A study of the agonistic behaviour of the long-tailed field mouse (Apodemus sylvaticus) and the bank vole (Clethrionomys glareolus)

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A study of the agonistic behaviour of the long-tailed field mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*)

by

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The long-tailed field mouse

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I. INTRODUCTION

The two species of small mammals, *Clethrionomys glareolus* and *Apodemus sylvaticus*, have been the subjects of numerous ecological studies in late years. In one of the most recent of these ASHBY (1967) found evidence of cyclical fluctuations in the density of field populations of *Clethrionomys* and postulated that one of the causes of these cycles might be the effects of social stress. The field vole, *Microtus agrestis*, is another species which exhibits population cycles and the work of CHITTY (1952) led him to suggest that the most important factors limiting population growth in this species were the effects of intraspecific strife. The same conclusions were also reached by CLARKE (1955) in his study of two experimental populations of *Microtus*.

SADLEIR (1965) and HEALEY (1966) have demonstrated the importance of adult aggressive behaviour in the regulation of population size in the deermouse, *Peromyscus maniculatus*, in which recruitment of juveniles into the population is maintained at a low level until the end of the breeding season. ASHBY (1967) believes that a similar mechanism may operate in *Apodemus* populations where he too found that juvenile recruitment was low during the main part of the breeding season. He also noticed that *Apodemus* and *Clethrionomys* individuals were more difficult to handle and had a greater tendency to bite the experimenter in the breeding season than at other times of the year, and he assumes that this behaviour is indicative of aggression.

BROWN (1966) suggests that aggressive behaviour of adults is the main cause of mortality among young Apodemus. She further maintains that the social structure of populations of this species is based on a dominant male animal at the head of an established social hierarchy.

Unfortunately, up to the present time, there has been little experimental evidence to back up such theories regarding the role played by social behaviour in the population dynamics of Apodemus and Clethrionomys. One of the main reasons for this is the lack of detailed knowledge of their behaviour. The present study attempts to partially fill this information gap.

It was considered that an investigation of the agonistic behaviour of the two species should be preceded by a study of their general individual behaviour to provide a basis from which to work. The activity of the two species in the laboratory was also examined. Later experiments were designed to show how agonistic behavioural activities varied within and between the species under different conditions, and to elucidate which factors were responsible for these variations. This work was confined to adult behaviour.

II. MATERIALS AND METHODS

1) The Animals and Methods of Culture

Two common species of wild rodents, the bank vole (Clethrionomys glareolus (Schr.)), and the long-tailed field mouse (Apodemus sylvaticus (L.)), were used in this study. Members of these two species, hereafter described as voles and mice respectively, were caught as adults with Longworth traps in mixed woodland near Durham. Only adults which were in breeding condition when trapped were brought into the laboratory. Juveniles used in the encounter experiments were first generation laboratory bred animals.

In the laboratory the animals were kept singly and in unisexual and bisexual colonies in wire mesh cages. These rested on metal trays containing sawdust which was changed each fortnight. The cages containing only one or two animals measured 37 x 21 x 16cm, while colonies comprising three or more animals were housed in larger cages measuring 41 x 26 x 21cm. Each cage contained a food dish, a water bottle, and a plentiful supply of hay and cotton wool for nesting material. The animals were fed on a mixture of crushed oats and wheat supplemented with cabbage once a week. Drinking water was supplied in inverted bottles fitted with glass drip-delivery tubes. An excess of both food and water was maintained in all the cages.

Glass jam jars with the lids removed were provided as refuges. These lay horizontally and were maintained in position by a length of rigid wire wrapped around the neck to form a projecting arm which rested on the wire mesh base of the cage. The smaller cages were supplied with a single refuge and the larger cages with two.

The temperature in the laboratory was not rigorously controlled but ranged between 18°C and 24°C. The mean value did not vary with season. Breeding condition was maintained by providing the laboratory with 15 hours of light each day, supplied from two 100 watt bulbs. The lights, which were controlled by an automatic switch, came on at 0400 hours and were turned off at 1900 hours.

When each colony was formed the component individuals were strangers to each other and to the cage and had experienced a period of adjustment to laboratory conditions of at least two weeks. Recognition of individual mice and voles in the colonies was facilitated by clipping the body fur in different patterns and, in addition, all experimental animals were permanently marked by toe-clipping.

Any individuals which died in the colonies were examined for external injury.

2) <u>The Observation of Behaviour</u>

(i) <u>General Behaviour</u>

The general individual behaviour of adult mice and voles was studied mainly in the home cages of the subjects. As *Apodemus* is largely nocturnal this involved watching during the evening after the onset of darkness. The cages were illuminated by red light to which *Apodemus* is insensitive (SOUTHERN 1955), provided by lamps screened with red gel plates. The voles, being more diurnal in their habits, were usually watched during the day. Regular use of the laboratory and the fact that the room overlooked a busy highway carrying a good deal of heavy traffic quickly accustomed the voles to noises made by the observer, and their activity during observation periods soon became normal without resorting to the use of screens.

(ii) Activity

A study was made of the activity of *Clethrionomys* and *Apodemus*. It was found to be possible to observe six individual animals of each species simultaneously and to note the times at which each animal emerged from and later re-entered the nest. Observation periods were either two or three hours in length and recordings were not made until the animals had had 20 minutes to settle down after the observer had entered the laboratory. Watching was carried out on different days and, over a fortnight, covered one 24 hour cycle. During the hours of darkness observations were made under red light.

(iii) Encounter Experiments

Encounters were staged between two animals of known weight and of the same species in either the home cage of one, or in a cage of similar size which was familiar to neither contestant. This neutral cage had a solid floor covered with sawdust and contained a food dish. In an encounter in the home cage the nest jar was removed approximately three hours before the contest. After this period the cage was transferred to an observation platform and the resident individual allowed to settle down for 10 minutes before the second animal was introduced. In the neutral cage encounters both animals were introduced simultaneously. In all contests the animals were watched for 15 minutes through a slit in a dark cloth screen. Details of ensuing behaviour were spoken into a tape recorder using a verbal shorthand and the information transcribed later. No individual was used in encounters more than once in a week, more than four times in all, or, with certain exceptions (page 43), met a given individual more than once.

A difficulty met with during trial encounters, that of the contestants being disturbed by the voice of the observer and the noise of the tape recorder, was resolved by providing continuous background noise from a portable radio.

(iv) Transcription of the Tape Recordings

After each encounter the tape was played back and, with the aid of a stop-clock, the recorded elements of behaviour coded on the tape were entered in sequence onto a score sheet. This showed the time at which the elements actually occurred and by which contestant they were performed. As some responses were often repeated quickly, making it difficult to perceive whether or not they were discrete elements, any such response by a given individual occurring more than once within

10 seconds, and without a different response intervening between the repetitions, was recorded as a single component.

(v) Photography

Visual observations were supplemented by photography using a single-lens reflex camera with an electronic flash and a 16mm cine camera with a long-focus zoom lens. Illumination for filming was provided by six 100 watt bulbs. The subjects were placed in a cage specially constructed for photographic work. This had wire mesh side-walls, a sheet alloy back-wall painted white, and sloping glass plate front to exclude reflected light. All the drawings of acts and postures have been taken directly from the films.

3) Terminology

Many authors of literature dealing with aