in length, and which had no scars to indicate fighting experience. Voles born at the end of the breeding season commonly fail to come into breeding condition in the year of their birth, and first become sexually mature at the beginning of the next breeding season; animals born at the beginning of the breeding season may become sexually mature very quickly at a very low weight. Although a physiological definition of immaturity was used in the present study, the results are in agreement with the general hypothesis that male aggressive behaviour is chiefly under the control of testicular androgens, which are present in the immature animal at extremely low levels.

Unlike the castrates, immatures were much less wary of each other than were adults, and approached each other in significantly more of the encounters. Again however, there was relatively little difference between the amount of investigative behaviours of the two groups, once an approach had been made.

In general, immatures and castrates did not behave very differently, except in the case of the number of encounters observed with an approach, where immatures approached each other more than castrates. The factor that, in the neutral arena, keeps more adults apart from adults, and more castrates apart from castrates, than immatures apart from immatures, is not clear. The work of Jones and Nowell (1973b) on the aversive olfactory cue present in dominant but not repeatedly defeated male mouse urine, and its possible relationship to pituitry-adrenocortical function, may be of relevance, since pre-pubertal castration has the well known effect of causing the retention of the X-zone of the adrenal cortex in mice, as well as causing adrenal hypertrophy; however, the complexity of the relationships between adrenocortical and gonadal influences and behaviour, which are not well understood, preclude any conclusions being drawn.

Section 2.4.2. Discussion of Section 2.3.2. - Comparisons of the ways in which the behaviour of a particular class of animal varied when confronted with different sorts of opponent.

In broad terms, it has been easy to show that adults are more aggressive than castrates or immatures, simply by measuring the incidence or duration of those behaviours which represented high levels of aggression. In the present study these were MUTUAL UPRIGHT, WRESTLE, CHASE and DOMINATE, combined into a composite aggressive behaviour MWCD; many of the mouse studies described in the introduction (2.1) have used similar methods, slightly more or less refined. For example, Dixon (1973) scored a total of 48 elements of behaviour, but then only analysed the results of his experiments in terms of four major groups of elements (Non-social, Social investigation and mating, Aggression and Flight). When the amount of overt aggression is low, however, these relatively crude measures are not sufficient to describe differences between groups. In the following sections therefore, whilst the gross differences in both aggressive and social and investigative behaviours will be discussed, the differences in individual elements, particularly those aggressive elements displayed by immatures and castrates which appear to prevent escalation to higher levels of aggression, will also be discussed.

Section 2.4.2(a) Discussion of section 2.3.2(a) - Comparisons of the behaviour of adults confronted with castrates, immatures or other adults.

The results obtained in this section were as expected from previous studies on mice. It has been shown in the introduction that testicular androgens appear to have two distinct concurrent effects on aggressive behaviours of rodents:-

(a) Through the modification of the production of olfactory cues.

(b) Through central motivational effects on fighting, presumably acting on brain tissues.

Several authors have shown that castrated male mice are less susceptible to attack by trained fighters than are intact males (Lee and Brake, 1971; Mugford and Nowell, 1970, 1971b; Brain and Evans, 1974(a) and (b)), and that immature males are similarly immune (Mackintosh, 1970; Dixon, 1973). Androgen replacement therapy restores proneness to being attacked (Lee and Brake, 1972; Mugford, 1974; Brain and Evans, 1974(a)). The reason for this appears to be that an aggression releasing substance is present in the urine of adult male mice, and is under androgenic control; immature males and castrates do not possess it. The urine of females has been shown to have an aggression inhibiting quality (Mugford and Nowell, 1970, 1971a; Dixon and Mackintosh, 1971; Svare and Gandleman, 1975); this does not appear to be the case with the urine of castrates and immatures, since the urine from both these groups does not prevent adults from being attacked, or attenuate aggressive behaviour in potentially aggressive situations (Dixon, 1973). Thus it was to be expected that adult male voles would attack and fight with other adults, but would not fight with castrates or immatures, and the results have shown this to be the case. The differences between the behavioural reactions of adults to castrates and immatures was not marked.

Section 2.4.2(b). Discussion of section 2.3.2(b) - Comparisons of the behaviour of castrates confronted with adults, immatures or other castrates.

The results of the comparison of the behaviour of castrates confronted with different opponents were much less clear cut than those described in the previous section because, in general, castrates were not overtly aggressive.

The function of certain behavioural elements in preventing the escalation of behaviour to higher aggressive levels, either by causing an approaching animal to retreat immediately, or by preventing the approach in the first place, appeared important in the behaviour of castrates. Thus, lunging at an approaching opponent (LUNGE-RETALIATE), with no bodily contact, was commonly sufficient to cause the approaching animal to retreat. This behaviour is morphologically very similar to the lunge of an animal that has approached another (LUNGE-ATTACK) but the motivation for the two appeared to be quite different; the former appeared to have a deterrent effect, the latter to be overtly aggressive. LUNGE-RETALIATE was exhibited by castrates to both approaching immatures and adults; with adults it was often accompanied by a squeal, and appeared to be more effective as a result. This behaviour is clearly described and drawn in Clarke's (1956) study of the field vole Microtus agrestis, although he associated squealing with weaker rather than more effective retaliation by subordinate animals. TEETH-CHATTER was observed in all three classes of animal, in all test situations, and seemed to act effectively as a deterrent to approach; it was commonly observed in encounters where no approach at all was made. Clarke (1956) said that teeth gnashing was a threatening behaviour commonly observed when two voles of equal status met, but also in unequal encounters. Turner and Iverson (1973) scored all vocalization together, but distinguished between squealing and teeth chattering. They claimed that squealing was heard during the breeding season, and teeth chattering when encounters between animals not in breeding condition were staged; in the present study this was not the case, and although squealing and teeth chattering were observed under very different circumstances, the same animal

frequently exhibited both in the same interaction.

Although the numbers of encounters in the three groups (C vs Ad, C vs C, C vs I) containing an approach was not significantly different (see Table 2.3.2(b)(i)), castrates tended to approach and indulge in amicable behaviours more with immatures than with adults or with other castrates. The former was, at least in part, as expected from the studies on the aggression facilitating olfactory cues of adult males previously discussed (Lee and Brake, 1971; Mugford and Nowell, 1970, 1971b; Brain and Evans, 1974 a, b), although all these studies monitored actual attacks by trained fighter mice on test animals and have not considered, at least directly, the action of olfactory cues on the social and investigative behaviours of non-aggressive animals. Whether the fact that castrates approached and investigated adults significantly less than immatures was the result of an aggression facilitating or an aversive pheromone of the adults (Jones and Nowell, 1973a), is open to question. Similarly, the reasons for castrates huddling with and grooming adults less than they did with other castrates may also be due to either an aversive cue from the adults, or to an aggression facilitating cue, also from the adults, acting at a lower threshold than has previously been suggested. Castrates approached adults significantly sooner than they did other castrates, which suggests that an aversive pheromone was not acting.

The fact that castrates approached and investigated immatures significantly more than they did other castrates cannot be explained in terms of the current knowledge of aversive and aggression - facilitating and inhibiting olfactory cues.

Section 2.4.2(c). Discussion of section 2.3.2(c) - Comparisons of the behaviour of immatures confronted with adults, castrates or other immatures.

As expected, immatures very rarely exhibited high levels of overt aggressive behaviour, whatever the opponent.

The behaviour of one animal in an encounter is obviously affected by the behaviour of the other, and this is demonstrated in this section; castrates, as has already been discussed, tended to lunge at approaching and investigating adults and immatures, and this behaviour appeared to prevent the level of aggression rising, since it usually resulted in an immediate retreat. Immatures however, appeared less affected than adults by this retaliatory lunge, and after retreating, commonly approached again only to be lunged at again, and so on. As a result, immatures confronted with castrates tended to show high levels of locomotion and investigatory behaviours. In immature-immature encounters, approaches were few because the two animals settled down fairly quickly after an initial bout of mutual investigation. The possible existence of both an aggression eliciting pheromone, present in adult males but not in castrates or juveniles, and an aversive pheromone, which has been shown to be more effective in dominant adult males than in subordinates, has been discussed above in the context of both adults and castrates reaction to different opponents. These two olfactory cues also appear to have been acting in mediating the behaviour of immatures in the present study, demonstrated by the reactions of castrates and adults to immatures, and the fact that immatures were so amicable with each other. Turner and Iverson, (1973) scored 'Time together' in their study of Microtus pennsylvanicus, regardless of whether animals were aggressive or amicable, and a similar measure in the present study could have demonstrated how much different classes of animal avoided each other. The only real measure in the present study of highly amicable behaviour was HUDDLE, but immatures were commonly very active, and did not exhibit this behaviour very frequently.

Sections 2.4.3. and 2.4.4. Discussion of section 2.3.3., (Supplementary behaviour study of animals removed from enclosures at the end of experiment ENCL 4) and section 2.3.4, (Comparison of results from main and supplementary behaviour studies).

The aim of these two sections of the results was to demonstrate :-
2.4.3.: that the adults, castrates and immatures used in experiment ENCL 4 (see Chapter 4) behaved differently from each other (Results section 2.3.3) and
2.4.4.: that any differences demonstrated in section 2.3.3. were broadly comparable to the differences demonstrated in the main behaviour study (Results sections 2.3.1 and 2.3.2).

Both these aims were achieved with one or two exceptions. As expected, adults removed from the enclosures at the end of experiment ENCL 4 fought with each other, whereas castrates and immatures did not, and adults removed from the left enclosure at the end of experiment ENCL 4 did not behave very differently from adults from the main behaviour study. Although there was no difference in the aggressive behaviour of immatures from ENCL 4 and immatures from the main study, and similarly no difference in the aggressive behaviour of castrates from ENCL 4 and castrates from the main study, (there was virtually no aggression in any of the four groups), both castrates and immatures removed from the enclosures were more active and exhibited more social and investigative behaviour than animals from the main study. Like animals from the main study, all animals from ENCL 4 were isolated for a minimum of two weeks before behaviour testing, and were otherwise treated in exactly the same way. However, animals used in the main study were wild-caught animals, which had grown up under normal bank vole social conditions. Animals from the enclosures, on the other hand, had been subjected to a very atypical environment and high population densities (see Chapter 4 for details). The marked effects of social experience on subsequent behaviour has already been mentioned (King and Gurney, 1957; Bevan et al., 1960), and it is likely that this would have most effect on the immatures, all born in the enclosures. The castrates in the main study had all been isolated at castration, several weeks before behaviour testing; the castrates

from ENCL 4 had spent 10 months living in the enclosures with other castrates, adult and immature males and females, and were only isolated after removal from the enclosure. It is not really possible, therefore, to be more specific about the reasons for the differences between the behaviour of animals removed from the enclosures and that of animals used in the main behaviour study except that their previous social experience had been clearly very different. This does not alter the fact most pertinent to the present study, that both castrates and immatures removed from the enclosures at the end of experiment ENCL 4 were significantly less aggressive than the intact adult males removed from the enclosures at the same time. In other words, overall levels of aggressive behaviour in the right, experimental enclosure were significantly less than the levels of aggressive behaviour in the left, control enclosure.

CHAPTER 8

Field observation of bank vole behaviour

3.1. INTRODUCTION

Between June and October 1973, observations were made of behavioural interactions under field conditions. It was felt that the techniques of laboratory observation of behaviour, described in Chapter 2, might be poorly reflecting both the qualitative and quantitative nature of field agonistic interactions. Field observation of behaviour is very common in studies of larger mammals; largely because of the secretive nature however, behavioural observations of rodents under field conditions have been few (Finley, 1959; Andrzejewski and Olszewski, 1963; Kikkawa, 1964; Ashby, 1967; Brown, 1969; Greenwood, 1974; Garson, 1975). In none of these studies have behavioural components been accurately defined or quantified, and only in two (Brown, Garson) were individuals identified. Andrzejewski and Olszewski (1963) observed 818 appearances of bank voles (Clethrionomys glareolus) at a bait point (as well as 521 appearances of yellow-necked mice, Apodemus flavicollis), of which 85 were interactions between two bank voles. They divided these interactions into three types, tolerant and aggressive meetings, and meetings with mutual flight, and they stated that, in bank voles, aggressive interactions were more frequent than tolerant or mutual flight interactions. Percentages of each type are given in their paper, but contradict each other, and therefore no comparison with the present study can be made. Kikkawa (1964) and Ashby (1967) both mention brief field observations of bank voles, Brown (1969) and Garson (1975) observed Apodemus sylvaticus in the field, and Greenwood (1974) observed both species, Jewell (pers.comm.) watched A. sylvaticus in drystone chambers on Hirta, St.Kilda; in none of these studies were behavioural components described in detail or quantified.

Similarly, although some observations have been made of the behaviour of small mammals in large enclosures, the incidence of individual behavioural components has not been quantified (e.g.Clarke, 1955; Southwick, 1955(b); van Wijngaarden, 1960; Crowcroft, 1966; Crowcroft and Rowe, 1963; Lidicker, 1973 and others). Southwick (1955b)scored the number of aggressive interactions per hour, and Crowcroft (1966) and Crowcroft and Rowe (1963) interpreted their

detailed descriptions and observations of the behaviour of individuals in Mus musculus populations in large indoor pens in terms of social structure within the pens, but did not quantify individual components. More detailed observations have been made on laboratory populations in large cages, but usually only in terms of the rates at which aggressive acts occurred (e.g. Lloyd and Christian, 1967; Terman, 1974; Lloyd, 1975). Thus it can be seen that studies containing systematic observation of the behavioural components of small mammals outside the confines of small laboratory arenas have been almost non-existent. The object of the present study was not primarily to quantify in detail differences between behaviour observed in the two enclosures used in the ecological part of this study (see Chapter 4 for full details), and the differences between behaviour observed in them and in the field, but to determine the relationship between the behaviour patterns observed in the laboratory arena tests and those observed under more natural conditions.

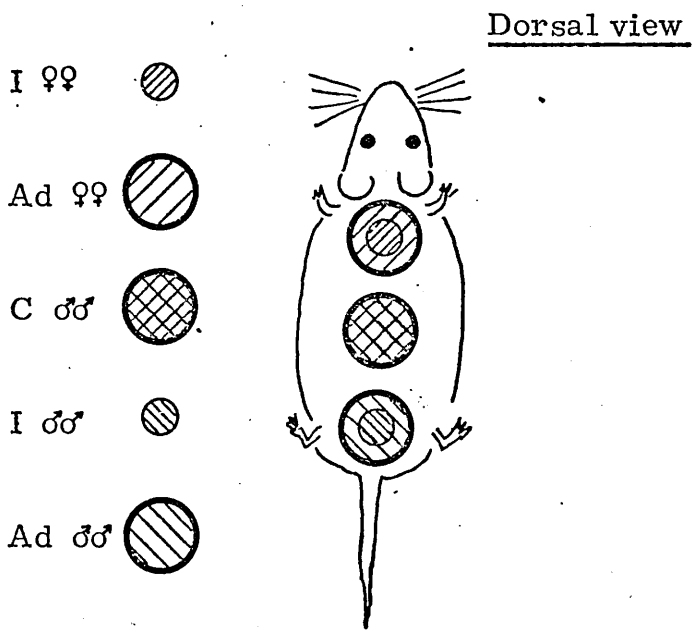
3.2. METHODS

Observations were made at three locations.

1. Left enclosure } Zoology Department, Royal Holloway
2. Right enclosure } College.
3. Oakfield, Burghfield, nr.Reading, Berks.

The two enclosures (each 550 m^2 in area) are described fully in Chapter 4. Observations at Oakfield were made in the middle of a grid in an area of mixed woodland being regularly live-trapped as part of another study. Because all three areas were being trapped regularly, it was possible to mark captured animals by clipping the fur. Clipping the guard hairs exposes the black under-fur, and if distinct patches are clipped, animals can be identified at a distance. Animals were fur clipped as shown in Fig. 3.2(i).

Fig. 3.2(i). Fur clipping.



Ad = Adult
I = Immature
C = Castrate

During the period of observation, the left enclosure contained approximately 25 adult males, 20 adult females and 45 each of immature males and females. The right enclosure contained

approximately 20 castrated males, five adult males 20 adult females and 65 each of immature males and females. Estimated density of animals at Oakfield was approximately 80 voles/ha. (T.D.Healing, personal communication).

In order to facilitate observations, a bait point was set up on each of the three sites. This consisted of a large tin filled with oats with a small opening at the bottom from which voles could feed. Voles at this point were observed through binoculars from a range of about 10 metres. All observations were in daylight between 07.15 and 19.10, and, although it is obviously not possible to assess the effect of an observer on the levels of activity of animals in the field, it is assumed that the quality of interactions was not changed by an observer's presence; commonly, voles started moving around and feeding within a very short time of my arrival and on no occasion was one seen to pay any attention to me. Encounters observed were simply recorded in full, with particular attention being payed to recording the 20 behaviours already described in Chapter 2. The additional category of MUTUAL AVOIDANCE was also scored. On many occasions, two animals saw each other from a range of a half to one metre and immediately rushed off in opposite directions. Clearly this could not occur in the laboratory arena tests previously described, but in the field constituted a definite interaction, without an APPROACH or any aggression occurring. MUTUAL AVOIDANCE was, of necessity, a blanket term, and in effect covered all interactions conducted at a distance, before an APPROACH occurred. SQUEAL was scored whenever it was heard, even if it was not part of an interaction under observation at the bait point.

3.3. RESULTS

Although trapping within the enclosures was intense (see Chapter 4), many animals were caught relatively infrequently, and because fur clips are lost at moulting, a fairly high proportion of the populations were not marked at any one time. Also, voles move very quickly, and an interaction was frequently over before the marks could be definitely distinguished. Consequently, in the majority of the interactions observed, neither the sex or age of either one or other of the participants is known. Trapping at Oakfield was considerably less intense (five days trapping every six weeks) and as a result, observed interactions containing marked animals were very few. During the course of the field observation of behaviour, the following components of agonistic behaviour described in Chapter 2 were observed:- LUNGE-ATTACK, LUNGE-RETALIATE, SQUEAL, LOCOMOTION, GROOM-SELF, APPROACH, STRETCH-ATTEND, NOSE, SNIFF, CHASE, FLEE. The following behaviours were not observed:- MUTUAL UPRIGHT, WRESTLE, DOMINATE, SUBMIT, CROUCH, GROOM-OTHER, HUDDLE. TEETH-CHATTER could not have been heard at the range from which observations were made, and so it is not known whether or not it occurred. The results of this field study of behaviour are summarised in Tables 3.3(i), (ii) and (iii).

Table 3.3(i). Summary of field observations of behaviour.

	Total observation time (mins)	No.of times SQUEAL heard	No.of inter-actions observed	Behaviour	Proportion (and number) of interactions	
					with:-	without:-
Right enclosure (experimental)	275	7	21	MUTUAL AVOIDANCE	0.52 (11)	0.48 (10)
				APPROACH	0.48 (10)	0.52 (11)
				All agonistic behaviour	0.14 (3)	0.86 (18)
				CHASE	3	-
Left enclosure (control)	625	113	57	MUTUAL AVOIDANCE	0.39 (22)	0.61 (35)
				APPROACH	0.61 (35)	0.39 (22)
				All agonistic behaviour	0.32 (18)	0.68 (39)
				CHASE	10	-
				LUNGE-ATTACK	1	-
				LUNGE-RETALIATE	7	-
Oakfield	1010	0	20	MUTUAL AVOIDANCE	0.35 (7)	0.65 (13)
				APPROACH	0.65 (13)	0.35 (7)
				All agonistic behaviour	0.10 (2)	0.90 (18)
				CHASE	1	-
				LUNGE-RETALIATE	1	-

For full details see text

Table 3.3(ii). Field observation of behaviour. Details of interactions observed between animals of different age and sex classes (combined data for two enclosures and Oakfield).

	Ad ♂♂	I ♂♂	Ad ♀♀	I ♀♀	Age and sex not known
Age and sex not known	4 0.50(2) 0.50(2) 0.75(3) 0.75(3)	17 0.59(10) 0.41(7) 0.12(2) 0 (0)	3 0.67(2) 0.33(1) 0 (0) 0 (0)	5 0.20(1) 0.80(4) 0.20(1) 0 (0)	44 0.38(17) 0.61(27) 0.25(11) 0.05(2)
I ♀♀	1 0 (0) 1.00(1) 0 (0) 0 (0)	8 0.50(4) 0.50(4) 0.13(1) 0 (0)	0 - - - -	0 - - - -	
Ad ♀♀	0 - - - -	1 0 (0) 1.00(1) 0 (0) 0 (0)	0 - - - -		
I ♂♂	7 0.29(2) 0.71(5) 0.43(3) 0.29(2)	6 0.33(2) 0.67(4) 0 (0) 0 (0)			
Ad ♂♂	2 0 (0) 1.00(2) 1.00(2) 1.00(2)				

Key: Each line in this block corresponds to a line in each of the cells in Table 3.3(ii) above

V
W (w)
X (x)
Y (y)
Z (z)

V = Number of interactions observed.
W(w) = Proportion (and number) of interactions with MUTUAL AVOIDANCE
X(x) = Proportion (and number) of interactions with APPROACH
Y(y) = Proportion (and number) of interactions with agonistic behaviour.
Z(z) = Proportion (and number) of interactions with agonistic behaviour, excluding CHASE.
Ad = Adult.
I = Immature.

Table 3.3(iii). Field observation of behaviour. Details of interactions of different age and sex classes, irrespective of opponent.

Interactions involving:-	Ad ♂♂	I ♂♂	Ad ♀♀	I ♀♀	Age and sex not known
Number observed	14	39	4	14	73
Proportion (and number) with MUTUAL AVOIDANCE	0.29(4)	0.46(18)	0.50(2)	0.36(5)	0.44(32))
Proportion (and number) with APPROACH	0.71(10)	0.54(21)	0.50(2)	0.64(9)	0.56(41)
Proportion (and number) with agonistic behaviour	0.57(8)	0.15(6)	0 (0)	0.14(2)	0.23(17)
Proportion (and number) with agonistic behaviour, but with CHASE excluded	0.50(7)	0.05(2)	0 (0)	0 (0)	0.07(5)
Comparison of all encounters with/without observed agonistic behaviour	$\chi^2 = 25.2$, df = 1 $p < 0.001$ $\chi^2 = 3.5$, df = 1 $p < 0.10$ $\chi^2 = 9.2$, df = 1 $p < 0.01$ Other comparisons between groups all non-significant.				
Comparison of only those encounters with an APPROACH with/without agonistic behaviour	$\chi^2 = 12.1$, df = 1 $p < 0.001$ $\chi^2 = 3.5$, df = 1 $p < 0.10$ $\chi^2 = 9.8$, df = 1 $p < 0.01$ Other comparisons between groups all non-significant.				

Tables 3.3(i), (ii) and (iii) show the following:-

(1) Overt aggressive behaviour was rarely observed at any of the bait points, the majority of interactions being completely peaceful. These peaceful interactions were of two sorts:- (a) those where an APPROACH was made, and the animals came within approximately 15cms of each other, and (b) those where the animals were aware of each other, but there was MUTUAL AVOIDANCE. MUTUAL AVOIDANCE occurred in 40 out of the 98 interactions observed.

(2) The difference between the frequencies at which interactions were observed in the two enclosures was not marked (approximately one every 11 minutes in the left enclosure, one in every 13 minutes in the right enclosure). Interactions were observed on average approximately once every 20 minutes at Oakfield.

(3) By far the commonest component of aggressive behaviour observed in the field was CHASE (and hence also FLEE). Those components most commonly observed in high level aggressive interactions in the laboratory arena (that is MUTUAL UPRIGHT, WRESTLE, DOMINATE)were not observed at all in the field.

(4) It has already been said (Chapter 2) that SQUEAL, when observed in the laboratory arena, occurred, in males, during the periods of high levels of agonistic behaviour; it can be seen from Table 3.3(i) that SQUEAL was very frequently heard in the left enclosure (on average approximately once every 5½ minutes), much less frequently in the right enclosure (approximately once every 39 minutes) and not at all at Oakfield.

(5) Table 3.3(ii) shows that only two encounters between two adult males were observed; in both, and APPROACH was made, and in both, aggressive behaviour (not CHASE) was observed.

(6) Table 3.3(iii) shows that when the interactions of each age or sex class are considered irrespective of opponent, it is amongst the adult males that aggressive behaviour is most evident. The differences in the proportions of interactions with MUTUAL AVOIDANCE and APPROACH between the different age and sex classes are not significant.

3.4. DISCUSSION

The results have shown that no encounters involving castrates were observed in the right enclosure; it is obviously not therefore possible to draw any conclusions about the behaviour of the castrated males in the enclosures from the present study. It will be shown however, (in Chapter 4), that at the same time as this field behaviour study was being conducted, adult intact males in the enclosures were significantly more wounded than castrated or immature males, and all females; it therefore seems reasonable to assume that the low levels of aggression observed in laboratory arena tests in the castrated males from the right enclosure, compared with the levels observed in intact adults from the left, (see Section 2.3.3(a)) were operating during the period of field observations described here. The relatively small numbers of interactions observed, and the difficulty in identifying sex and age of participants, mean that detailed conclusions about the differences in the incidence of behavioural components between the different age and sex classes cannot be drawn. The results suggest however, that, in agreement with the laboratory study of male behaviour, it is the adult males who indulge in more aggressive behaviour than immature males or adult and immature females. These differences are exhibited when, as in the laboratory study, either all encounters were considered or only those in which an APPROACH was made (Table 3.3(iii)). In spite of the fact that the results of the field study appeared to parallel those of the laboratory study with respect to the general levels of aggressive behaviour of different age and sex classes, and with respect to the form of the behavioural components observed, it was very soon noticed that as a result of the lack of confinement of field interactions compared with laboratory interactions, individual encounters observed in the field were not the same as those observed in the laboratory. This is exemplified by the need to create a new behavioural category for the field study, MUTUAL AVOIDANCE; 39% of the interactions observed in the field contained this behaviour. The essential difference was, of course, the fact that animals in a laboratory arena could not get more than about 25cms away from each other. There was absolutely no possibility of escape in the arena, whereas, in the field, MUTUAL

AVOIDANCE, following long range audial or visual detection of another animal, was easy. It would appear that, in the field situation under observation, MUTUAL AVOIDANCE functioned as a method of avoiding highly aggressive encounters, so that as a result of the physical differences between the laboratory arena and the bait point, much less aggressive behaviour was observed at the latter.

The fact that, of the behavioural components considered to be most highly aggressive in the laboratory (MUTUAL UPRIGHT, WRESTLE, CHASE, DOMINATE), CHASE was observed frequently (in 14% of all interactions observed, in 24% of encounters in which an APPROACH occurred, and in 61% of encounters containing any agonistic elements), and the other three not at all, also pointed to the marked difference observed between laboratory and field interactions. It would appear that CHASE, when observed in the field, represented a lower level of aggressive interaction than when observed in the laboratory arena where it was very rarely observed, where a flight reaction leading to effective escape was not possible, and where it represented an extremely high level of aggression.

It will be shown (Chapter 4) that, in field populations during the breeding season of 1976, adult males showed significantly higher levels of fresh wounds than did immature males, adult females or immature females; in the enclosures, adult males were more wounded than castrated and immature males and adult and immature females. Commonly, more than 50% of adult males had fresh wounds at any one time. In all these cases, it is not known who inflicted the wounds; the results of many behavioural studies on mice and voles on both aggressive and sexual behaviour (see Eleftheriou and Sprott, 1975 for a review) suggest however, that the wounds found on adult males are inflicted chiefly by other adult males. Since no fighting was observed at the bait point, because avoidance or escape were possible, it would seem likely that the wounds were inflicted either during the many CHASE-FLEE interactions observed, or where an escape from an attacker was not easy, for instance down the burrows. Several authors have noted that chasing mice commonly bite at the rump of a fleeing mouse, and that a cornered animal will often turn and bite at an attacker; these retaliations and flights are often accompanied

by squealing by the subordinate animal (e.g.Clarke, 1955; Crowcroft, 1966; Lloyd and Christian, 1967); this last parallels the association between SQUEAL and high levels of aggression observed in the laboratory arena (Chapter 2). The results have shown that SQUEAL was most frequently heard in the left enclosure containing the adult males, whose wounding record has shown to have been fighting the most. Clearly, since the animals doing the squealing were rarely observed, it is not possible to draw any firm conclusions about the interactions that gave rise to them; if however, many of the interactions involved animals other than adult males, higher levels of wounding might have been expected in the other classes than were observed. It would seem reasonable therefore, to assume that a majority of them involved at least one adult male. The second explanation for the existence of wounding is that they were sustained in encounters where avoidance or flight were thwarted, for instance down burrows. This also seems a reasonable proposition and, if it is the case, it suggests a situation which the laboratory arena-testing experiments are able to mimic far better than they do the interactions at the bait point.

The fact that female behaviour, and its role in vole population dynamics, has received almost no attention, and the reasons for this neglect, have been discussed in Chapter 2. That female rodents are much less aggressive than males is well known (see Beach, 1948), and the results of the present study corroborate this. It can be seen from Table 3.3(ii) that female voles, both adult and immature, were observed to indulge in very little aggressive behaviour; the fact that even a little was observed however, means that female behaviour in the field warrants further study.

In conclusion, the present study demonstrated marked differences between the content of aggressive interactions observed at a field

bait point and those observed in a laboratory arena; individual components of behaviour were not different, but, whereas close-quarter behavioural components inevitably predominated in the laboratory arena, many long-distance interactions were observed at the bait point. However, the high incidence of wounding of adult male voles in the field confirms the incidence of close-quarter interactions, which are probably equivalent in content to the interactions observed in the laboratory arena.

CHAPTER 4

Enclosure study of bank vole ecology.

4.1. INTRODUCTION

This chapter describes a study of the role of male aggressive behaviour in mediating demographic variables in communities of bank voles enclosed in two large (550m^2) outdoor enclosures. Full details of the study are given in the Methods section of this chapter (4.2. below); briefly, the broad aim of a series of experiments conducted in the enclosures was to manipulate overall levels of aggressive behaviour in a population established in one enclosure ('the experimental enclosure') with respect to a population of the same sex- and weight-structure established in the other enclosure ('the control enclosure') and to investigate the demographic consequences.

It has been shown (Chapter 2) that, in laboratory arena tests, castrated male bank voles were significantly less aggressive than adult males. The artificial difference in levels of aggressive behaviour between the two enclosures was therefore achieved by castrating a large proportion of the adult males prior to introduction into the experimental enclosure; none of the males in the control enclosure were castrated. The subsequent fate of each population was determined by live trapping.

The role of intrinsic factors, mediated by social behaviour, in the control of the demography of rodent populations has been reviewed in Chapter 1; these factors must ultimately cause changes in one or more of the four processes of birth, death, immigration and emigration. In particular, the importance of the role of dispersal (emigration) from unenclosed populations has been discussed. It has, however, been a common ploy to eliminate the processes of immigration and emigration by using either naturally or artificially enclosed groups of animals, and to concentrate on the birth and death processes. The results of thwarting emigration can be demographically spectacular, as has been described in Chapter 1. In particular, as a result of frustrated dispersal, the densities observed in enclosed populations of both voles and mice have been consistently much higher than those observed in the field. (e.g. Clarke, 1955; Louch, 1956; Crowcroft and Rowe, 1957; Van Wijngaarden, 1960; Krebs et al, 1969; Lidicker, 1976). The

question then arises as to whether results obtained from studies of enclosed populations at artificially high densities have any relevance to the processes of population regulation operating in natural populations. This question is discussed in Chapter 5.

Most of the studies on rodents described in Chapter 1 consisted solely of introducing founder animals into one or more enclosures, and following the fate of the resultant population(s) (e.g.Brown, 1953; Southwick, 1955(a); Lidicker, 1965, 1976 amongst others). In some, an attempt was made to manipulate the populations or their surroundings (e.g.Crowcroft and Rowe, 1963; Petrusewicz, 1957, 1963). In very few studies however, has an attempt been made to manipulate the behaviour of individual animals with a view to determining the effect on population variables.

There are two major exceptions. Vessey (1967) administered the drug Chlorpromazine (a tranquilizer), mixed with food, to laboratory populations of mice which had reached an asymptote in total numbers, as a result of reproductive inhibition of adult females and infant mortality. There was a marked decrease in aggressive behaviour, and population growth was renewed as a result of increased infant survival. Removal of the drug caused a rise in aggression and a decline in numbers due to renewed infant mortality. Mortality of adults did not vary significantly with population size, nor was it affected by the administration or removal of the drug. Reproduction in the original populations, before the administration of the drug, had almost ceased; the effect of the drug was to allow the few young being born to survive better, but it had no apparent effect on renewing breeding in the reproductively inhibited adult females; Vessey suggested that this might have been because the drug was administered for a relatively short time, and that, had it been continued for several months, reproduction might have been resumed. He also suggested that the two mechanisms (of infant mortality and reproductive inhibition) might operate sequentially, with the increase in infant mortality being the one more sensitive to aggressive behaviour.

The second major example of an indirect attempt at

experimental manipulation of behaviour is the study by Gaines et al (1971) in which populations of Microtus ochrogaster were established in three, two-acre field enclosures; each of the founding populations was composed of 20 voles, all of one genotype (determined from gel electrophoresis of marker genes in plasma), and each introduction was replicated three times, once into each enclosure. Previous work (Tamarin and Krebs, 1969; Gaines and Krebs, 1971) had shown that frequencies of these three genotypes were related to the phase of the population cycle of this vole, and that levels of aggressive behaviour were also linked to population phase (Krebs, 1970). Attempts to discover the link, if any, between genotype and aggressive behaviour in voles have not, however, been successful, (Krebs, 1970), although Lagerspetz (1964) has shown that it is possible to select aggressive and non-aggressive strains of male laboratory mice within two generations, indicating that, in mice, aggressive behaviour is at least in part under genetic control. The central tenet of Chitty's behavioural-genetic hypothesis for control of population cycles in Microtine rodents (summarised in Chapter 1, fig. 1.1.) is that animals from different phases of the cycle are different, genetically and behaviourally. Gaines and his colleagues hoped, therefore, that populations of different genotypes introduced into the enclosures would exhibit different rates of population growth, as a result of their different genetic and behavioural make-up. This, unfortunately, proved not to be the case; there were no statistical differences between the populations in the rate of population increase, the percentage of lactating females, an index of recruitment, or survival rates. Particular genotypes did, however, appear to be selected against. This experiment failed either because an animal's genotype and those behavioural components which are concerned with the control of population variables are not linked, or, if they are linked, because those behavioural components are unimportant during the phase of population growth in enclosures. Because of this uncertainty, the experiment failed to confirm either the theory that social behaviour is involved in vole population processes, or the more specific behavioural-genetic hypothesis of Chitty.

In addition to these two major efforts to modify behaviour and to determine its ecological consequences, attempts rather akin to behavioural manipulation have been made with vole populations on several occasions; these have involved the selective removal of individuals from populations. (Houlihan, 1963; Krebs, 1966; Smyth, 1968; Krebs et al, 1969; Watts, 1970). Some of these studies have involved the selective removal of adult males, and so bear a direct comparison with the present study, where the aggressive behaviour of most of the adult males in the experimental enclosure was depressed by castrating them, but the animals themselves were still physically present. Unfortunately, the experiments of Krebs (1966) and Smyth (1968) were carried out on unenclosed study areas in more or less continuous habitat, and extensive induced immigration from the surrounding uncropped population compensated for the removal. However, in 120ft^2 outdoor enclosures, Houlihan (1963) maintained a control population of Microtus californicus at around 20 individuals by monthly cropping, whilst allowing an experimental population to grow freely. The proportion of females either lactating, pregnant or in breeding condition was consistently higher in the control pen than in the experimental. However, there was a temporary severe food and cover shortage half way through the experiment, following decimation of the natural vegetation by the voles, and even though food was then provided in excess, there was a subsequent population 'crash' in the experimental control enclosure, which was associated with marked behavioural and physiological changes. Unfortunately, these problems mean that comparisons of Houlihan's results with those of the present study are not really possible.

Krebs et al (1969) cropped one third to one half of all adults from populations of Microtus ochrogaster and Microtus pennsylvanicus in 0.8ha enclosures, in an attempt to test the suggestion of Chitty (1960) that a cropped population should remain in the increase phase of the normal regular 3 - 4 cycles exhibited by these voles. The result of cropping was an increased rate of population growth for both species, significantly higher than the growth rate exhibited in an unenclosed, uncropped control area, and high enough to compensate for the removals. At the same time, an uncropped

enclosed population, not given supplementary food, rose to very high levels, resulting in overgrazing and a resultant sharp decline in numbers; this decline meant that detailed comparison between this uncropped, enclosed population and the cropped enclosed population was not really possible; both however showed the very high initial rates of population increase commonly associated with newly enclosed populations, and both reached the very high densities, relative to unenclosed populations, associated with frustrated dispersal. Cropping one enclosed population appeared to prolong the increase phase and avoid the mortality, associated with overgrazing, that was observed in the other uncropped population. Thus, these experiments demonstrated that, in large field enclosures, the presence of adult animals was alone sufficient to depress the population growth rate, and the data presented suggest that this was due to enhanced survival of juvenile animals in the cropped population. However, since both male and female adults were cropped, it is not possible to say whether either or both sexes were having the significant effect.

A final example of cropping a vole population is that of Watts (1970) and is of particular interest because the species used was the North American red-backed vole Clethrionomys gapperi, which is both ecologically and structurally very similar to Clethrionomys glareolus (Corbet, 1966) and because the cropping programme involved the removal of adult males only. Watts' study area was a strip of forest 2400m long and 50-80m wide bounded on its two long sides by unsuitable red-backed vole habitat. He removed adult males from half of each of the four 600m x 50-80m quarters of his whole study area, thereby replicating the experiment four times. The object was to test the hypothesis that dominant adult male voles killed or drove out juveniles during the breeding season (Chitty and Phipps, 1966; Watts, 1969). Although the minimum numbers known to be present was greater, when compared with the control areas, in three out of the four areas from which adult males had been removed, Watts attributed this not to the increased reproduction or decreased mortality, as a result of the absence of the dominant males on the experimental areas, but to the fact that young animals entered the traps sooner in life on the experimental areas, because the presence

of the uncropped dominant males on the control areas was inhibiting the initial capture of the young animals. This interpretation, based on analysis of the populations weight-structures, showed that, although juveniles appeared to be absent on the control areas, the numbers of sub-adults subsequently caught was not different between the two areas; since there was very little detected movement between the areas, the young animals must have been there on the control areas all the time, but were just not being caught. A simple model, in which 80% of the juveniles evaded capture on the first occasion that they were large enough to have entered the traps, was sufficient to mimic the results obtained in the field. This result is clearly important for all studies of the role of social behaviour in the population dynamics of rodents which use live trapping techniques, and will be discussed, in light of the results of the present study, in sections 4.3.4.(f) and 4.4. below.

In conclusion, although previous attempts have been made to affect rodent population dynamics by experimental manipulation, these have mostly been unsuccessful, for a variety of reasons. Vessey's (1967) study was the only one in which experimental manipulation of the behaviour of individuals resulted in measurable changes in demographic variables.

4.2. METHODS

4.2.1. Construction of Enclosures.

During the course of this study, the enclosures used had to be extensively modified as a result of loss of voles from, and transfers between the two enclosures, and as a result of immigration of Brown Rats, Rattus norvegicus. Plates 4.2.1(i) and (ii) show the enclosures at the end of the study in November 1975, by which time the modifications necessary to remedy all these defects had been carried out. These modifications will not be described in detail, but presented in a series of figures with footnotes.

Figure 4.2.1(i) gives a plan showing original dimensions and areas, and a section through the enclosure wall showing the original construction is given in Fig.4.2.1(ii).

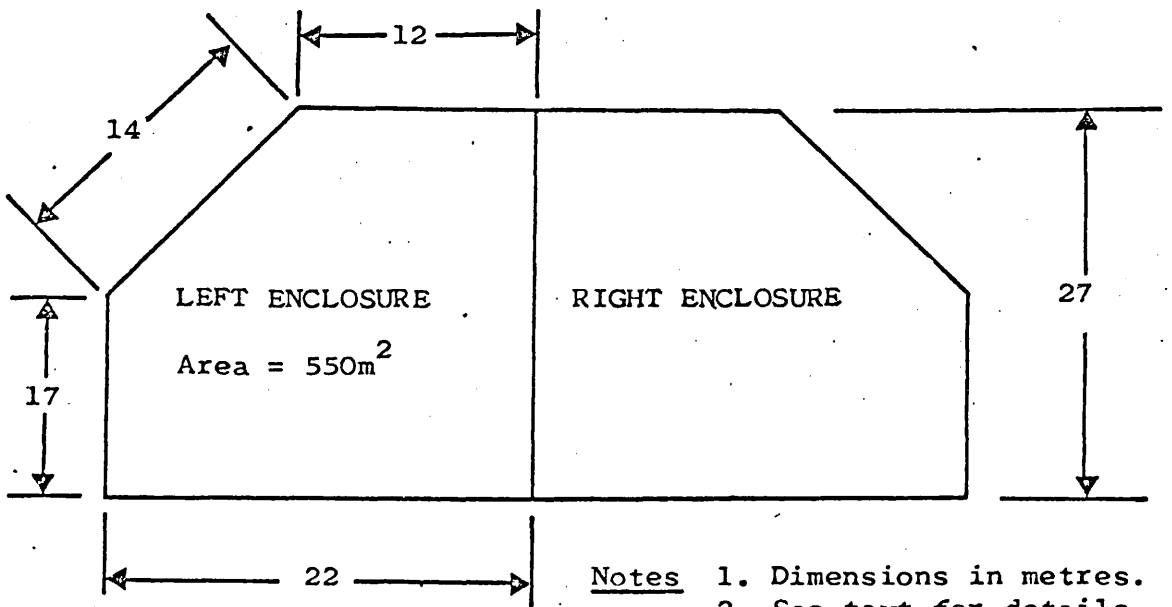
Fig. 4.2.1(iii) shows a section through the wall following the first modifications, necessitated by mass escape of experimental animals through newly dug mole runs extending under the walls and by immigration of non-experimental animals in February, 1974, and Fig. 4.2.1(iv) shows a plan of the enclosures following these modifications, which were carried out in May-June,1974.

Following immigration of rats into the enclosures in January, 1975, the further modifications shown in Fig. 4.2.1(v) were made. A side elevation of the same modifications is given in Fig.4.2.1(vi) (See also Plate 4.2.1(i)). The aim of this modification was to prevent immigration of rats over the overhang and through the original 1½" mesh; following the modification, the rat now had to climb the fine ½" mesh after jumping up the original galvanised wall, and then found a foot of vertical galvanised sheet to negotiate.

In July, 1975, a pair of rats burrowed down through the gravel between the plastic sheeting and the original galvanised wall, and so into the right enclosure. In November 1975, therefore, this gravel round the perimeter was covered to a depth of two inches with concrete. (See Fig.4.2.1(vii) and plate 4.2.1(i)). Following some transfers of experimental animals between the enclosures in June, 1973, the gravel between the galvanised and plastic sheeting of the central partition between the two enclosures was also concreted over.

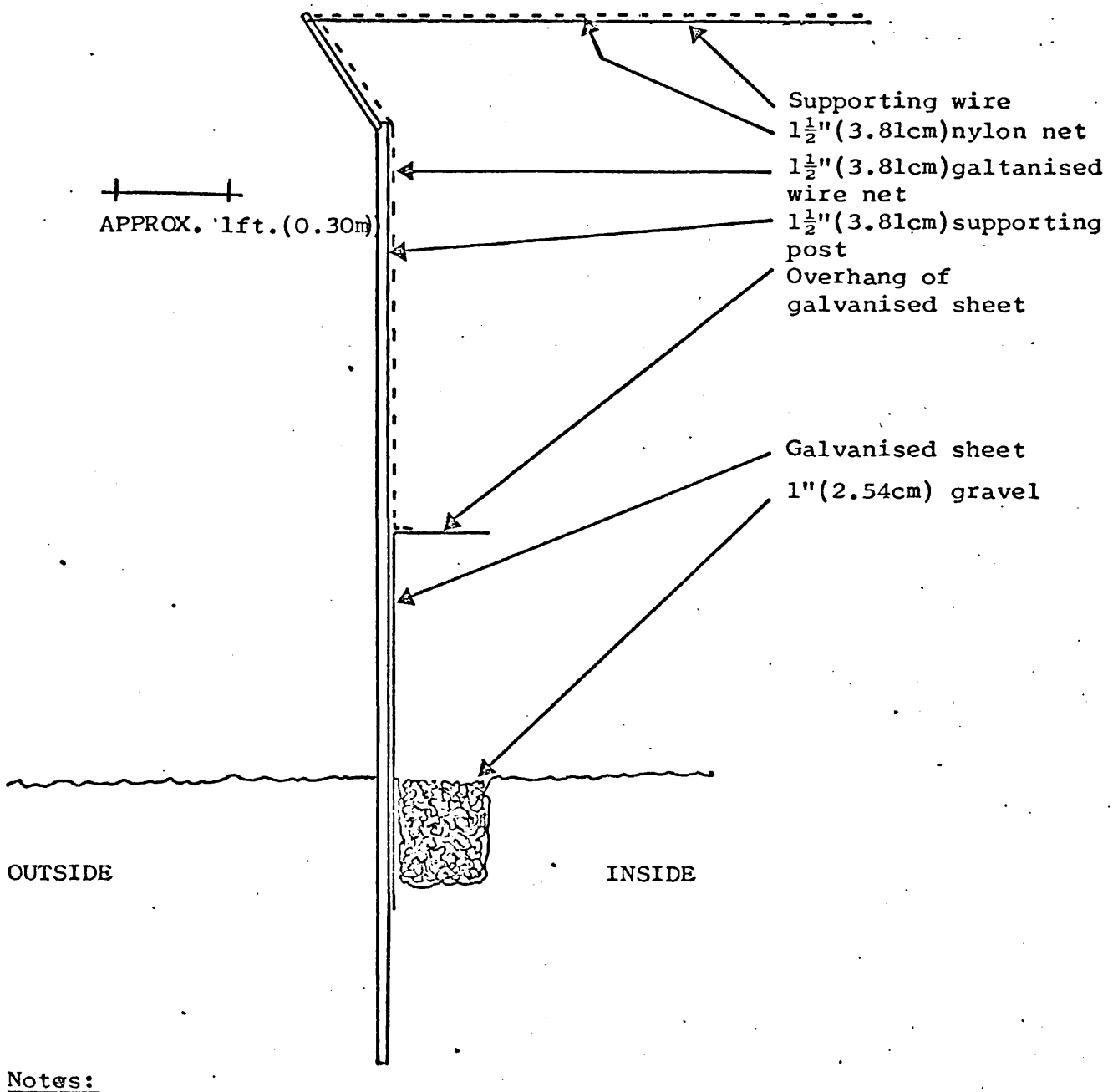
Plates 4.2.1. (i) - (ii)

Fig. 4.2.1.(i) Enclosures (plan), original construction, October, 1973



Notes 1. Dimensions in metres.
2. See text for details.

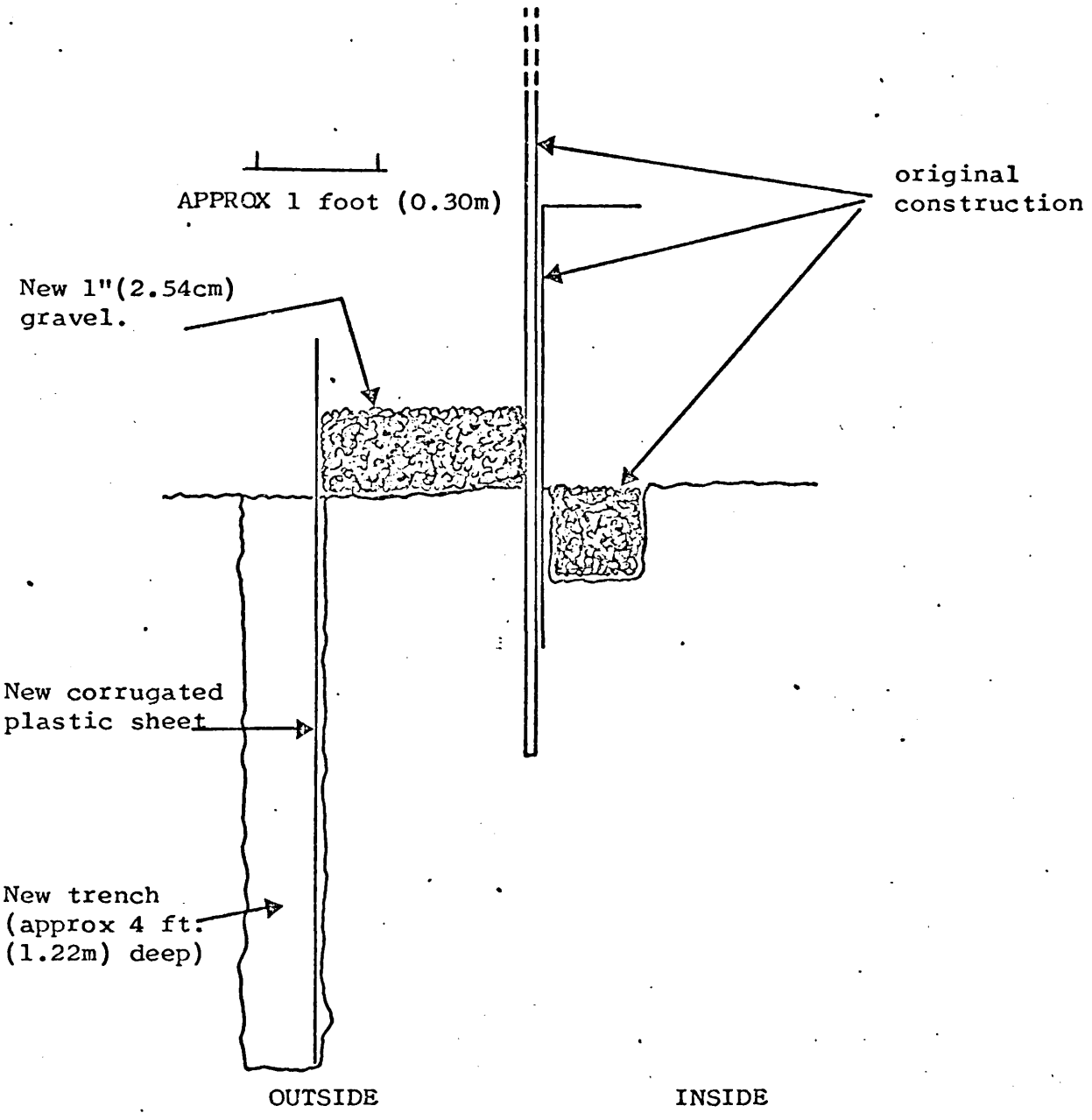
Fig. 4.2.1.(ii) Enclosure wall (section)
original construction, October, 1973.



Notes:

1. Supporting posts set every 8feet(2.44m) round perimeter (See fig. 4.2.1.(i)).
2. Galvanised sheets 8 feet long(2.44m), 4feet wide(1.22m); 1 foot(0.30m) overhang, 2 feet(0.60m) above ground, 1 foot (0.30m) below ground.
3. Nylon net to exclude avian predators (owls etc.).
   Galvanised net to exclude terrestrial predators (cats etc.).
   Galvanised sheet to prevent escape of experimental animals and to exclude immigrants.
   Gravel to discourage tunnelling around enclosure edges.
4. See text for details.

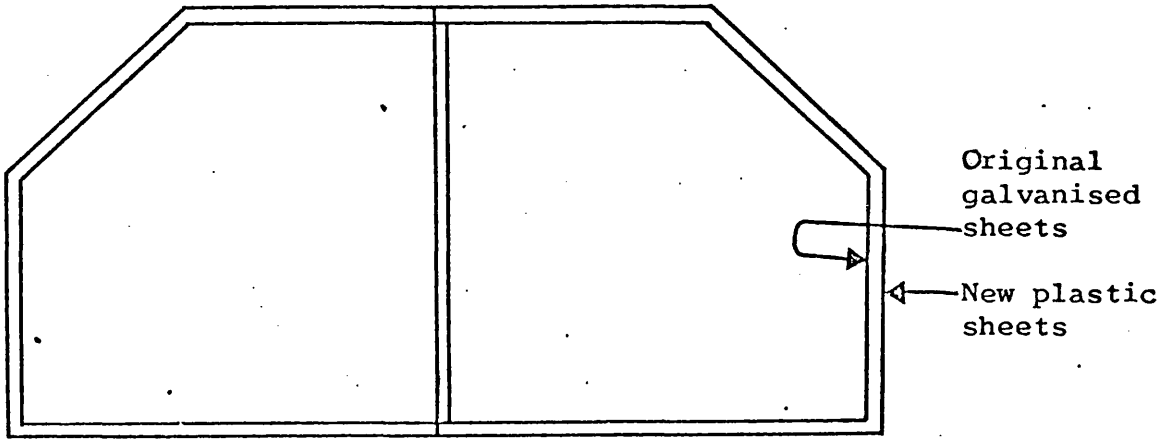
Fig. 4.2.1.(iii) Enclosure wall (section), including modifications, May-June, 1974.



Notes:

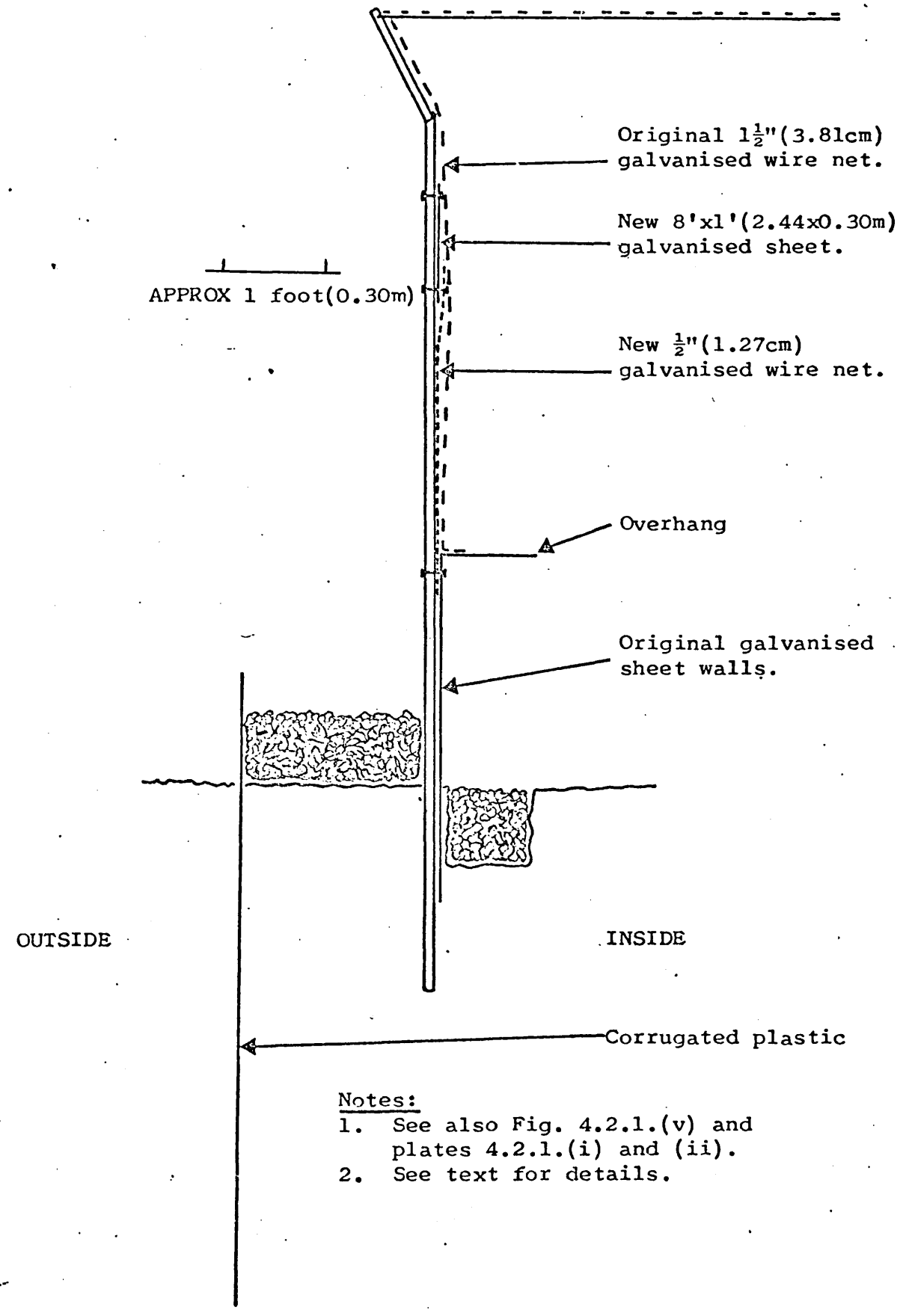
1. 4 foot(1.22m) trench dug using Davis TF700 trench digger.
2. Corrugated plastic sheet 4 feet(1.22m) below ground, 1 foot above.
3. Same modification carried out on central partition dividing the two enclosures.
4. See text for details.

Fig. 4.2.1.(iv) Enclosure (plan), including modifications May - June, 1974.



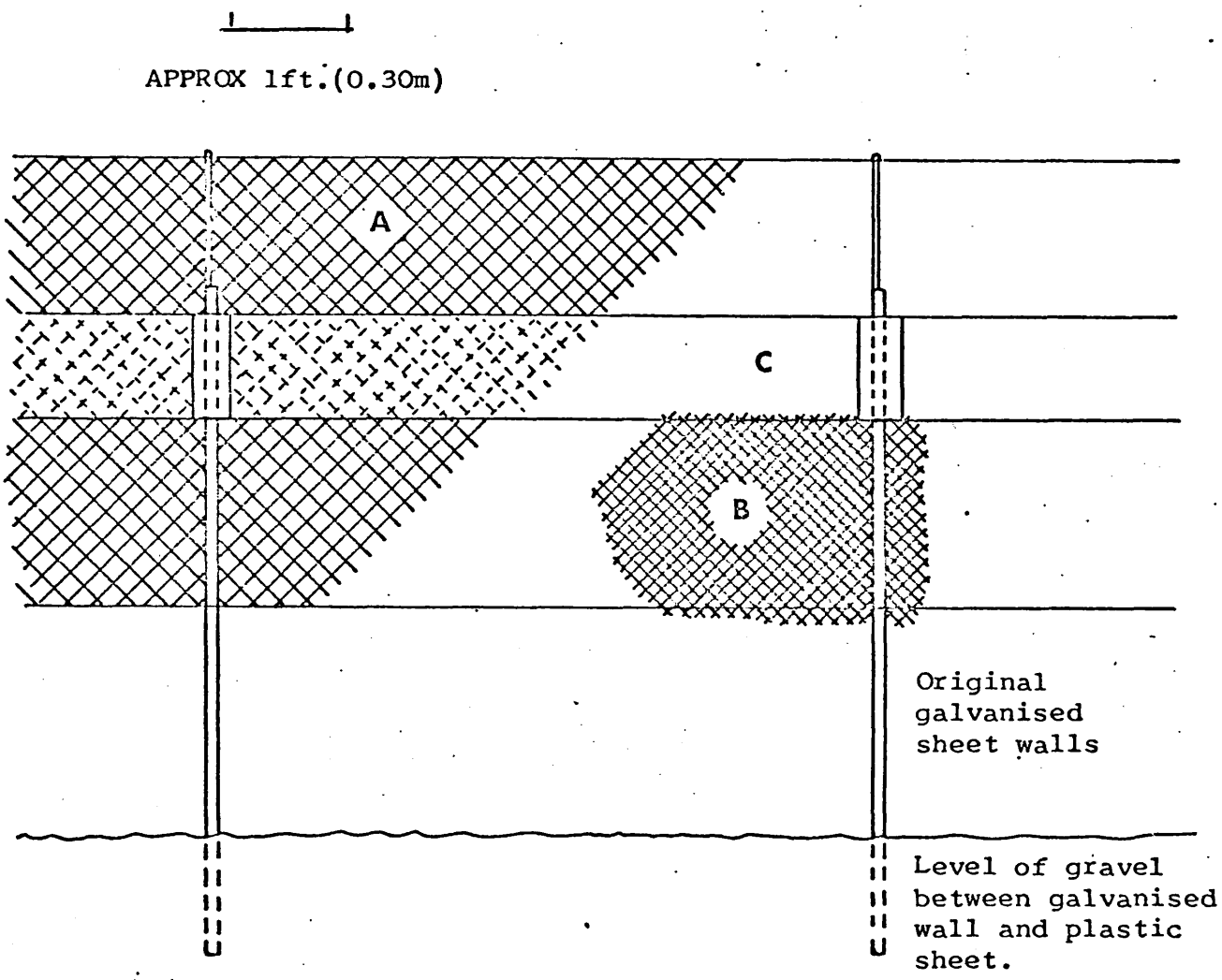
Notes:
1. Dimensions as for Fig. 4.2.1.(i).
2. See also Fig. 4.2.1.(ii).
3. See text for details.

Fig. 4.2.1.(v) Enclosure wall (section), including modifications, February, 1975.



Notes:
1. See also Fig. 4.2.1.(v) and plates 4.2.1.(i) and (ii).
2. See text for details.

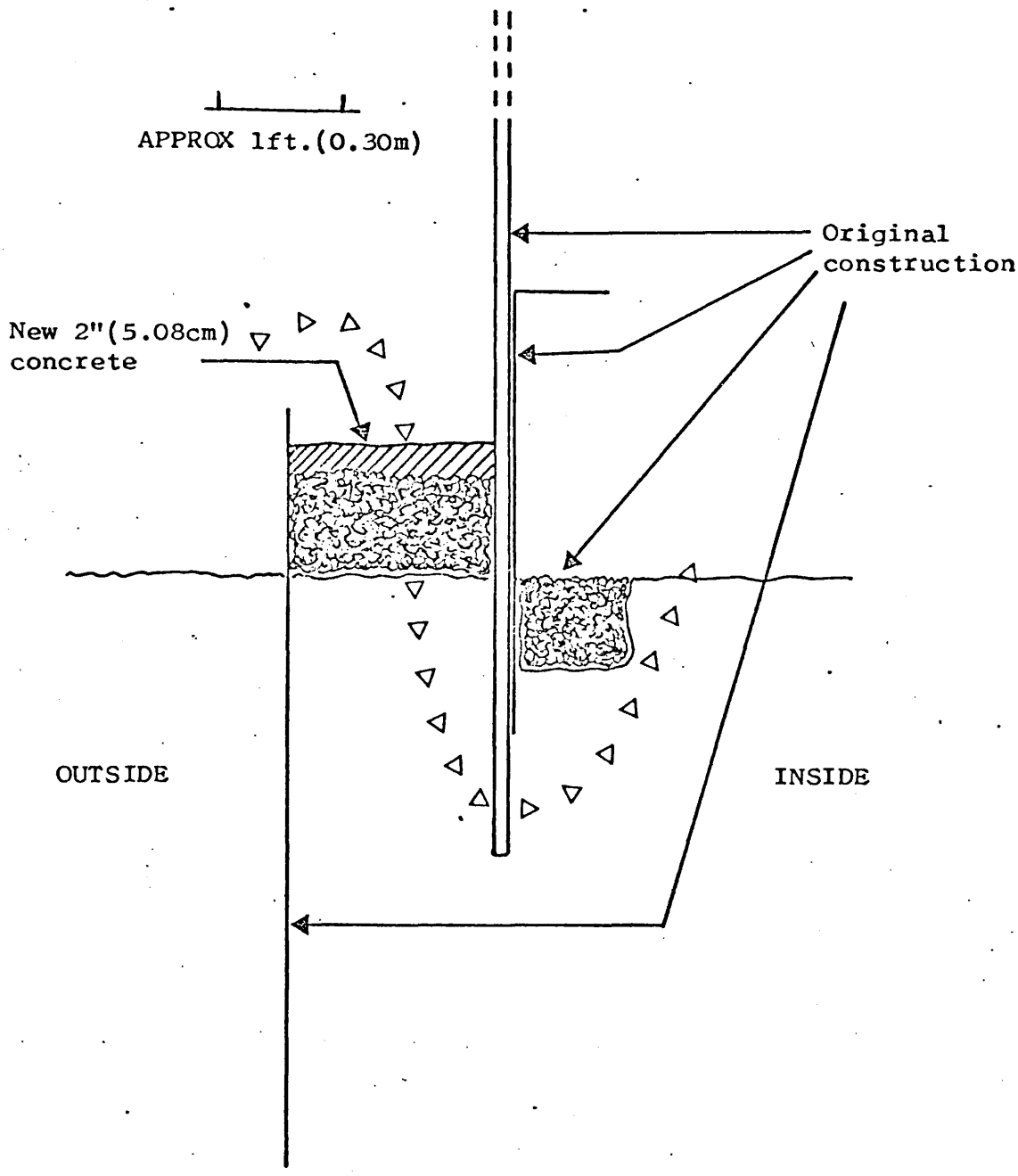
Fig. 4.2.1.(vi) Enclosure wall (side elevation), including modifications, February, 1975, viewed from outside.



Notes:

1. A = Original $1\frac{1}{2}$"(3.81cm) galvanised wire net
   B = New $\frac{1}{2}$"(1.27cm) galvanised wire net
   C = New 8'xl'(2.44xO.30m) galvanised sheet
2. See text for details
3. See also Fig. 4.2.1.(v) and Plates 4.2.1.(i) and (ii)

Fig. 4.2.1.(vii) Enclosure wall (section) including modifications, November, 1975



Notes:

1. New concrete to prevent burrowing by rats into the enclosures along arrowed path.
2. See text for details.

4.2.2. Introduction of animals into the enclosures.

Animals for introduction into the experimental enclosures were captured from various sites in the Crown Estates near Windsor, Berkshire, from the grounds of the Forestry Commission Research Station at Alice Holt, near Farnham, Surrey or from the grounds of Royal Holloway College, Egham, Surrey. If animals from more than one source were used in any introduction into the enclosures, care was taken to partition animals from each source equally into each half, to ensure that the genetic composition of the two starting populations was not artificially made different. Similarly, the sex ratio and weight distribution of the two starting populations was made as similar as possible. Table 4.2.2(i) gives a summary of the experimental introductions of the animals into the enclosures. After capture from the field, animals were housed individually before release. Castration and sham operations were carried out as described in Chapter 2, Section 2.2.1.

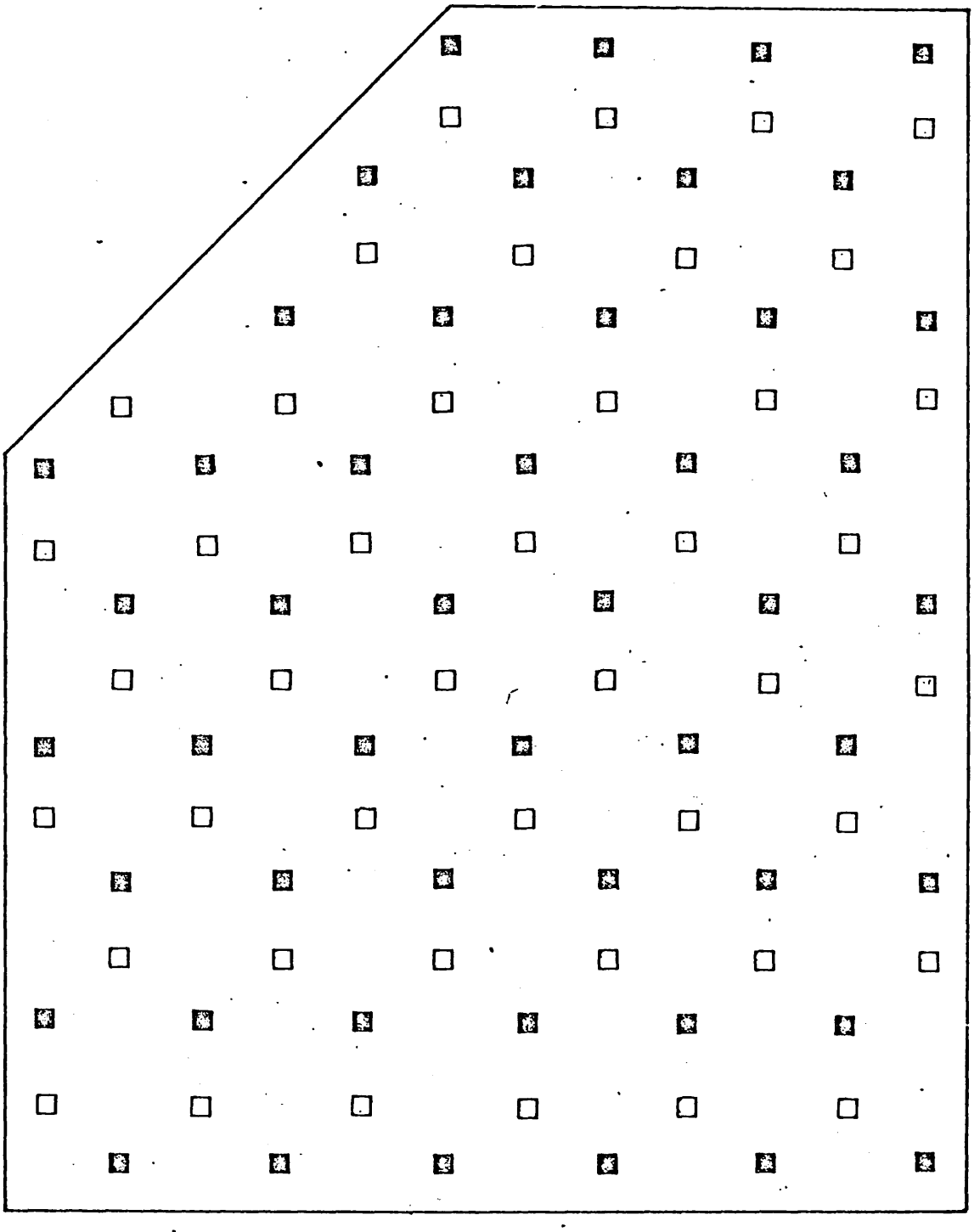
Table 4.2.2(i). Summary of introductions of animals into the enclosures.

Experiment number		Dates	LEFT ENCLOSURE ♂	LEFT ENCLOSURE ♂	LEFT ENCLOSURE ♀	RIGHT ENCLOSURE ♂	RIGHT ENCLOSURE ♂	RIGHT ENCLOSURE ♀	NOTES:- (for full details see text)
	ENCL1	Feb - Mar 1974	22		22	22		22	Discontinued March 1974 - transfers of voles, escapes. Modifications shown in Fig. 4.2.1(iii) and Fig. 4.2.1(iv) (perimeter and control partition trench, and plastic sheeting)
	ENCL2	July 1974 - Feb 1975	23				23		Jan 1975. Rats in both enclosures Modifications shown in Fig.4.2.1(v) and Fig.4.2.1(vi) and Plate 4.2.1(i). (new galvanised sheeting and fine mesh)
	ENCL3	April - July 1975	5	19	19	24		19	July 1975. Rats in enclosures Modifications shown in Fig. 4.2.1(vii) and Plate 4.2.1(i) (concreting over perimeter gravel)
	ENCL4	Feb - Dec 1976	24		20	5	18	20	July 1976, some transfers between enclosures. Modification - concreting over central partition gravel.

4.2.3. Supplementary food and water.

Figs. 4.2.3(i) and (ii) show plans of both left and right enclosures, giving the positions of nest boxes and feeding sites. Food (Dixons Diet 86) was provided at the points shown in empty wine bottles with the top 1-2 inches of the neck removed, lying on their sides. During dry periods, water was provided daily either in shallow aluminium trays or by thoroughly spray-wetting the vegetation in both enclosures.

Fig. 4.2.3.(i) Left enclosure (plan)



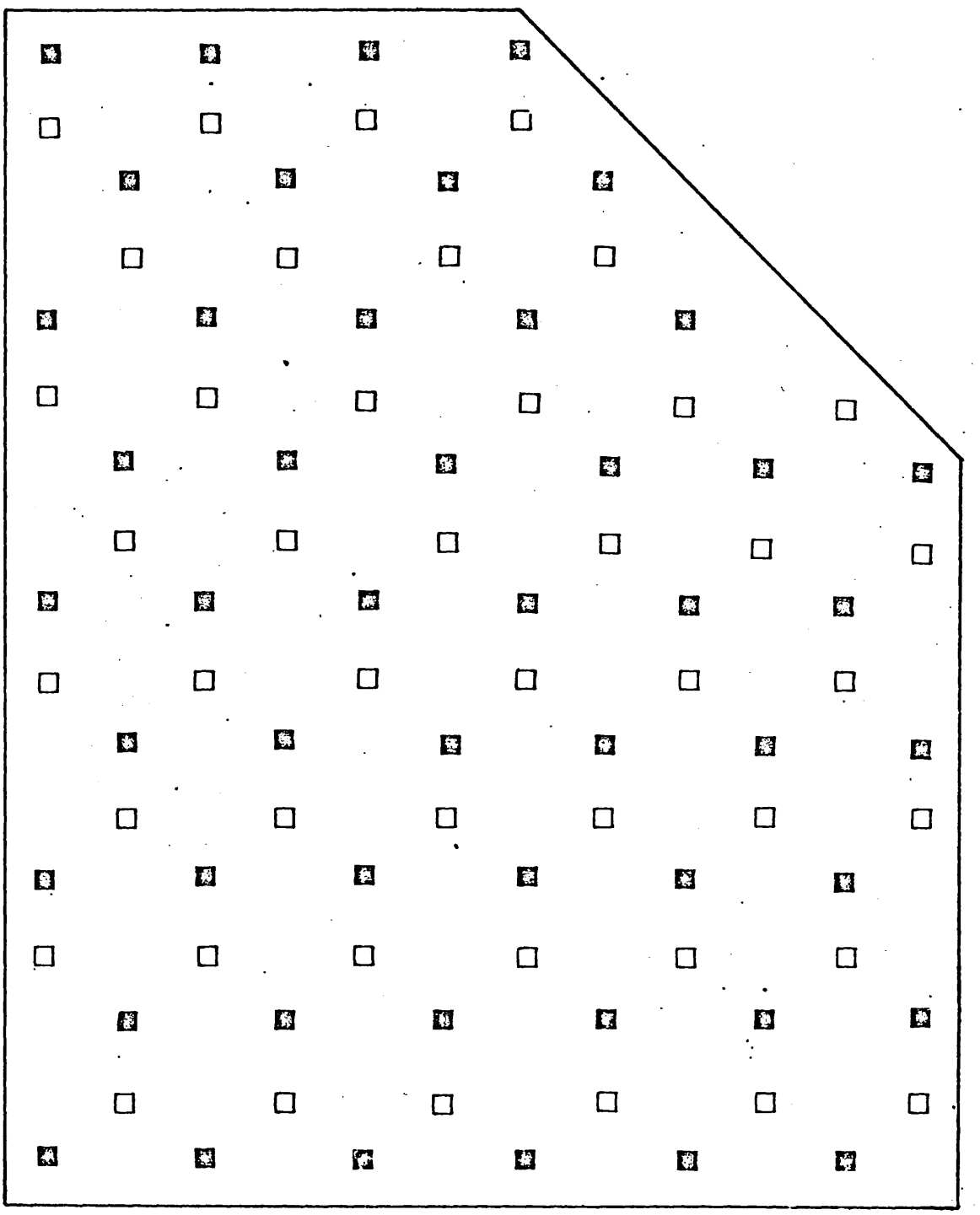
Key:-

■ = Trapping point

□ = Nest box/Feeding site

APPROX. 1m.

Fig. 4.2.3.(ii) Right enclosure (plan)



Key:-

■ = Trapping point

□ = Nest box/Feeding site

APPROX. 1m.

4.2.4. Trapping.

4.2.4(a). Trap layout.

The layout of trapping points is shown for each enclosure in figs. 4.2.3(i) and (ii). Traps were placed within approximately one metre of each trapping point, with enough traps at a point to ensure that only about half the traps set were full. This reached a maximum during experiment ENCL 4, when three traps were set per point.

Each enclosure was trapped using Longworth traps, without pre-baiting, for two nights in alternate weeks. Traps were left in the enclosures permanently, locked open when not in use.

Traps were set in the afternoon, checked and reset the following morning and afternoon, and checked and locked open the third morning. During hot weather, traps were set to catch overnight only, to prevent trap deaths due to overheating.

4.2.4(b). Information collected on the trap round.

All animals released into the enclosures were given individual numbers by toe-clipping before release, and all animals caught for the first time within the enclosures (i.e.born there) were also toe-clipped. If a female had a litter inside a trap, the size of her litter was noted. The young then had their tail tips clipped, (see also Section 4.2.5(c) below), both mother and litter were returned to the trap, and the door was propped open; the female usually removed her litter within a few minutes.

The following data were collected from each animal caught:-

1. Position of capture (see Figs.4.2.3(i) and (ii)).
2. Weight in grams.
3. Sex (♂, ♀, or castrated ♂).
4. The presence if any, of new wounds. The face, tail and lower abdomen were particularly carefully scrutinized for fresh wounding; only new wounds were scored, old scars were disregarded.
5. Breeding condition.

Males: The position of the testes was noted, and scored as scrotal, pushable into the scrotal sac by gentle pressure on the ventral abdomen, or abdominal. A subjective assessment was also made of the testis size, and the testes classed as small (approx. $\frac{3}{4}$cm in length), medium (approx. $\frac{3}{4}$-1cm), or large (1cm). All males with medium or large testes were classed as being in breeding condition.

Females: Vagina; perforate or imperforate. Pregnancy was diagnosed in the field by enlargement of the abdomen, or the presence of blood or mucus in the vagina. Increase in weight corroborated these two other diagnostic features. The presence of vaginal plugs was also noted. Lactation was diagnosed by study of the mammary glands (whether or not they were engorged with milk) and the nipples (whether or not they were hairless or enlarged through suckling). Females were defined as being in breeding condition if they were either pregnant or lactating, or the vagina was perforate.

4.2.4(c). Analysis of trapping data.

The trapping data were analysed using the Calendar of Captures method (Petrusewicz and Andrzejewski, 1962).

For each enclosure and each age and sex class, minimum numbers present, the proportion of animals in breeding condition, the number of pregnancies observed, and recruitment into, and losses from, the trappable population, were estimated directly from the calendar of captures, and the results for the two enclosures compared.

All these comparisons were made to test the hypothesis that different social conditions in each enclosure would lead to differences in the population dynamics between the communities of voles in each enclosure.

Despite the enormous efforts put into increasing the reliability and accuracy of methods for estimating the numbers of small mammal populations (see Smith et al, 1975 for a review), Krebs (1966) has demonstrated and discussed at length the inapplicability of mark-recapture techniques for estimating small mammal populations, and he subsequently used direct enumeration methods. Enumeration of enclosed populations is clearly much easier and more efficient than enumeration of unenclosed populations, since in the former, immigration and emigration are eliminated, and the only processes affecting the population size are births and deaths.

Also calculated direct from the calendar of captures was the proportion of each age and sex class exhibiting fresh wounds at each trapping session; this calculation was done to determine directly whether there was any difference in the levels of fighting occurring in the two enclosures, and to determine which age and sex classes were indulging in close-quarters aggressive encounters.

From the raw trapping data, two further variables, linked to the social organisation within the enclosures, were calculated. These were the distances between captures for each age and sex class, and the trap revealed home range.

The inadequacy of live-trapping techniques for obtaining information on movements and home ranges of small mammals has long been recognised (Jewell, 1966; Randolph, 1973). Firstly, once caught, the animal is immobilised and it can only reveal one point within its home range on each trapping occasion. Secondly, different age and sex classes have been shown to react differently to traps (Kikkawa, 1964; Tanton, 1965; Brown, 1969). Other factors such as trap spacing, size of trapping area, and the number of times an individual is captured have also been shown to affect movement and home range calculations (see Kikkawa, 1964; and Sanderson, 1966 for reviews). As an alternative, several tracking techniques have been developed (e.g. Justice, 1961; Adamczyk and Ryszkowski, 1968; Randolph, 1973). In the present study, however, live-trapping was the only method available for following the populations in the enclosures, and collection of data on movement and home ranges was of secondary importance to the collection of demographic data.

The distances between all the captures of all the individuals of each age and sex class were compared with other age and sex classes using the Mann-Whitney test (Siegel, 1956); a non-parametric test was used because it has been shown (Flowerdew, 1971) that the frequency distribution of distances between captures is markedly skewed. This calculation was made to test the hypothesis that the different social conditions in each enclosure would affect the freedom of movement of different groups of animal differently, within and between enclosures. Obviously, the distance between captures is an extremely crude measure of this, and in the present study, because the traps were so close together, the distance between captures could have in no way represented the actual movement between the two captures; also the enclosures were small enough for a vole to cross in a very few

minutes and were no longer than previously reported bank vole home range lengths (e.g.Zejda and Pelikan, 1969: approximately 20-40m). Because of these limitations, it was felt that any sophisticated analysis of distances between captures would have been inappropriate, and so only gross comparisons were made between all the distances between captures for each class and each other class, with complete disregard for the time interval between captures.

In the present study, the home range area was defined as the total area enclosed by the smallest convex polygon containing all the capture points to date, plus the area of a boundary strip around this polygon whose width was equal to half the distance between traps.

A great deal of effort has been devoted to finding a method of estimating home range areas accurately and consistently from scarce data (Hayne, 1949; Stickel, 1954; Calhoun and Casby, 1958; Mazurkiewicz, 1968; Jennrich and Turner, 1969; Wierzbowska, 1972; Andrzejewski and Mazurkiewicz, 1976; Randolph, 1977).

In the present study, however, a relatively simple system of analysing the trapping results was used because of the very small trap-spacing and because of the confinement of the enclosures; it was thought that, as outlined above in connection with the analysis of distance between captures, a complex analysis would have been inappropriate.

The accumulation of home range area with successive captures was calculated for each animal (for a discussion of this method see Andrzejewski and Mazurkiewicz, 1976) and each age and sex class in the experimental enclosure compared, using the Mann-Whitney test (Siegel, 1956), with the equivalent age and sex class in the control enclosure. This calculation was made to test the same hypothesis tested by the calculation of distances between captures, namely that the different social conditions in the two enclosures would affect the freedom of movement of equivalent groups in each enclosure differently.

Finally from the trapping data, the mean weight at first capture of each sex in each enclosure was calculated to test the suggestion by Watts (1970) concerning the influence of adults on the trappability of juveniles, discussed in the Introduction to this Chapter (4.1. above).

4.2.5. Nest boxes.

a) Nest boxes were provided at the points marked on Figs. 4.2.3(i) and (ii).

b) The general design of the nest boxes is shown in Fig.4.2.5(i). The boxes were made of wood, with a perspex lid. Each box was surrounded by bricks on three sides, with a tile at an angle over the fourth to cover the entrance. A concrete slab rested on the three bricks and the box top. It was hoped that the animals would use these boxes and that frequent inspection would reveal information about litter sizes. However, they were used relatively little, probably because they tended to get rather damp during wet periods.

c) Periodic tours of the nest boxes were made. Litters found had their tail-tips clipped (toe-clipping is not possible at this early age). Thus, any animal trapped for the first time with its tail tip missing was known to have been seen as a nestling. Tail-tip clipping was also done to litters born in Longworth traps.

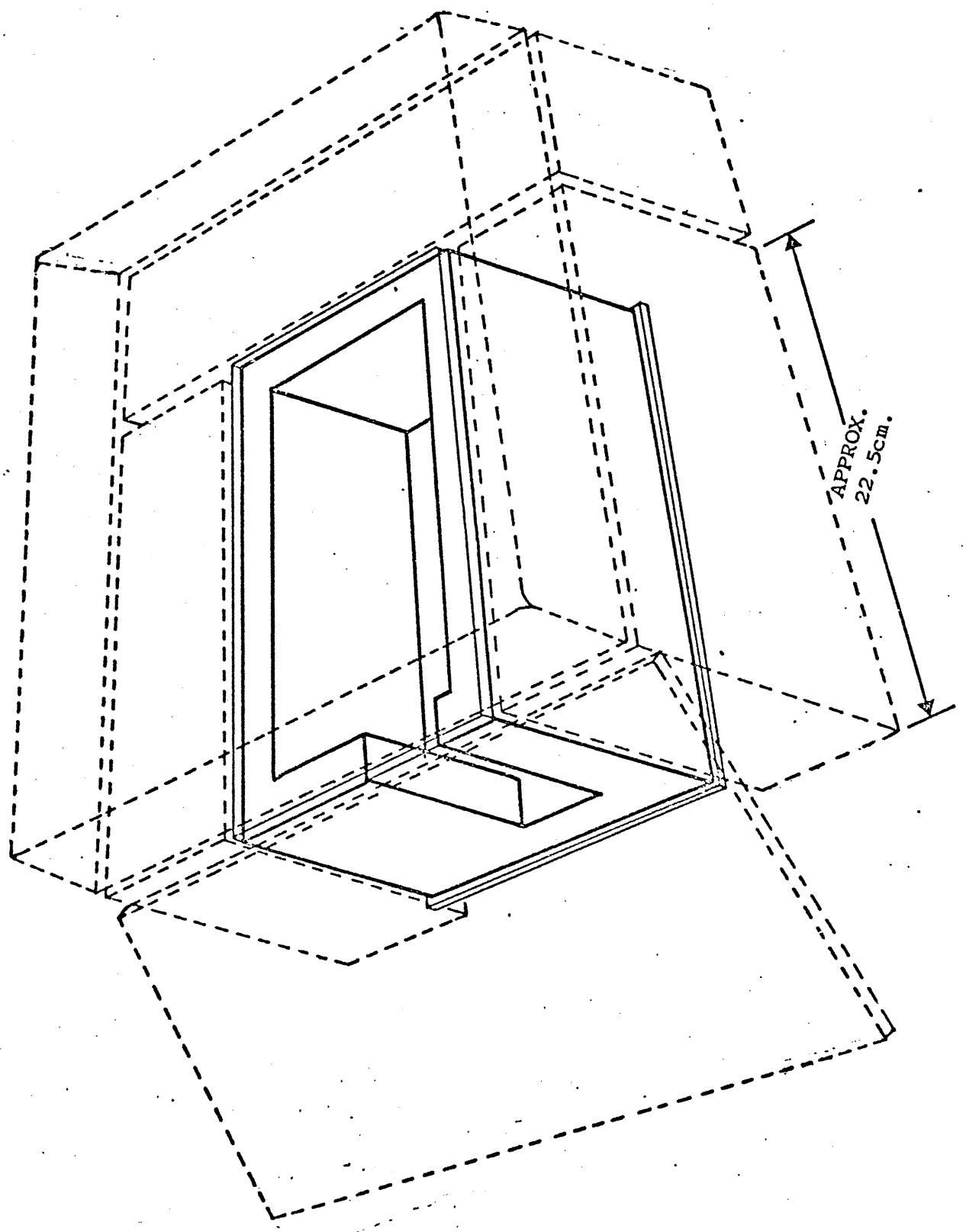


Fig. 4.2.5.(i) Nest box.
(See text for details)

4.3. RESULTS

4.3.1. Experiment ENCL 1.

22 males and 22 females were introduced into each enclosure in February, 1974. It very soon became clear that many animals were escaping, that unmarked voles and mice were entering the enclosures, and that voles were transferring between the enclosures. The experiment was terminated in March, 1974, any remaining voles were removed, and the modifications described in 4.2. above were carried out. No results were obtained from this experiment.

4.3.2. Experiment ENCL 2.

In July, 1974, 23 adult males were introduced into the left enclosure and 23 castrates were introduced into the right enclosure, with the intention of determining if there were any differences in survival between the two types. In January, 1975 rats got into the left enclosure, and the experiment was terminated.

4.3.2(a). ENCL 2 - Survival

The last trapping occasion before the rats got in was on the 7th December, 1974. Table 4.3.2(i) shows the survival between July and December 1974; the difference between adults and castrates is not significant.

Table 4.3.2(i).

	No. introduced	Known survivors to 5.12.74	
L enclosure (adults)	23	18	$\chi^2 = 2.31$ df = 1 n.s.
R enclosure (castrates)	23	22	

Note: Five losses in L. enclosure include one trap death, not included in analysis of difference in survival between the two enclosures.

4.3.3. Experiment ENCL 3.

Experiment ENCL 3 was started in April, 1975 with five intact males, 19 castrated males and 19 females in the left enclosure and 24 intact males and 19 females in the right enclosure; trapping had been going on for twelve weeks when a pair of rats got into the right enclosure. Following this immigration and failure to catch the rats, numbers of voles in the right enclosure sharply declined, presumably killed by the rats, and the experiment was terminated in August, 1975. No useful results were obtained from this experiment.

4.3.4. Experiment ENCL 4.

Experiment ENCL 4 was started in February 1976 with five adult intact males, 18 castrated males and 20 adult females introduced into the right, experimental enclosure, and 24 adult intact males and 20 adult females introduced into the left, control enclosure. The experiment lasted 42 weeks, until the beginning of December, 1976.

Presentation of the results of experiment ENCL 4 will be divided into the following parts:

(a) Estimated numbers of animals in each enclosure.

(b) Processes affecting the numbers of animals in each enclosure.

- (i) Breeding condition.
- (ii) Births.
- (iii) Recruitment into the trappable population.
- (iv) Losses.

(c) Wounding.

(d) Distances between captures.

(e) Trap revealed home-range areas.

(f) Weights at first capture.

4.3.4(a). The estimated numbers of animals in each enclosure.

The initial numbers in the two enclosures in February, 1976, introduced at the start of experiment ENCL 4, are shown in the methods section above, in Table 4.2.2(i). Figure 4.3.4(i) shows the total numbers of animals in each enclosure between February and December, 1976.

It can be seen that the maximum number reached in the right enclosure (172) (initially containing five intact and 18 castrated males and 20 females) is greater than the maximum number reached in the left control enclosure (142) (initially containing 24 intact males, no castrates and 20 females). The difference approaches, but is not significant ($\chi^2 = 2.87$, df = 1, $0.10 > p > 0.05$). If however, each line on the graph of numbers against trapping week (Fig.4.3.4(i)) is divided into two sections, the first corresponding to the period of increase in each enclosure, the second corresponding to the period of relative stability of numbers, it can be seen that the rates of increase in the two enclosures, (represented by the slopes of the lines) are different, whereas the periods of increase were the same (approximately 14 weeks). The formulae for the regression lines of N (Total numbers) against T (Trapping week) for the two graphs of total numbers against trapping week between trapping weeks 7 and 23 inclusive are given on Fig.4.3.4(i) as are values of r, the instantaneous rate of population growth per week for the same period. The slopes of the regression lines are significantly different, ($F = 83.35$, df 1, 15, $p < 0.001$). In other words, the overall rate of increase in total numbers in the right (experimental) enclosure was significantly higher than the overall rate of increase in the left (control) enclosure during the period of increase in both populations.

Figure 4.3.4(ii) shows the total numbers of adults and immatures of both sexes combined in each enclosure between February and December, 1976. It can be seen that the major part of the difference between the numbers in each enclosure was the result of more immature animals entering the trappable population in the right, experimental enclosure, than the left, control enclosure. Loss of adult introduced animals was however, rather higher in the

Key to graphs

Throughout this chapter, the following convention has been employed.

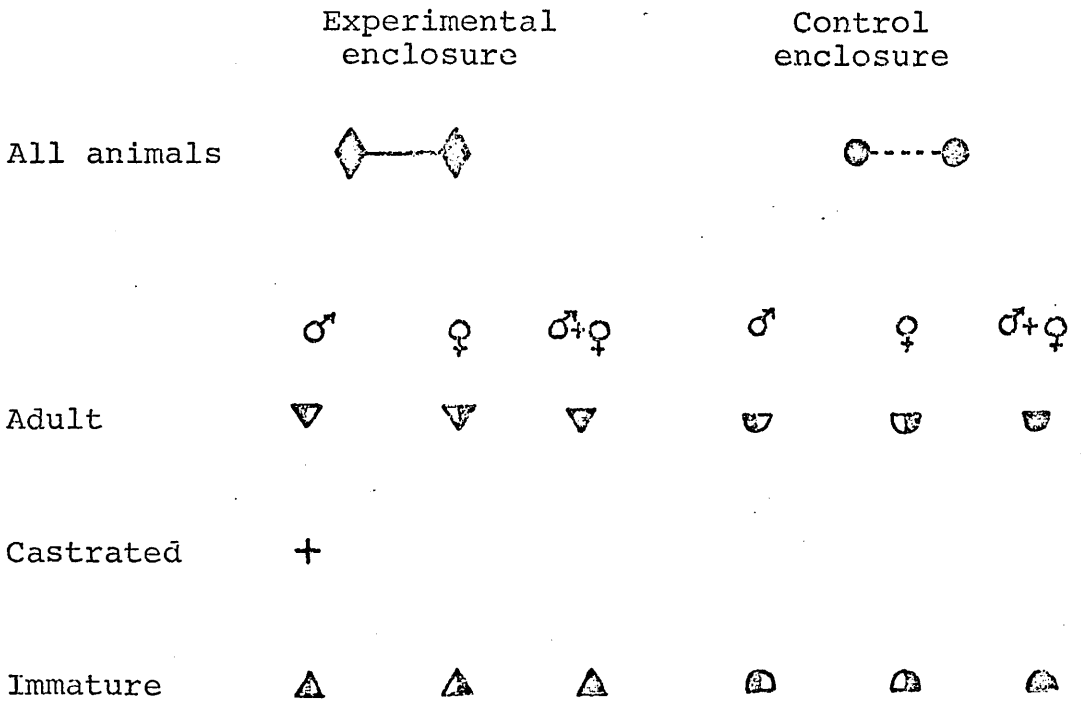


Fig. 4.3.4.(i) The total estimated numbers of trappable animals in each enclosure during experiment ENCL 4 (See text for full details).

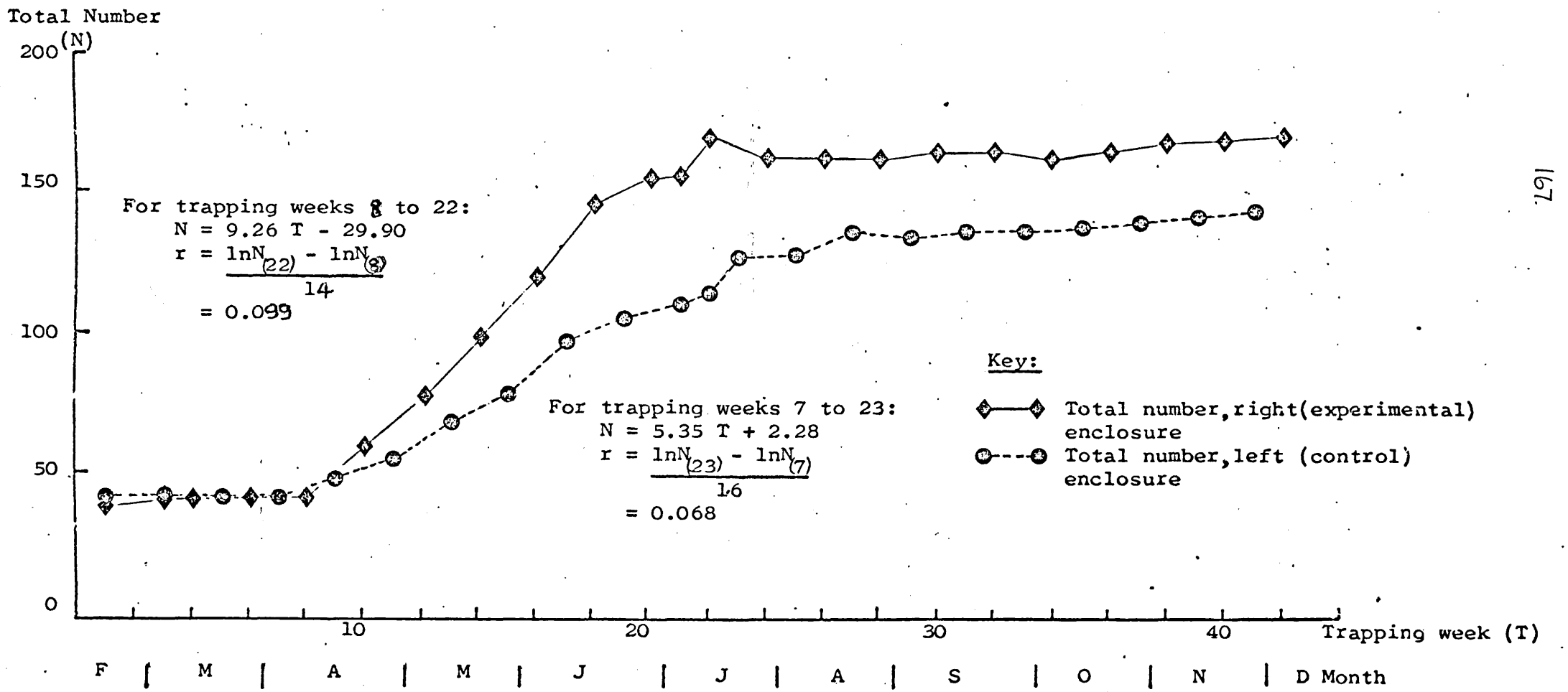
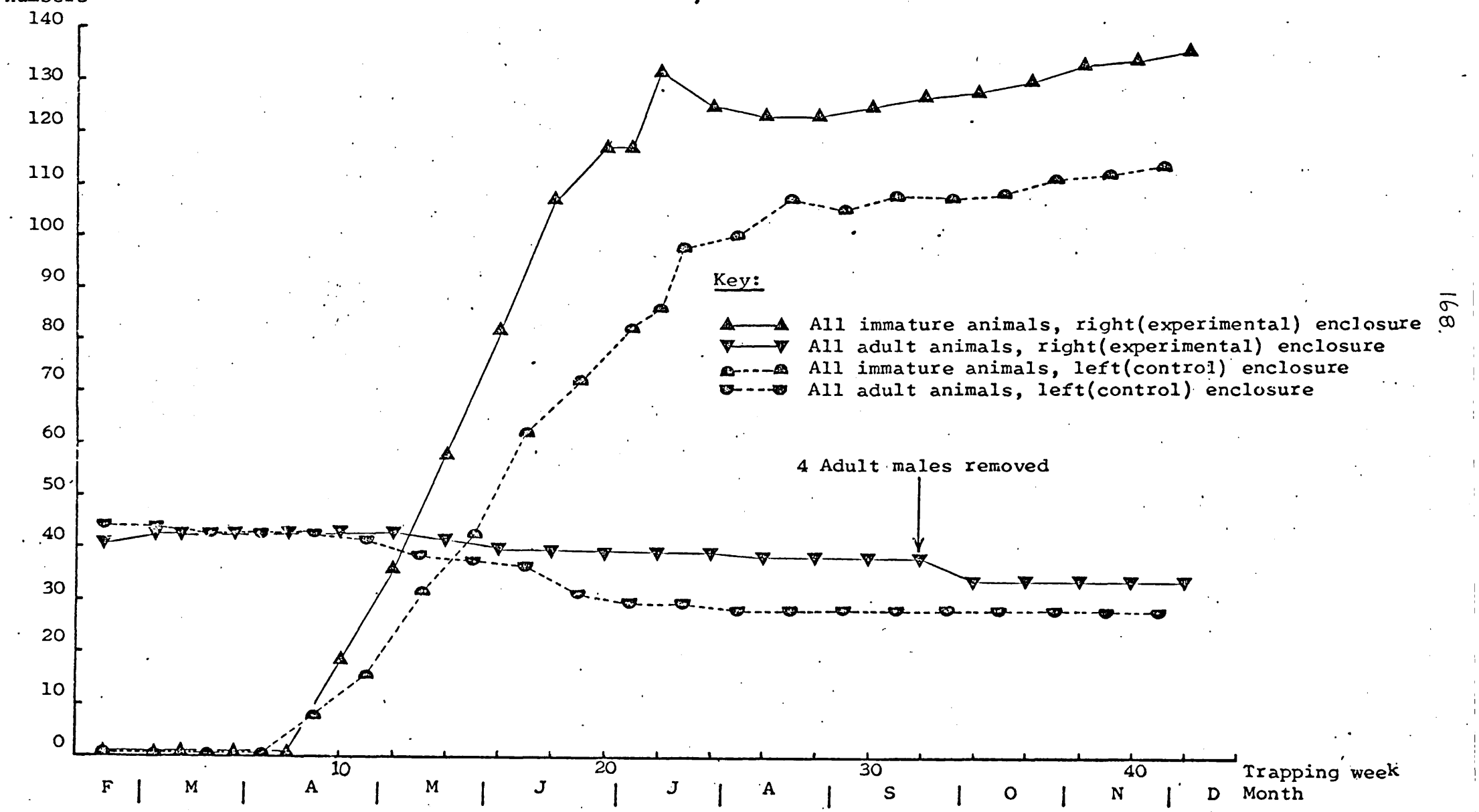


Fig. 4.3.4.(ii) The total estimated numbers of trappable adult and immature animals in each enclosure during experiment ENCL 4. (See text for full details).



left enclosure than the right, and this also contributed to the observed difference in absolute numbers.

Figure 4.3.4(iii) shows the numbers of adults and immatures of each sex in each enclosure between February and December, 1976, and again it can be seen that the rate of increase of numbers of both immature males and females in the right, experimental enclosure, was higher than the rate of increase of either immature males or females in the left, control enclosure. The differences in final numbers between immature animals of each sex have no obvious explanation.

Results concerning recruitment to and losses from the populations are presented in section 4.3.4(b) below.

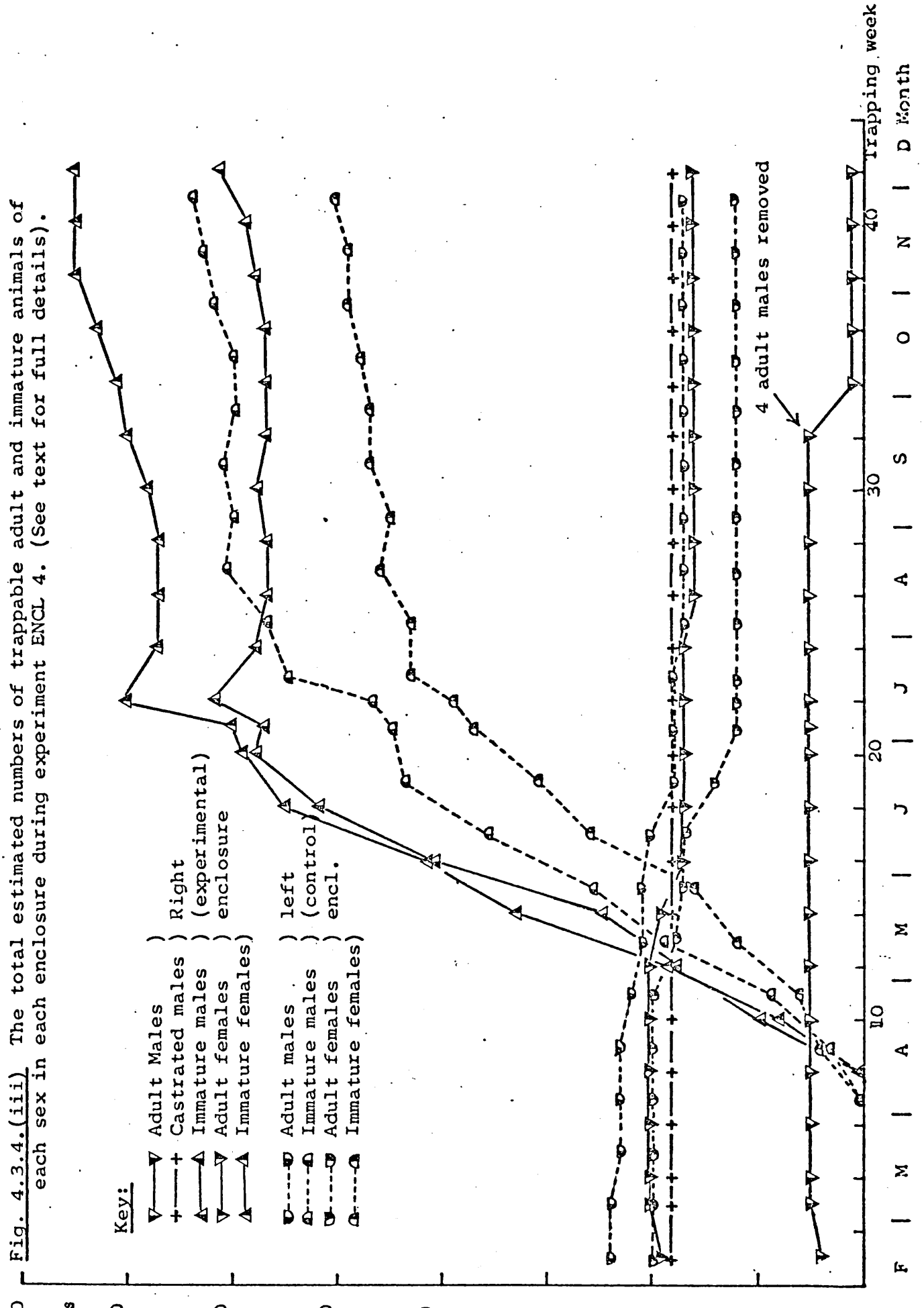


Fig. 4.3.4.(iii) The total estimated numbers of trappable adult and immature animals of each sex in each enclosure during experiment ENCL 4. (See text for full details).

4.3.4(b)(i). Breeding condition of animals in the enclosures.

Figure 4.3.4(iv) shows the proportion of females caught at each trapping occasion in different age classes in breeding condition as defined in section 4.2.4(b). It can be seen that in both enclosures, the proportion of adult introduced females in breeding condition started to markedly decline well before the end of the normal bank vole breeding season. At Oakfield (where part of the field study of behaviour was being carried out), all females over 15g, and many less than 15g, were still in breeding condition at the time of the marked decline within the enclosures, and the usual seasonal decline in the proportion of females found in breeding condition did not start until around September/October. (T.D.Healing, personal communication).

Figure 4.3.4(iv) also shows the proportions of females born in the two enclosures with perforate vaginas (none of the females born in either enclosure became pregnant). It can be seen that in both enclosures the numbers were extremely low.

Figure 4.3.4(v) shows the breeding condition of the males in each enclosure. It can be seen that the proportion of adult males in breeding condition in the left enclosure declined steadily after the end of July; this was roughly two months later than the start of the decline in breeding in the females, and, as in the case of the females, earlier than the decline in the Oakfield population (T.D.Healing, personal communication). This difference between males and females in the enclosures may, however, be artificial; assessment of breeding conditions in the males was of necessity arbitrary and subjective (see methods section, 4.2.4(b) above). Although this assessment, along with body weight and general size, enabled animals to be classed in pre- or post-pubertal, it was almost certainly not sensitive enough to accurately detect cessation of breeding in animals with regressing gonads, since the exact point at which such an animal becomes reproductively incapable is not known. Fig. 4.3.4(v) does show however, that a marked decline occurred in the proportion of adult males with medium or large testes; in many of the animals in the latter part of experiment ENCL 4 (September 1976 onwards) the testes were abdominal, and too small

Fig. 4.3.4.(iv) The proportion of females in breeding condition in experiment ENCL 4. (see text for details)
(Proportion in breeding condition = Number in breeding condition / Number caught at each trapping occasion)

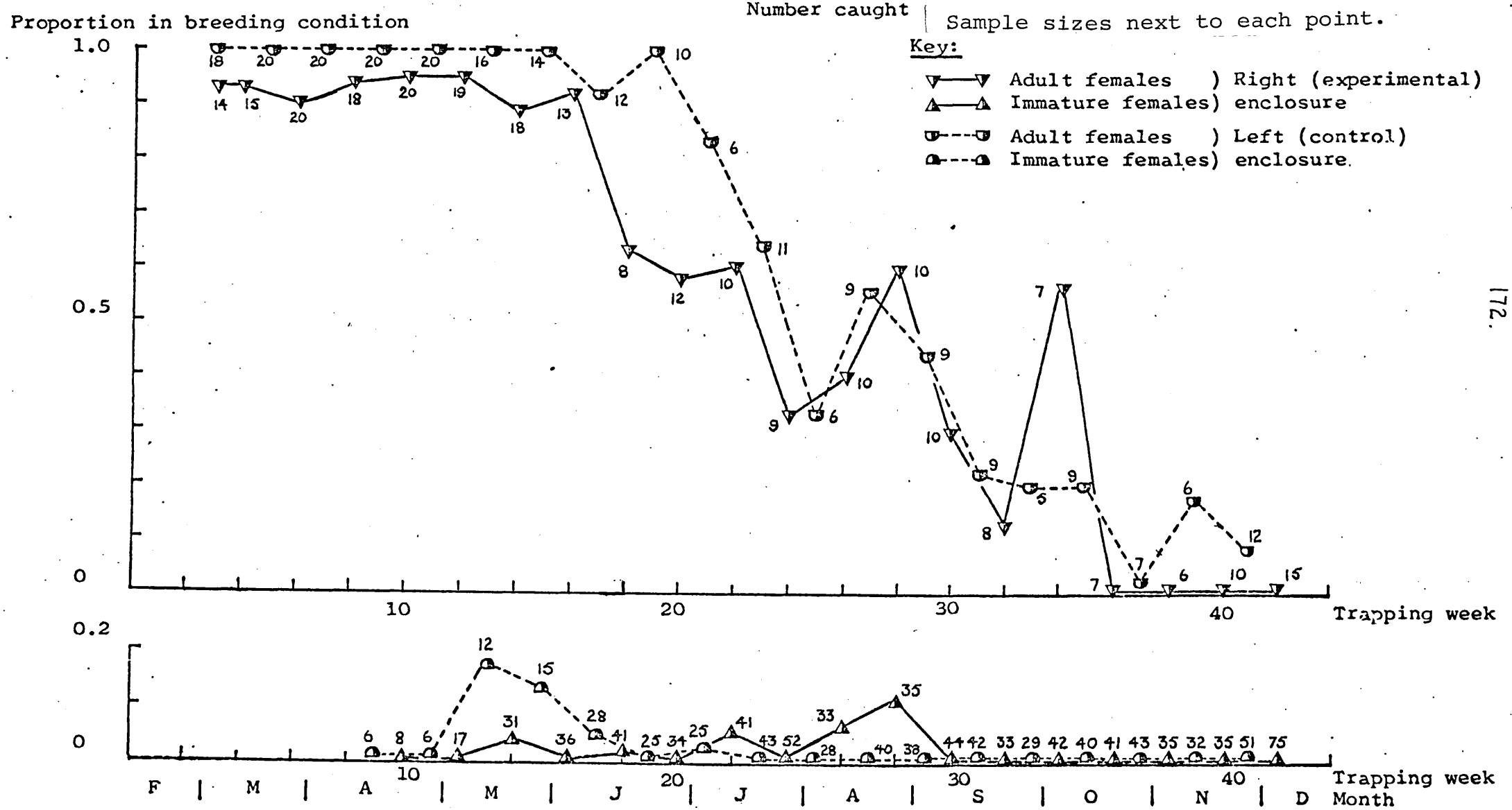
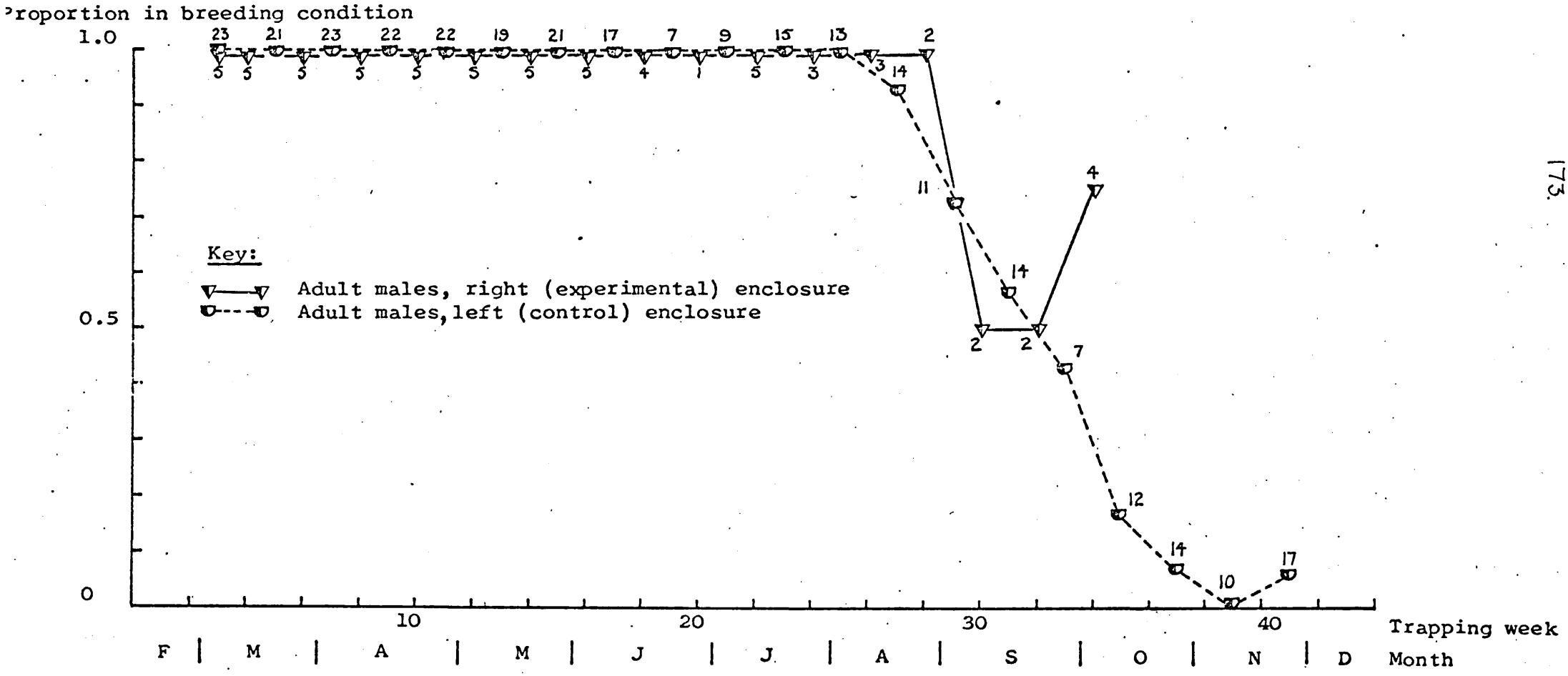


Fig. 4.3.4.(v) The proportion of males in breeding condition in Experiment ENCL 4 (see text for full details) (Proportion in breeding condition = Number in breeding condition / Number caught at a particular trapping occasion). Sample sizes next to each point.



to be detected at all by palpation of the lower ventral abdomen.

Figure 4.3.4(v) also shows the proportion of adult males in the right enclosure, (containing initially five adult intact males, [illegible] castrated males and 20 females) which were in breeding condition; this is really only included for completeness, since the numbers caught were always very small. No males born during experiment ENCL 4 in either enclosure was assessed as having medium sized testes, and so it is concluded that none came into breeding condition.

Gross examination of the gonads of animals removed from the enclosures at the end of experiment 4 corroborated the field evidence presented in figs. 4.3.4(iv) and (v) ; all females born in either enclosure had thread-like uteri, all males born in either enclosure had very small testes (none greater than approximately 3-4mm in length). All the adult females which had been introduced into the enclosures in February 1976, and which were removed in November-December 1976, also had thread-like uteri. Adult males removed from the left enclosure all had very small, regressed testes, and none of the castrated males removed from the right enclosure showed any evidence of testis-regeneration. It must however be remembered that these examinations were done in December 1976 and January 1977 (after some of the animals had been used for behaviour testing, see Chapter 2), and also after the end of the normal breeding season of the bank vole; it was therefore to be expected that the gonads of all the animals would have tended to regress into the non-breeding condition.

4.3.4(b)(ii). Births.

From the calendar of captures of animals, using the criteria for detecting pregnancy described in Section 4.2.4(b) above, it was possible to estimate the total number of pregnancies in each enclosure. A total of 57 pregnancies were detected amongst the 20 females originally introduced into the left enclosure (in which all the males were intact), and 46 pregnancies amongst the 20 females originally introduced into the right enclosure (in which 18 of the 23 males were castrated). The mean number of pregnancies/female was 2.85 ± 1.35 for the females introduced into the left enclosure, and 2.30 ± 1.63 for the females introduced into the right enclosure. This difference is not significant (t_{42} = 1.11, $p>0.10$). No pregnancies were detected in any of the females born in either of the enclosures.

Thirteen freshly born litters were found in nest boxes or in traps in the two enclosures during experiment ENCL 4, eight in the left enclosure, five in the right. A further eleven females, caught in the wild at around the same time, subsequently gave birth in the laboratory. The mean litter sizes of these females are summarised in Table 4.3.4(i).

Table 4.3.4(i).

	Litter size mean	SD	Sample size
(a) Experiment ENCL 4			
(i) Left enclosure (control)	3.25	1.28	8
(ii) Right enclosure (experimental)	3.80	2.17	5
(b) Field caught females	3.45	0.93	11
(a)(i), (a)(ii) and (b) combined	3.46	1.32	24

The differences in mean litter size between the two enclosures, and between them and the field caught animals, are not significant.

4.3.4(b)(iii). Recruitment into the trappable population.

Figure 4.3.4(vi) shows,

(a) The numbers of animals caught for the first time at each trapping session in each enclosure.

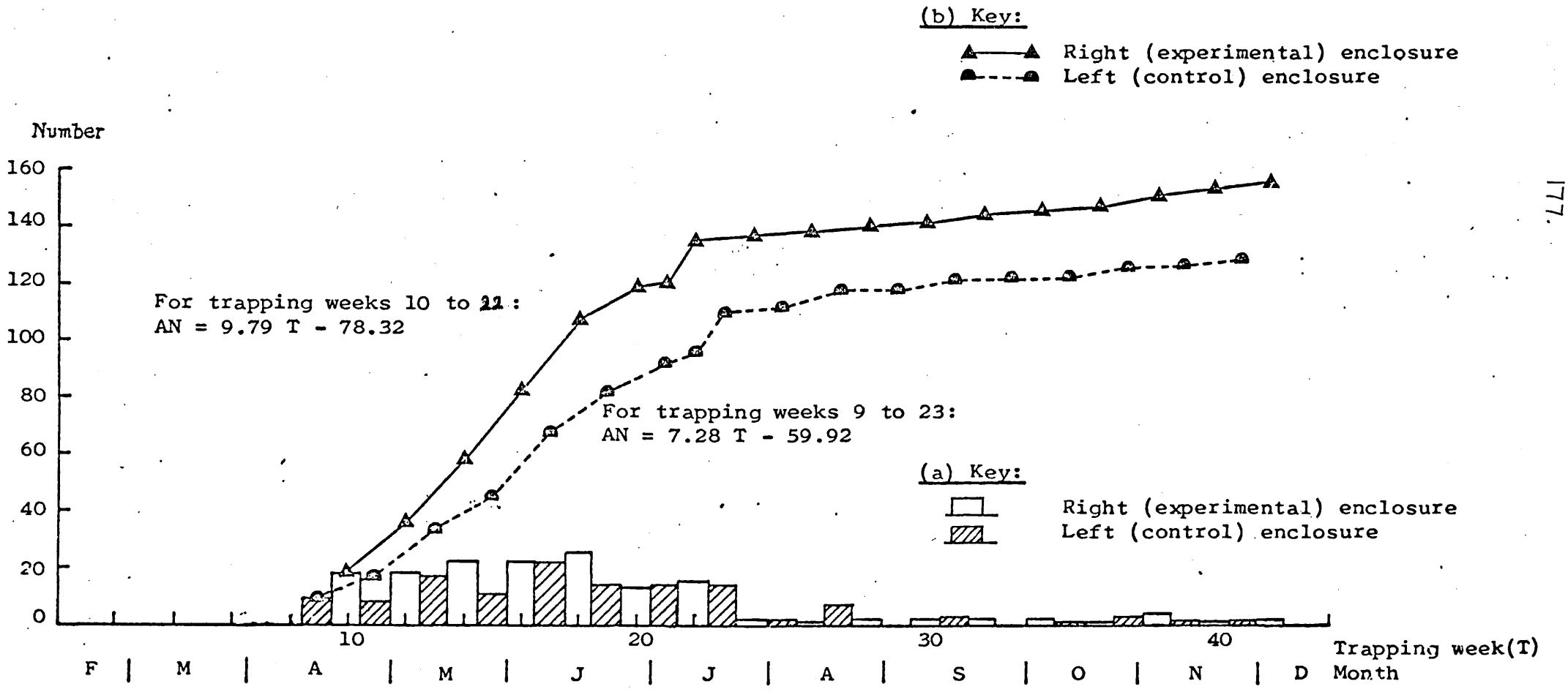
(b) The accumulated numbers of animals caught for the first time at each trapping session in each enclosure.

The numbers do not necessarily represent the numbers of animals born into the populations, since the Longworth traps used cannot catch animals weighing less than around 7-8g (the mean weight of animals at first capture in both enclosures combined was 13.78g $\pm$ 2.56, see 4.3.4(f) below); results concerning mortality of the pre-trappable population is presented in section 4.3.4(b)(iv) and discussed in 4.4. below.

The figure shows that the accumulated total number of recruits into the trappable population in the right enclosure was greater than the accumulated total in the left; these accumulated totals represent the numbers of enclosure-born animals that would be present in each enclosure at any one time if no mortality of this group had occurred (see 4.3.4(b)(iv) below for details of mortality of the trappable population). Thus the slopes of the initial parts of each curve represent the overall potential rates of increase in numbers of enclosure-born, trappable animals in each enclosure. The formulae for the regression lines of AN (accumulated numbers) on T (Trapping week) for the two graphs of accumulated numbers caught for the first time against trapping week between trapping weeks 9 and 23 inclusive are given in Fig.4.3.4(vi). The slopes are significantly different, ($F = 24.73$, $df = 1,13$, $p<0.001$). In other words, significantly more young enclosure-born animals entered the trappable population in the experimental enclosure than entered the trappable population in the control enclosure.

Figure 4.3.4(vii) shows the accumulated number of new animals entering the trappable population at each trapping session, with each sex in each enclosure considered separately. It can be seen that the slopes of the lines for both sexes in the experimental enclosure are steeper than both the lines for both sexes in the control enclosure; the differences between the sexes has no obvious

Fig. 4.3.4.(vi) (a) Numbers of new animals entering the trappable population at each trapping session.
(b) Accumulated numbers (AN) of new animals that had entered the trappable populations at each trapping session.
(See text for full details).



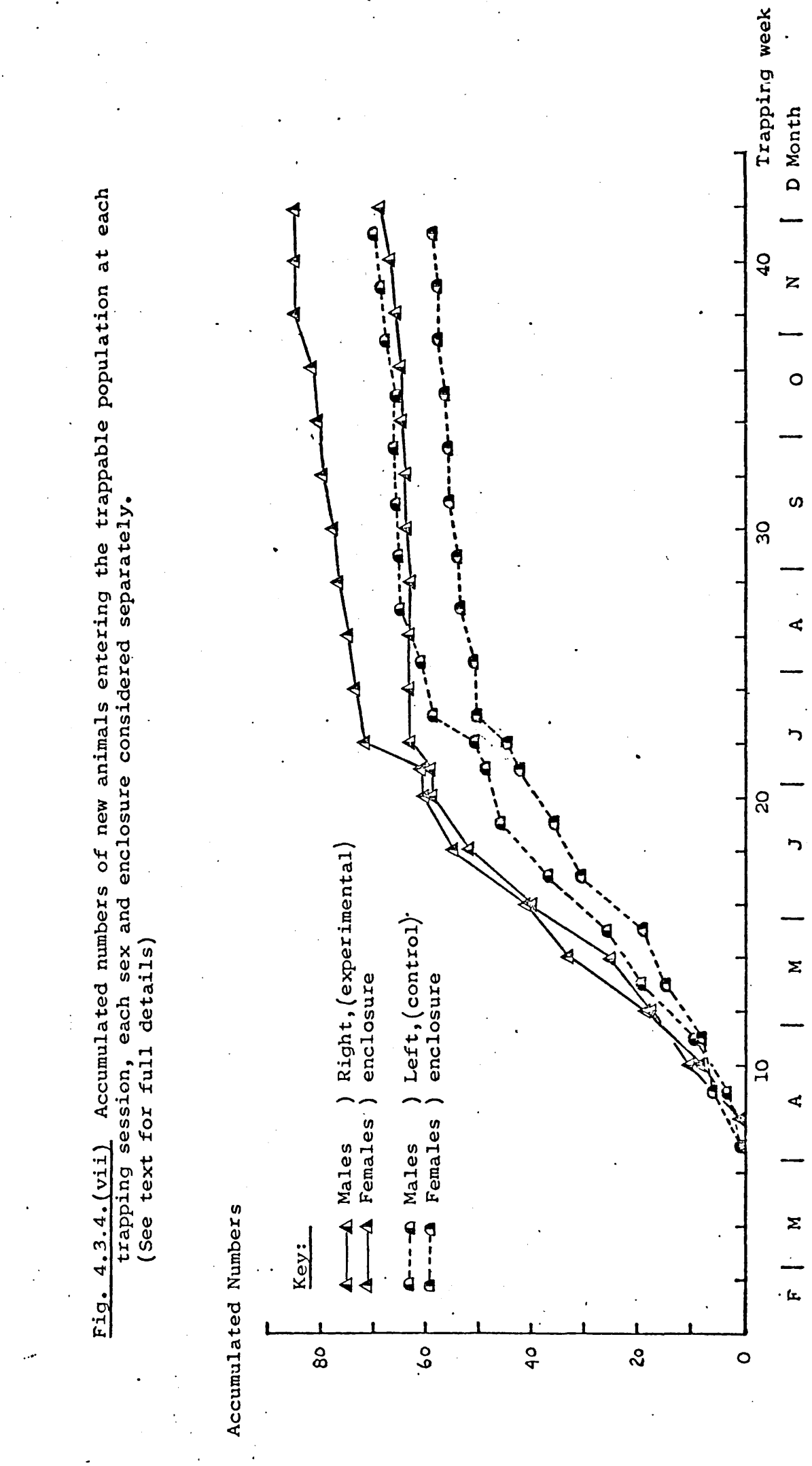


Fig. 4.3.4.(vii) Accumulated numbers of new animals entering the trappable population at each trapping session, each sex and enclosure considered separately.
(See text for full details)

explanation.

4.3.4(b)(iv). Losses.

Losses of toe-clipped animals.

Table 4.3.4(ii) summarises all losses of toe-clipped animals from the populations in the enclosures during experiment ENCL 4. It can be seen that there were more trap deaths than should have been acceptable; the study was carried out during the summer of 1976, when very hot weather and drought lasted several months. Although the trap round was always done early in the morning at this time, before the ambient temperature rose, and although the traps were always protected from direct sunlight, most of the trap deaths were presumably due to the animals becoming overheated in the traps.

Disappearance of toe-clipped animals, excluding trap deaths, is shown in Fig.4.3.4(viii). Animals were scored as having disappeared at the trapping session following the one at which they were caught for the last time, and it was assumed that this was as a result of the death of the animal. It can be seen that the mortality of marked animals in both enclosures was slight, and the difference between the total numbers that disappeared from each enclosure, compared in a 2 x 2 contingency table of the total numbers lost or not lost in each enclosure, is not significant ($\chi^2 = 1.02$, df = 1, $p > 0.10$). There are also no significant differences in the numbers of different sex and age classes that disappeared either within or between enclosures.

Losses of tail-clipped infants.

Neonatal animals, found in nest boxes or traps, had their tail tips clipped, since toe clipping was not possible in newly-born animals. (see 4.2.5(c) above). In Section 4.3.4(b)(ii) above, it was noted that eight newly born litters, consisting of 26 infants, were found either in traps or nest boxes in the left (control) enclosure,

Table 4.3.4(ii). Number of animals lost from the trappable population at each trapping session.

	Trapping week	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Totals	
	(month)	F		M					A				M				J					J				A				S					O					N			
Left enclosure	A ♂♂ trap deaths			1								1						2																								4	7
	A ♂♂ last time seen											1				1								1																		3	
	I ♂♂ trap deaths																	1																1								2	6
	I ♂♂ last time seen																			1		2								1												4	
	A ♀♀ trap deaths											2						2		1																						5	8
	A ♀♀ last time seen													1				1		1																						3	
	I ♀♀ trap deaths									1				1				1				1																				4	9
	I ♀♀ last time seen									1								1						2						1												5	
	All trap deaths			1						1		3		1				6		1		1												1								15	30
	All last time seen									1		1		1		1		2		2		2		3						2												15	
	Combined total lost			1		.				2		4		2		1		8		3		3		3						2				1									
Right enclosure	A ♂♂ trap deaths																																								0	0
	A ♂♂ last time seen																																								0	
	C ♂♂ trap deaths																																								0	0
	C ♂♂ last time seen																																								0	
	I ♂♂ trap deaths																					1			1										1							3	8
	I ♂♂ last time seen																				1				2	1							1								5	
	A ♀♀ trap deaths																										1														1	4
	A ♀♀ last time seen														1		2																								3	
	I ♀♀ trap deaths																				1				4	1															6	10
	I ♀♀ last time seen																								1			2											1			4	
	All trap deaths																				1	1			5	2									1						10	22
	All last time seen														1		2				1				3	1		2					1					1			12	
	Combined total lost														1		2				2	1			8	3		2					1		1			1			22	

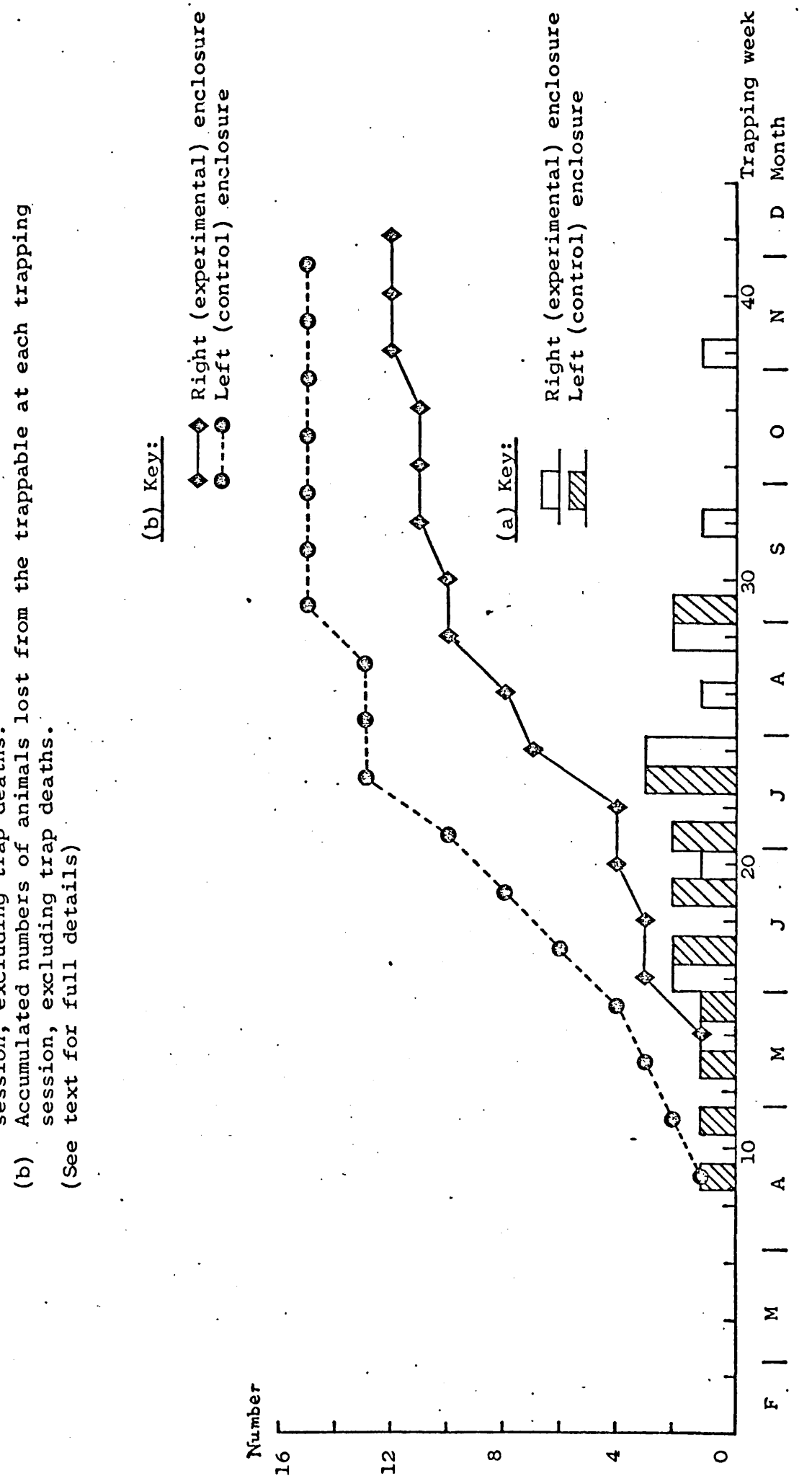


Fig. 4.3.4.(viii) (a) Numbers of animals lost from the trappable population at each trapping session, excluding trap deaths.
(b) Accumulated numbers of animals lost from the trappable at each trapping session, excluding trap deaths.
(See text for full details)

and five litters, consisting of 19 infants, were found in the right (experimental) enclosure. Of the litters found in the left enclosure, one litter of four was found dead, and another litter of two did not have their tail tips clipped. Thus, in the left enclosure, 20 neonatal voles had their tail tips clipped and were released alive; of these, 10 were subsequently recaptured as immatures in traps. In the right enclosure, 19 infants were tail clipped, and all were released alive; of these, all 19 were subsequently recaptured in traps. This result is summarised in Table 4.3.4(iii). The survival of tail clipped juvenile voles in the right, experimental, enclosure was significantly greater than the survival of tail-clipped juveniles in the left, control, enclosure ($\chi^2 = 12.9$, df = 1, $p < 0.001$).

Table 4.3.4(iii). Losses of infant voles, experiment ENCL 4.

	Left enclosure (control)	Right enclosure (experimental)
No. of neonates which had had their tail tips clipped.	20	19
No. of juveniles caught in traps with tail tips missing	10	19
No. of neonates which had had their tail tips clipped which were not subsequently caught in traps	10	0

$\chi^2 = 12.9$
df = 1
$p < 0.001$

Table 4.3.4(iv) summarises the demographic results obtained from experiment ENCL 4.

Table 4.3.4(iv). Summary of demographic results obtained from experiment ENCL 4.

		Left enclosure (control)	Right enclosure (experimental)
Animals introduced into the enclosures	Ad ♂♂	24	5
	C ♂♂	0	18
	Ad ♀♀	20	20
Number of pregnancies detected		57	46
Total number of recruits into the trappable population	♂♂	70	69
	♀♀	59	85
		129	154
Recruits/pregnancy		2.26	3.35
Losses (including trap deaths) from trappable population	Ad ♂♂	7	0
	C ♂♂	-	0
	I ♂♂	6	8
	A ♀♀	8	4
	I ♀♀	9	10
Number of infants tail clipped		20	19
Number subsequently live-trapped		10	19
Therefore, number lost as infants/ juveniles		10	0

4.3.4(c). Wounding.

Figure 4.3.4(ix) shows the proportion of males of different age classes caught at each trapping session showing fresh wounds. Fig. 4.3.4(x) shows the same for females. It can be seen that a much larger proportion of adult males from both enclosures showed fresh wounds than did castrated or immature males, and adult and immature females. Immatures of both sexes showed very low levels of fresh wounding, as did adult females. Most importantly, castrated males in the experimental enclosure also showed very low levels of wounding, when compared with adults in their own enclosure or with the adults in the control enclosure.

4.3.4(d). Distances between captures.

Table 4.3.4(v) shows the results of Mann-Whitney test (Siegel, 1956) comparisons between measured distances between successive captures for each sex and age class in each enclosure. The distances between all captures for each individual have been combined with the distances between all captures for all other members of the same class. Within each enclosure, comparisons have been made between each age and sex class and each other class. Between enclosures, like has been compared with like, except that, in addition, the castrates from the right enclosure have been compared with adults from the left. Comparisons within the right enclosure are in the top left-hand quadrant of Table 4.3.4(v), those within the left enclosure are in the bottom right-hand quadrant of the table. Comparisons between enclosures are in the top right- and bottom left-hand quadrants. The results given in Table 4.3.4(v) are summarised in fig. 4.3.4(xi).

Within the right enclosure, it can be seen from Fig.4.3.4(xi)(a) that adult females tended to be caught significantly closer to their previous capture than all other classes, and successive captures of castrated males were significantly closer than those of both adult and immature males, but not significantly different to females. All

Fig. 4.3.4.(ix) Proportion of males of different age classes caught at each trapping session showing fresh wounds. Sample sizes next to each point.
(Proportion wounded = $\frac{\text{Number wounded}}{\text{Number caught}}$ at each trapping session)
(See text for full details)

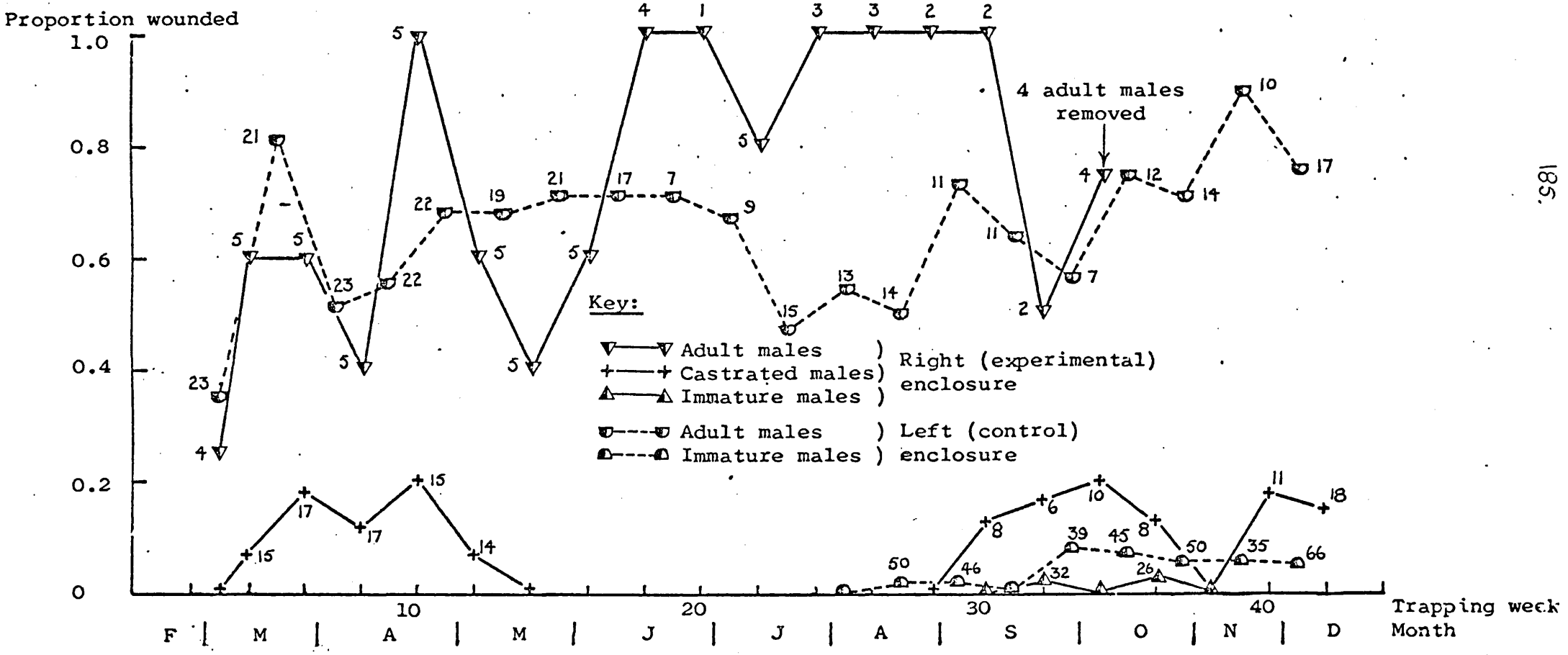


Fig. 4.3.4.(x) Proportion of females of different age classes caught at each trapping session showing fresh wounds. Sample sizes next to each point.
(See text for full details). (Proportion wounded = $\frac{\text{Number wounded}}{\text{Number caught}}$ at each trapping session)

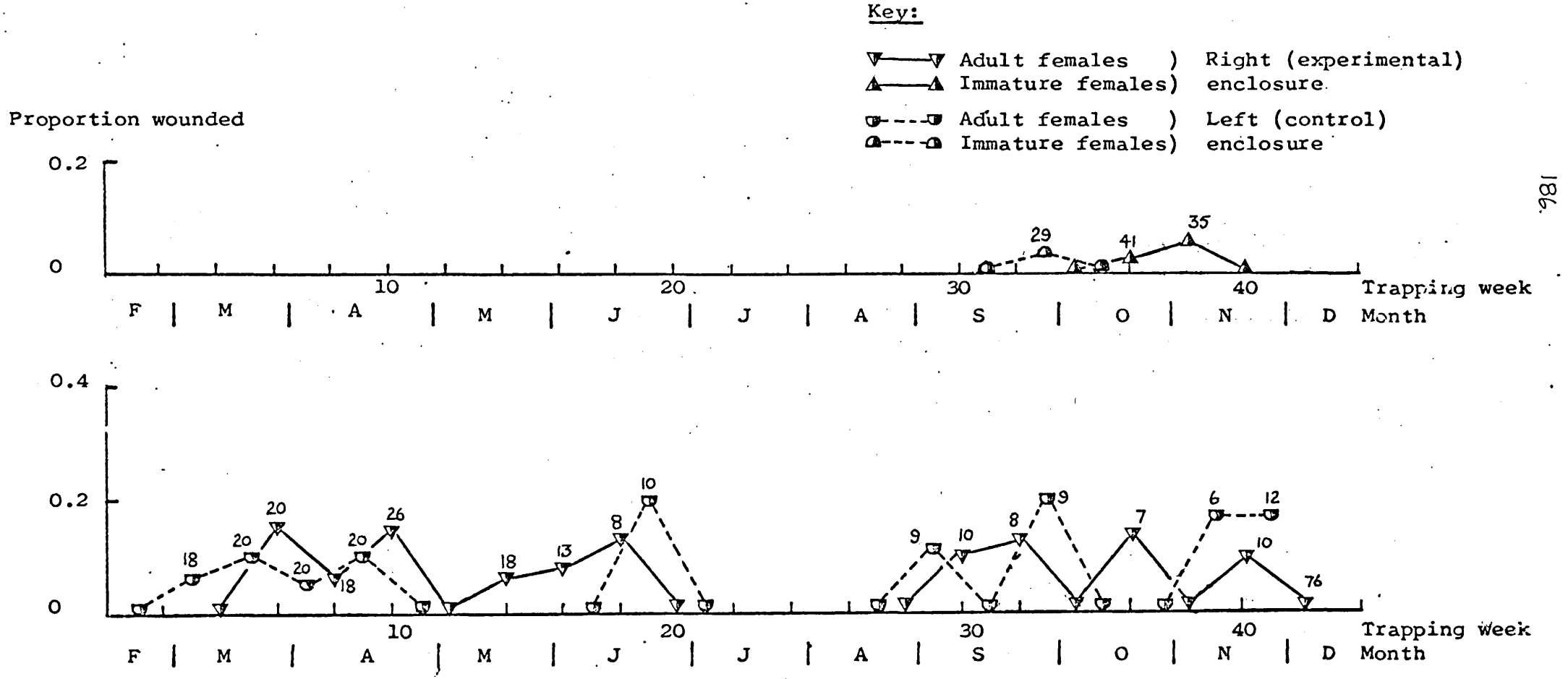


Table 4.3.4(v). Values of U of the Mann-Whitney test and probability p associated with differences in the distances between captures of adult, castrated, and immature males, and adult and immature females during experiment ENCL 4.

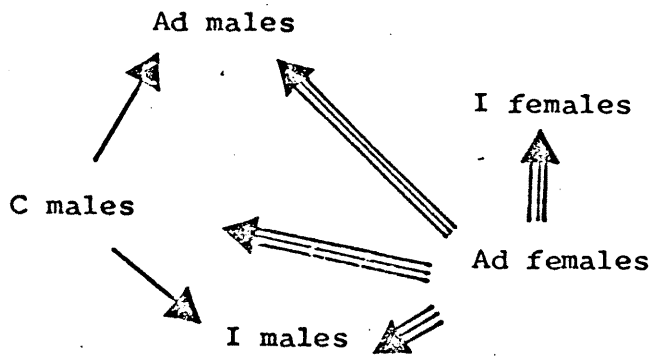
	RIGHT ENCLOSURE					LEFT ENCLOSURE				
	Ad ♂♂	C ♂♂	I ♂♂	Ad ♀♀	I ♀♀	Ad ♂♂	I ♂♂	Ad ♀♀	I ♀♀	N
RIGHT ENCLOSURE. Ad ♂♂		8654·5 3 (←)	19317·0 n.s.	9455·5 1 (←)	20695·0 n.s.	18501·0 2 (←)				89
C ♂♂	8654·5 3 (↑)		46747·0 3 (↑)	29958·0 1 (←)	55310·5 n.s.	56300·0 n.s.				227
I ♂♂	19317·0 n.s.	46747·0 3 (←)		52516·5 1 (←)	112027·0 n.s.		93163·0 1 (←)			456
Ad ♀♀	9455·5 1 (↑)	29958·0 1 (↑)	52516·5 1 (↑)		643880 1 (↑)			644045 n.s.		323
I ♀♀	20695·0 n.s.	51310·5 n.s.	112027·0 n.s.	64388·0 1 (↑)					104548·0 1 (←)	514
LEFT ENCLOSURE. Ad ♂♂	18501·0 2 (↑)	56300·0 n.s.					119087·5 n.s.	82839·0 1 (←)	110648·5 1 (←)	511
I ♂♂			93163·0 1 (↑)			119087·5 n.s.		86121·0 1 (←)	112642·0 3 (←)	491
Ad ♀♀				64404·5 n.s.		82839·0 1 (↑)	86121·0 1 (↑)		92468·5 2 (↑)	416
I ♀♀					1045480 1 (↑)	110648·5 1 (↑)	112642·0 3 (↑)	92468·5 2 (←)		494

Key:-

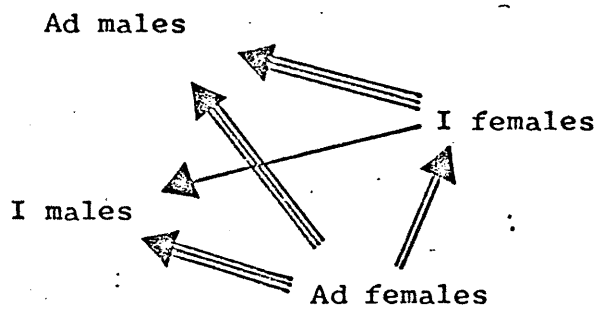
1. N = number of movements used for the analysis.
2. Significant levels shown as follows:- $p<0.001 = 1$, $p<0.01 = 2$, $p<0.05 = 3$.
3. The arrow in the bracket (←) or (↑) points to the group with the higher values.
4. Ad = Adult.
   C = Castrate.
   I = Immature.

Fig. 4.3.4.(xi) Summary of table 4.3.4.(v)

(a) Comparisons within right (experimental) enclosure



(b) Comparisons within left (control) enclosure



(c) Comparisons between enclosures

Left enclosure.		Right enclosure.
Adult males	⟹	Adult males
Castrated males	n.s.	Adult males
Immature males	⟹	Immature males
Adult females	n.s.	Adult females
Immature females	⟹	Immature females

Key:

1. Ad = Adult, C = Castrate, I = Immature
2. Significance levels shown as follows:-
   $p < 0.001$ = ⇗, $p < 0.01$ = ⇗, $p < 0.005$ = ↗
3. The arrow points towards the group with higher values

other comparisons were non-significant. Within the left enclosure, successive captures of females were closer than those of males, and, as in the right enclosure, adult females tended to be caught much closer to their previous capture than all other classes.

Comparisons between the enclosures show that the distances between captures of the castrated males in the right enclosure were not significantly different to the distances between captures of the adults in the left enclosure. However, adult males, immature males and immature females all were caught significantly further apart between captures in the right, experimental enclosure than they were in the left, control enclosure.

4.3.4(e). Home range areas.

Figures 4.3.4(xii) - 4.3.4(xv) show means and standard deviations of accumulated trap-revealed home range areas for each age and sex class, in each enclosure, for captures one to twelve. Only those animals caught twelve or more times are included.

It can be seen from all four figures that the means of home ranges of animals from the right, experimental enclosure, increased consistently faster with number of times caught than did the means of home ranges of animals from the left, control enclosure.

In the case of the comparison between adult males from the control enclosure and castrated males from the experimental enclosure, (fig.4.3.4(xii)) the difference is significant at the 5% level (Mann-Whitney test) at twelve captures; the differences between the means of the home ranges of immature males from each enclosure (fig.4.3.4(xiii))is significant after eleven and twelve captures. Although the means of the home ranges of adult females from the right enclosure are higher than the means of the home ranges of adult females from the left enclosure from four to twelve captures, (fig.4.3.4(xiv))none are significantly different.

Finally, comparison of the means of the home range of

Fig. 4.3.4.(xii) Means and standard deviations of accumulated home range areas against number of captures (adult and castrated males). (see text for full details).

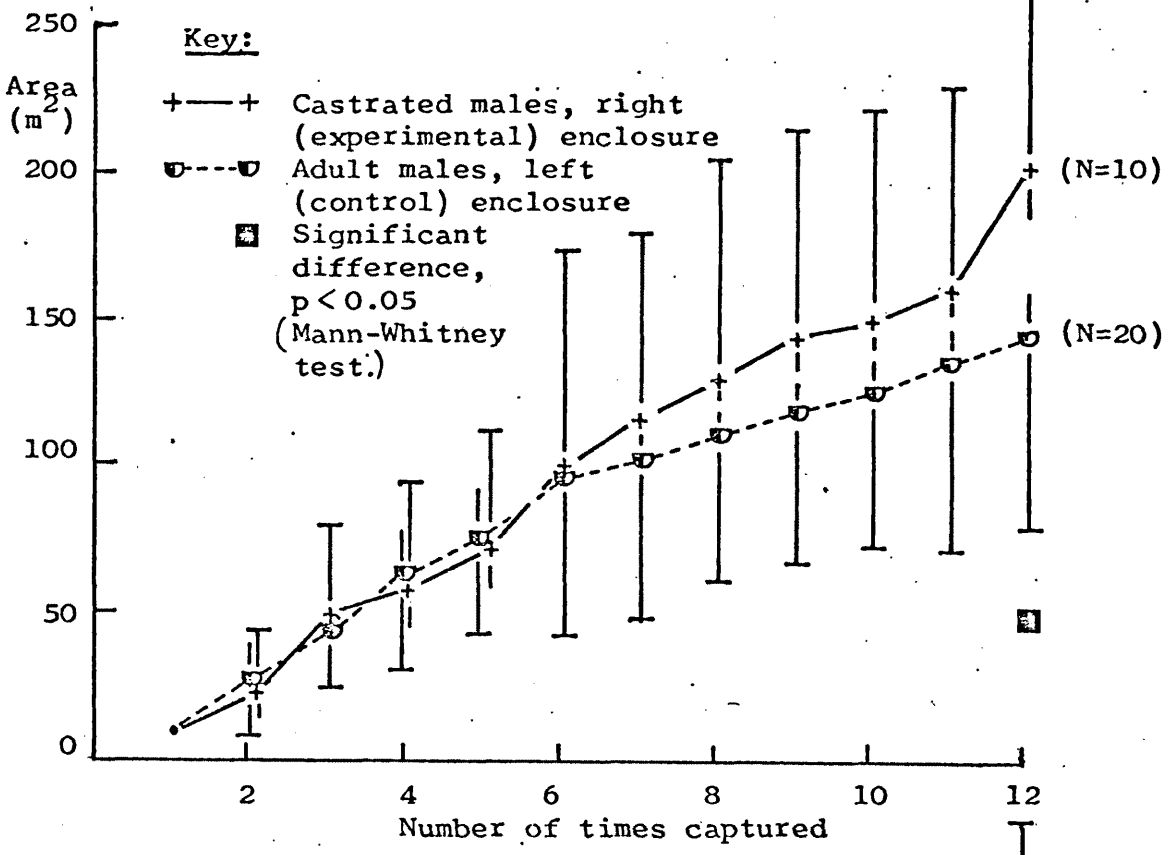


Fig. 4.3.4.(xiii) Means and standard deviations of accumulated home range areas against number of captures (immature males). (See text for full details)

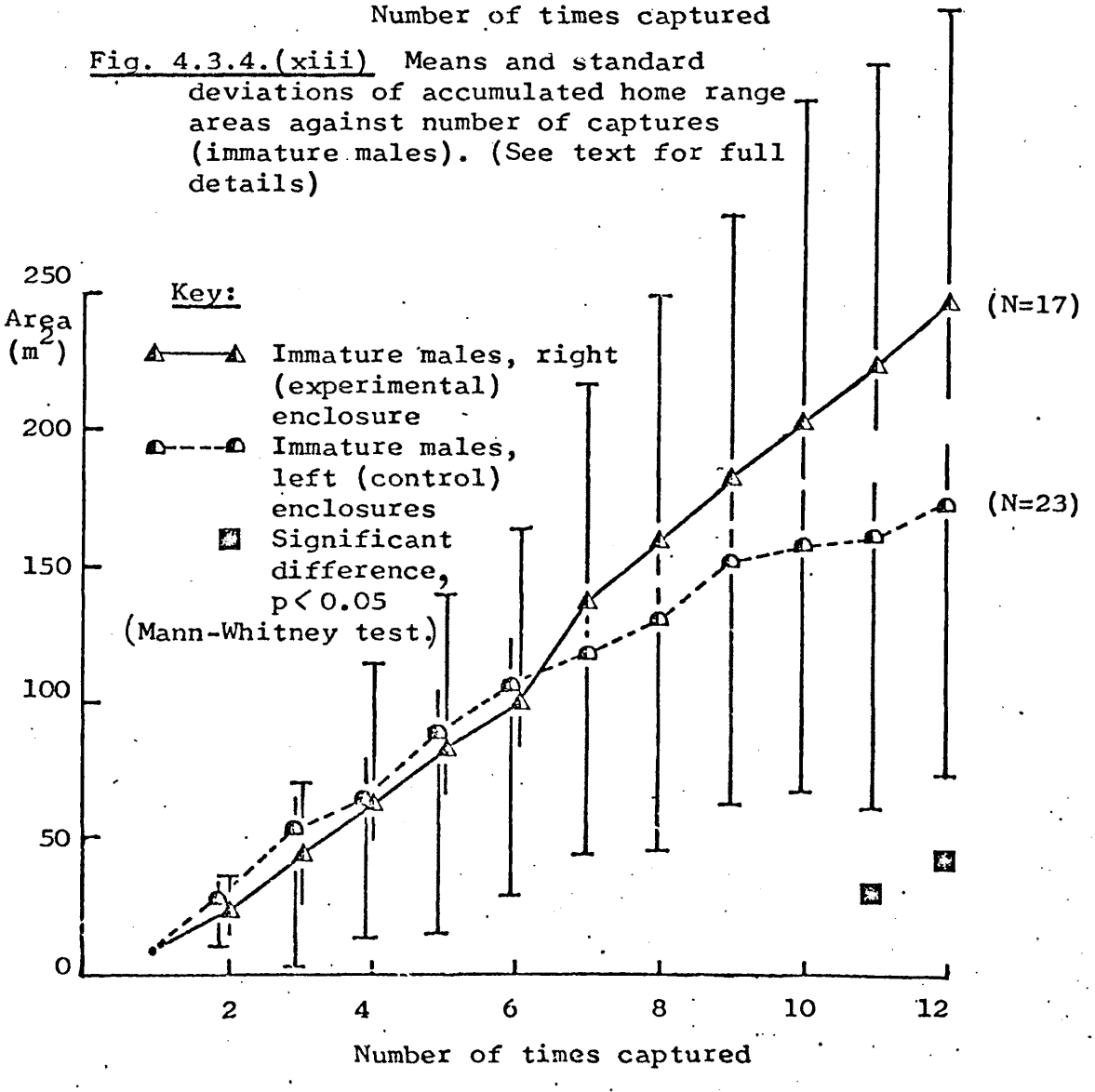


Fig. 4.3.4. (xiv) Means and standard deviations of accumulated home range areas against number of captures (adult females). (See text for full details).

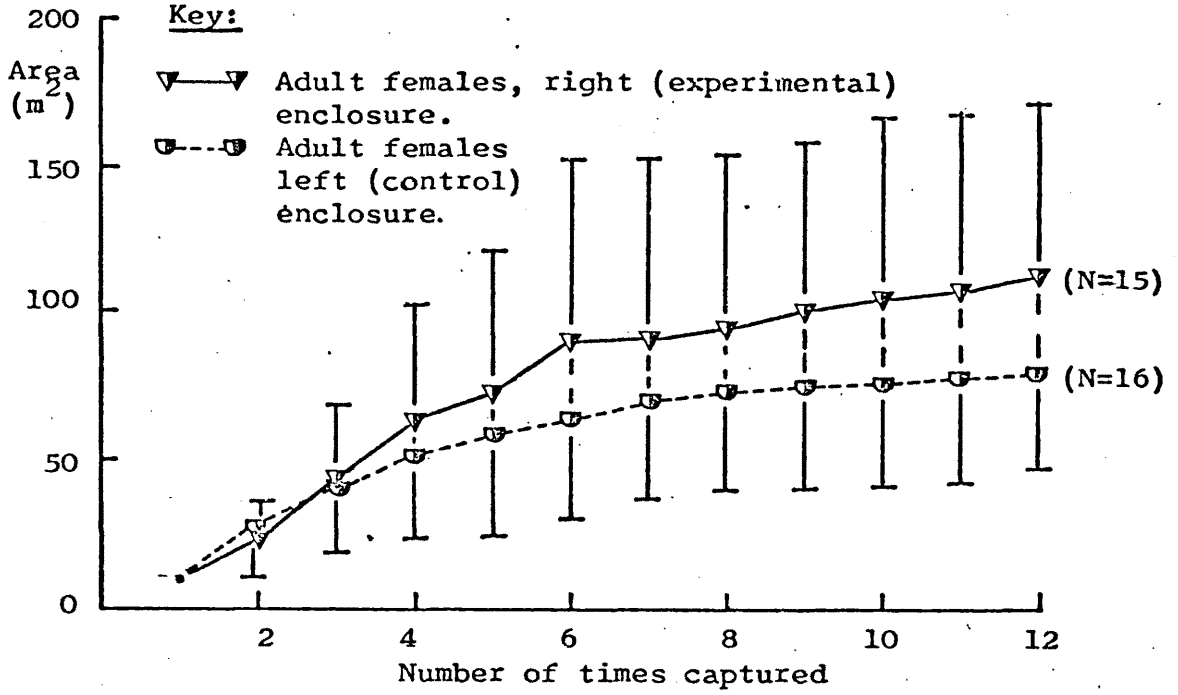
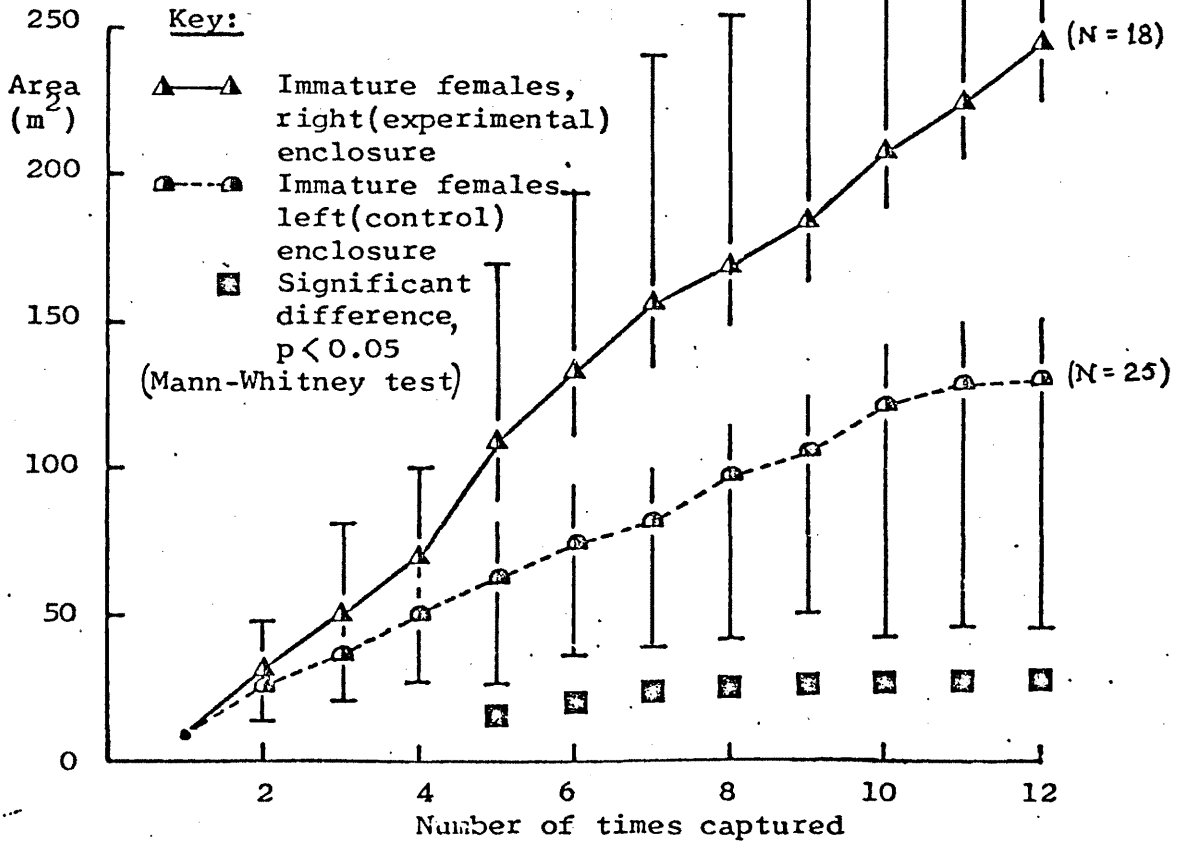


Fig. 4.3.4.(xv) Means and standard deviations of accumulated home range areas against number of captures (immature females). (See text for full details).



immature females in each enclosure (fig. 4.3.4(xv)) shows that the differences are significant at the 5% level from captures five to twelve.

4.3.4(f). Body weights at first capture.

In order to test Watts' (1970) suggestion (discussed in the introduction to this chapter, section 4.1) that the behaviour of dominant adult males had inhibited the age of first capture of young on his control areas, and thereby had presented a false picture of total numbers present, the mean body weights at first capture of immature males and females from both enclosures were calculated. The results are shown in table 4.3.4(vi). The assumption that has had to be made is that weight is positively correlated with age; this is true for the first four months of life of bank voles (Zejda, 1964).

Table 4.3.4(vi). Body weight at first capture of immature males and females.

	Mean weight (g)	S.D.	N
LEFT ENCLOSURE			
MALES	13.61	2.45	48
FEMALES	13.77	2.47	41
RIGHT ENCLOSURE			
MALES	13.73	2.77	52
FEMALES	13.95	2.51	64

All the differences shown in table 4.3.4(vi), both within and between enclosures, are non-significant; therefore, the suggestion that the adults might in some way be affecting the age, and hence weight, at first capture is rejected in the present study.

4.4. DISCUSSION

Experiment ENCL 2 showed that castration had no significant effect on the survival of individuals under field conditions in the enclosures, when other age and sex classes were absent.

Experiment ENCL 4 was the only experimental introduction into the enclosures that produced any useful results upon which the original hypothesis, that male aggressive behaviour was an important factor in the demography of bank voles in field enclosures, could be tested. The results from this experiment have been presented in six sections, (4.3.4(a) - (f)) and each will be discussed in turn.

4.4.(a). Estimated absolute numbers of voles in each enclosure.

The effect of thwarting emigration by enclosing vole populations, described in Chapter 1 and in the introduction to this chapter, was clearly observed in the present study. The maximum numbers reached in the enclosures were 172 in the experimental enclosure, and 142 in the control enclosure. These represented, respectively, densities of 3127 and 2582 voles/ha. As far as I know, the highest estimated density in the literature of a field population is that of Newson (1963) whose maximum was 247/ha; commonly, field densities of bank voles range up to around 100/ha (French et al, 1975, give several estimates in their Table 4.2). Observed densities in the present study were of the order of 25-30 x normal density estimates, and 10 times the maximum estimate; other studies of enclosed vole (not Clethrionomys) populations have shown similar enclosed/ unenclosed density ratios of between 10: and 100:1 (Clarke, 1955; Van Wijngaardan, 1960; Houlihan, 1963; Krebs et al, 1969 amongst others). Thus, the first factor that this study has clearly shown to be important in regulating the numbers of Clethrionomys glareolus is, as expected from previous studies, dispersal. All subsequent discussion concerning the mechanisms by which bank vole numbers

are controlled is therefore necessarily based upon the fact that the populations under study were not natural populations under natural conditions.

Comparisons of densities reached in the enclosures with each other has shown that they were different, and that the reason for this difference was that the rate of increase of numbers in the experimental enclosure was significantly higher than it was in the control enclosure. The weekly rates of increase, in terms of new animals per week, was approximately 9.3 in the experimental enclosure and 5.4 in the control enclosure. These were equivalent to instantaneous rates of weekly increase, assuming geometric population growth, of 0.099 and 0.068 respectively. These values are similar to the rates observed in unenclosed populations of both bank voles and various Microtus species during the increase phase of the population cycle (Krebs and Myers, 1974, p.281 summarise values from many previous studies of unenclosed populations). They are also similar to values of r extracted from several studies of the initial phase of increase following the founding of enclosed vole populations. For instance, the values obtained from Clarke's (1955) Fig.4 are 0.11 and 0.06 respectively for his low and high starting-density populations of Microtus agrestis, those from Van Wijngaarden's (1960) Fig.1 are approximately 0.05 for the three populations that grew, those from Gentry's (1968) Fig. 1 approximately 0.09 for his enclosed population of Microtus pinetorum, and a value of approximately 0.09 is obtained from Fig.4 of Krebs et al (1969) for Microtus pennsylvanicus. Thus it would appear that the rates of increase in numbers commonly observed following the founding of populations in enclosures are similar to the rates observed during the increase phase of the normal Microtine population cycle. Notwithstanding this, the difference between the two enclosures was significant; the question of whether this difference was the result of differences in natality or mortality will be discussed in the next section.

4.4(b). Processes affecting numbers in the enclosures.

The factors that have been shown to be important in regulating the numbers of both mice and voles at high densities in enclosures have been discussed in Chapter 1; the two most frequently observed have been reproductive inhibition, both of adult and immature animals, and neonatal mortality.

Reproductive inhibition was very marked in both enclosures in the present study, so much so that no female born in either enclosure became pregnant, and very few came into breeding condition at all; this inhibition was observed in the animals born in the enclosures throughout the course of the experiment, even those born within the first few weeks. The relative importance of the initial density of the introduced population has not generally been evaluated in studies of enclosed vole populations. The initial population densities in the present study (approximately 700/ha) were already around 3 x denser than the previously reported maximum in field populations of bank voles, and reproductive inhibition of animals born into the enclosures was almost complete. Some authors have found that the first few young voles born into field enclosures have bred, and only later have animals been completely reproductively inhibited (e.g.Clarke (1955) who started with original densities of around 1 x and 6 x the previously recorded maximum for Microtus agrestis). On the other hand, some authors, starting with low initial densities, have found sporadic breeding by all cohorts, even though the overall reproductive rate was very low as a result of general inhibition (e.g.Krebs et al, 1969, who started with initial densities of Microtus ochrogaster much lower than are normally found). This sporadic breeding by all cohorts has also been observed in high density mouse populations in large enclosures (e.g.Lidicker, 1976). It would appear therefore, that the initial population density is important in determining the subsequent course of reproductive inhibition in field enclosures; n ot surprisingly, very high initial densites appear to cause the inhibition to be manifested soonest.

The majority of the adult females introduced into the enclosures also became non-fecund well before the end of the breeding

season. Almost all the adult females bred initially, leading to the initial sharp rise in numbers in both enclosures, and in neither enclosure did breeding amongst adult females cease completely. In previous studies of enclosed vole populations, breeding by different cohorts has not been distinguished, so that comparison with the present study is not possible.

Only in some studies of populations of mice or voles in field enclosures has reproductive inhibition of males been mentioned (e.g.Krebs et al, 1969; Lidicker, 1976); despite the fact that it was felt that objective assessment of the breeding condition of males was not achieved in the present study (see Methods section 4.2.4(b) above), no male born in either enclosure was ever judged to have come into breeding condition, and there was a steady decline in the proportion of the introduced adult males judged to be in breeding condition from the beginning of August onwards. These two facts suggest that the reproduction inhibiting factors operating upon the males closely paralleled those operating on the females, in both enclosures.

All this reproductive inhibition was almost certainly the result of the high levels of aggressive behaviour, as it has been shown to be in previous studies; the fact that there were no apparent differences between the enclosures means that simply rendering relatively non-aggressive the majority of the males in the experimental enclosure was alone not sufficient to prevent it. Whether, in the experimental enclosure, the aggressive behaviour of the five remaining intact males, or the residual aggression of the castrates, or the simple presence of so many animals (aggressive or not), was responsible for the reproductive inhibition observed could not be determined. Removal of four out of the five adult males at the end of 32 weeks was followed,at the following trapping occasion in week 34, by an increase in the proportion of adult females caught with perforate vaginas. However, (see fig.4.3.4(iv))the sample size was very small (four perforate out of seven caught) so no reliance can really be placed on this result.

Apart from reproductive inhibition, other factors that have been implicated in reducing the birth rate in rodent populations have been discussed in Chapter 1. One of these is reduced litter size;

there was no difference in litter size between the two enclosures in the present study, or between them and litters born to field-caught females trapped at the same time. All three estimates were obtained from counts of embryos, and they are, if anything, slightly lower than the previous estimates for litter size in field populations of bank voles also obtained from counting embryos (Brambell and Rowlands (1936): 4.11; Smyth (1963): 3.98; Zejda (1966): 4.90; Ryszkowski and Truszkowski (1970): 4.6, and Flowerdew (1971): 3.98). However, sample sizes in the present study were very small, with high standard deviations, so that they cannot really be relied upon.

As in previous studies, mortality of adult and immature, male and female toe clipped (i.e. trappable) animals was low. The mortality (including trap deaths) of adult females in the control enclosure was however rather higher, though not significantly so, than the mortality of adult females in the experimental enclosure (Table 4.3.4(ii)). Krebs and Myers (1974, p.309) have demonstrated that, in small mammal populations, the rate of population growth is very dependant upon survival rate of reproducing females; it might be thought, therefore, that the observed differences in population growth rate and final numbers observed between the enclosures in the present study were a result of this difference in adult female mortality between the two enclosures. It must be remembered, however, that in spite of this difference in adult female mortality, there were 57 detected pregnancies in the control enclosure, which had the greater number of adult female losses, and 43 pregnancies in the experimental enclosure, where fewer adult females were lost. Therefore, adult female mortality appears not to have been the factor that produced the observed differences between the numbers of animals entering the trappable populations in each enclosure.

The major factor, reviewed in Chapter 1, that has been observed to affect the total numbers of enclosed populations of small mammals has been mortality of neonates, and this clearly occurred in the present study, at least in the control enclosure.

Firstly, the fact that only 10 out of the 20 tail clipped infants in the control enclosure were subsequently trapped, whereas all 19 tail-clipped infants in the experimental enclosure were seen again in traps, showed that the presence of the adult males in the control enclosure had a significant effect on depressing infant survival. This is corroborated by the fact that 57 detected pregnancies in the control enclosure produced 129 recruits to the trappable population (an average of 2.26 recruits/pregnancy) whereas only 45 pregnancies detected in the experimental enclosure produced a total of 154 recruits (an average of 3.35 recruits/pregnancy). However, this difference might have been the result of either foetal resorption or neonatal mortality; the latter certainly occurred in the control enclosure, as has been demonstrated by the loss of tail-clipped infants, but the former cannot be ruled out. However, a mean litter size, calculated from counts of embryos, as low as 2.26 (the average number of recruits/pregnancy in the control enclosure) has not previously be recorded, whereas 3.35 (the average number of recruits/pregnancy in the experimental enclosure) is very close to the mean litter size calculated in the present study, (although rather lower than the previous estimate summarised above). This, therefore, also suggests that it was primarily neonatal mortality, rather than foetal resorption, that caused the lower numbers of recruits to the trappable population in the control enclosure.

The mechanism by which neonatal mortality occurs have been discussed in Chapter 1, and include cannibalism, abandonment, trampling, and nest disturbance. Clearly, in a live trapping study in large field enclosures, it is not possible to determine which mechanisms are operating. A question that is seldom asked, however, is the degree to which the observational techniques (trapping, litter-handling, etc.) contribute to infant mortality. Clearly, trap deaths are quantifiable, but the effect of depriving infants of their mother for varying lengths of time by incarcerating her in a trap (in other word, causing her to 'abandon' her litter) have not been determined. Certainly, observer interference has been shown to have marked effects on infant mortality in enclosed mouse populations (Crowcroft

and Rowe, 1957). In the present study, traps were set at dusk or at around 6-7p.m. whichever was earlier, and inspected at around 8-10a.m. the following morning; thus a vole could spend a maximum of about 16 hours in a trap during which time, if it was a lactating female, her litter would be deprived of warmth and nourishment. This problem must have affected all previous studies of small mammals in which overnight live-trapping has been done. However, of the 19 animals tail-clipped as neonates in the control enclosure, some of which must presumably have suffered this maternal deprivation caused by trapping, all 19 survived to be trapped, which suggests that the problem may not be as severe as was initially feared; it does, however, warrant further study.

This live trapping study in the enclosures has shown that there were significant demographic differences between the experimental and control enclosures, summarised in Table 4.3.4(iv). Since the experimental design ensured as far as possible that the only difference between the enclosures was the overall level of aggressive behaviour, it must be assumed that it was this factor that caused the observed effects. Results concerning social relationships within the populations, also obtained from the live trapping study, have been presented; these were wounding, distances between successive captures, trap revealed home range areas, and weights at first capture, and they have shown that the experimental manipulation did indeed have social consequences within the enclosures. These results will be discussed in the sections that follow.

4.4.(c). Wounding.

In populations of rodents, wounding levels have been shown to be associated with density (e.g.Rowe et al,1964; Southwick, 1955(b), 1958; Christian, 1971(a)), the population cycle in Microtine populations (also, in effect, density) (Krebs, 1964; Christian, 1971(a)), sex (Rowe et al, 1964; Batzli and Pitelka, 1971; Christian, 1971(a); Rose and Gaines, 1976), age or reproductive

condition (Christian, 1971(a), Lidicker, 1973; Rose and Gaines, 1976) and season (Lidicker, 1973). The introduction to Chapter 2 has also reviewed many factors, particularly endocrine, that have been shown to affect the aggressive behaviour of male rodents. In general, because of hormonal influences, adult males fight, castrated and immature males do not. This was demonstrated to be true for bank voles in Chapter 2, and the experimental design for the work in the enclosures depended upon it. The field study of behaviour (Chapter 3) also confirmed that immature males tend to fight less than adult males, but, because no interactions involving castrated males were observed in the field, no conclusions could be drawn from that study about the aggressive behaviour of castrates. The results presented in 4.3.4(c) above confirmed that, in the enclosures, adult males fought considerable more than either castrates or immatures, using the degree of wounding as a measure.

Mention was also made in Chapters 1 and 2 of the fact that female rodents generally exhibit less aggressive behaviour than males, but that their behaviour had been studied very little, and the results of the field study of behaviour, presented in Chapter 3, showed that females fought less than males in the enclosures and at the field study site; the wounding results from the enclosures confirm this. In at least one Microtine species, however (Microtus townsendii), females can be highly aggressive (C.J.Krebs, personal communication) even though they do not show many wounds in the field. Thus the role of female behaviour in Microtine population biology remains unclear.

4.4.(d). Distances between captures.

The rather crude method of comparing the distances between captures of one age and sex class with another has been described in the Methods section, 4.2.4(c) above. In spite of this, the results obtained were of interest, although difficult to interpret. Bearing in mind the problems associated with different trap response by different age and sex classes, mentioned in the Methods section

4.2.4(c) above, the results concerning sex differences were in agreement with previous studies of bank vole movements (e.g. Zejda and Pelikan, 1969; Crawley, 1969) in that females moved less far between captures than males. As far as I know, previous studies have not differentiated quantitatively between the distances moved by adult and immature animals. In the present study, adult females appeared extremely sedentary, more so than immature females, whereas there was no difference between adult and immature males in either enclosure. Castrated males in the experimental enclosure tended to be caught slightly closer to their previous capture than either immature or adult males in the same enclosure.

The results of comparisons of like with like between the enclosures have shown that adult males, and immature males and females, all moved more between captures in the right, experimental enclosure than they did in the left, control enclosure. There was no significant difference between the distances between captures of the adult females in the two enclosures, nor between the castrated animals in the experimental enclosure and the adult males in the control enclosure. It is therefore hypothesised that the lower levels of aggression in the experimental enclosure (the result of the castration of the majority of the males) enabled individuals to range more freely than in the control enclosure; in other words, the aggressive behaviour of the intact males in the control enclosure was in some way restricting the movement of the other classes (except adult females). The reasons that no differences in distances between capture were exhibited by adult females from the two enclosures is not clear, but may be associated with adult females restricting their movements to the immediate vicinity of a nest site, even after breeding had effectively ceased.

An interesting result is that there was no significant difference in the distances moved between captures by castrated males in the experimental enclosure and the distances moved by intact males in the control enclosure. The marked behavioural differences between these two groups demonstrated in the laboratory (Chapter 2) had encouraged the speculation that their movements between captures might be different also; the reasons for the absence of any observed

difference is not clear.

4.4(e). Home range areas.

It has been shown above (Results 4.3.4(e)) that, in the present study, the trap revealed home range area for a given number of captures, even within a particular age and sex class, was very variable, and this is in agreement with previous live-trapping studies of small mammals (for instance, see Fig.6 of Kikkawa, 1964); even using tracking techniques, where more information concerning each animal's movements can be collected over a much shorter time-period than is possible in live-trapping studies, and where it is possible to investigate temporal changes in range use, the same variability in home range area within age and sex classes has been shown (e.g. see Table 3 of Randolph, 1977). This great variability inevitably tends to mask any differences produced by experimental manipulation, and this appears to have been the case in the present study. However, even though the definition of home range area used in the present study was very crude, taking no account of time-interval between captures or possible home-range shifts with time, the results obtained in general confirmed the original hypothesis, that the different social conditions in each enclosure would affect the freedom of movement of different age and sex classes differently. In particular, the presence of adult males appears to have restricted the movement of other age and sex classes in the control enclosure, compared with the movements of animals in the right, experimental enclosure, containing the non-aggressive castrated males; this result clearly, and not surprisingly, corroborates the results of the analysis of distances between captures, discussed above.

The fact that, in previous studies of other species, adult dominant males have been observed to restrict the movement of subordinate animals, lends weight to this interpretation (Crowcroft, 1966; Brown, 1969). On the other hand, several studies of bank voles have shown that home range size is inversely related to population density (e.g. Myjda and Pelikan, 1969; Mazurkiewicz, 1971; Andrzejewski and Mazurkiewicz, 1976); apparently in direct

contradiction of these results, home range areas in the present study were greater in the experimental enclosure, which contained a higher total number of animals, than the control enclosure; the experimental enclosure did however, contain less adult, aggressive males than the control enclosure, because the majority of adult males were castrated; perhaps, in the previous studies, the observation that home range areas were inversely proportional to the density really meant that home range areas were inversely proportional to the density of aggressive adult males. Because of the artificially high densities that occurred in the present study, this hypothesis is tenuous when applied to natural populations, but deserves further investigation. As in the analysis of distances between captures, the reason for the lack of more marked difference between home range areas of adults and castrates is not clear.

Because of the atypical conditions inevitably present in enclosed populations at high densities, values of the mean home range areas are not comparable with previous estimates of home range areas obtained from studies of unenclosed populations of bank voles (e.g. those of Zejda and Pelikan, 1969 or Crawley, 1969); however, in agreement with previous studies, the ranges of adult females were markedly lower than those of adult males (figs.4.3.4(xiii) and 4.3.4(xiv)) (Zejda and Pelikan, 1969; Crawley, 1969; Mazurkiewicz, 1971; Andrzejewski and Mazurkiewicz, 1976), whereas the ranges of immature males and females were generally less different from each other than those of adults (figs. 4.3.4(xii) and 4.3.4(xv)) (Mazurkiewicz, 1971; Andrzejewski and Mazurkiewicz, 1976).

In conclusion, this study has shown that, in communities of bank voles in field enclosures, the aggressive behaviour of adult males had a significant effect on population dynamics. In agreement with previous studies of enclosed mouse and vole populations, reproductive inhibition occurred at high densities, but there was no observable difference between the degree of inhibition in the experimental and control enclosures. Neonatal mortality, the other process also previously suggested as important in regulating the numbers in enclosed small mammal populations, was observed to be significantly higher in the enclosure with all males intact than in the enclosure with castrated males, and was the cause of the difference in numbers between the enclosures. Other demographic processes that might have affected the numbers were not significantly different between enclosures. Certain measures of the social organisation (wounding, distances between captures, home range areas) were also shown to be different between enclosures. As expected, the incidence of wounding was highest amongst adult males. In general animals were less restricted in their movements in the presence of non-aggressive, castrated males in the experimental enclosure than in the presence of aggressive intact males in the control enclosure.

The implications of these findings for the study of population regulation in rodents in general, and Microtine rodents in particular, will be discussed in Chapter 5.

CHAPTER 5

CONCLUSIONS

The present study has shown that, during the course of a single season, adult male aggressive behaviour appeared to have a significant effect on population variables in communities of bank voles in large field enclosures. Four major questions however, remain.

Firstly, could experiment ENCL 4 have been repeated with the same result? Because of the time- and energy-consuming nature of live-trap studies of small mammal populations, replications in either time or space have been rare. In the present study, only two enclosures were available, and the problems encountered with them, described in Chapter 4, meant that only one long experiment, (spanning a breeding season) was possible. As a result, it cannot be said with certainty that the observed differences between the populations in the enclosures were not simply due to undetected habitat differences between the two enclosures, or between the populations initially introduced into them, rather than to the differences in social conditions produced experimentally by the castration of most of the adult males in the experimental enclosure. Previous studies of enclosed populations of rodents have shown that the numbers reached at asymptote can be very variable, even in apparently identical enclosures (e.g.Southwick, 1955(b); Petrusewicz, 1957, 1958, 1960; Lidicker, 1965; Vessey, 1967). In general, however, this variability has occurred in laboratory populations, in small enclosures or cages, with very few founding animals (sometimes a single bisexual pair); in other words, with extremely restricted stock. It is easy to imagine that behavioural or genetic differences between one founding pair and the next could cause marked differences in subsequent population growth and asymptote. In the present study, the founding populations were large (10 animals were introduced into each enclosure at the start of experiment ENCL 4) and animals caught from different areas were divided equally between the two enclosures, with the intention of starting the experiment with genetically mixed populations. Therefore, it is unlikely that the differences observed were due to initial differences between the populations. Similarly, it is felt unlikely that there were sufficient habitat differences between the two enclosures to account for the demographic differences, although this possibility cannot be completely ruled out.

Secondly, castration was demonstrated, using rather imprecise methods, to affect the behaviour of male voles. Which other aspects of adult male social behaviour were also affected by castration, and which other components of the behavioural repertoire of male voles are important in population processes? In this, and other studies, the terms 'aggressive behaviour' and 'social behaviour' have been used as blanket terms to cover, for the sake of simplicity, a multitude of individual behavioural components. The role and interplay of behavioural components in the field must, however, be extremely complex; Chapter 3 has shown that it is possible to observe and to quantify behavioural interactions of voles in the field. It would seem to be worth pursuing this approach with a view to determining, in finer detail, which aspects of behaviour are most important in mediating population processes. In particular, the detailed effects of experimental manipulation (such as the castration used in the present study) on field behaviour deserves further study.

Thirdly, what is the role of social behaviour of other age and sex classes in affecting population variables? Traditionally, it has been assumed that it is the behaviour of adult males that is the most important in socially-controlled population processes. This assumption has arisen for the two reasons mentioned in Chapter 2; firstly, that the behaviour of females is difficult to study because of the complicating effects of hormone fluctuations during the oestrus cycle, and secondly, that males are more aggressive than females in most small mammal species. However, there are indications that female social behaviour may also be important (Krebs, personal communication; Bujalska, 1970, 1971, 1973), and investigation of this aspect is overdue.

The final question, and probably the most important of the four, is: What is the relevance of the results of the present study, carried out on enclosed vole populations, to the population ecology of bank voles in natural populations? Artificially enclosed populations have usually been studied only during the relatively short initial period of high population growth, as was the case in the present study. Because of this, adult mortality has largely been discounted in previous studies of enclosed populations; in the wild however, very few voles live for two breeding seasons. Clearly, the short time-scale of most studies

of enclosed populations of rodents means that the relevance of their results to population processes in natural populations may be limited. It is also always possible to criticize studies of laboratory and enclosed populations of rodents on the grounds that the densities reached render them so artificial that they bear little or no relationship to the real world, and that the mechanisms of population regulation revealed by them are therefore of minimal importance in natural populations. Lidicker (1976), however, argues that reproductive inhibition at least, clearly observed in the present study, is probably 'more than a pathological manifestation of artificially high densities' since only those species of rodents known to reach high natural densities (if only occasionally) have 'such efficient physiological machinery for turning off reproduction'.

I feel that these problems can really only be resolved by long-term experimental studies of natural populations, at natural densities. In particular, I think that further attempts should be made to manipulate, in a quantifiable manner, the behaviour of individuals or groups within natural populations (for instance, by hormone implants); demographic consequences of the behavioural modification of different age- and sex-classes should then be determined by comparison with similar, but unmanipulated, control populations. Replication, by repeating the experiment in the same areas, but with experimental and control populations reversed to eliminate possible intrinsic differences between the two areas, should finally enable the role of social behaviour in the dynamics of natural populations of rodents to be clarified.

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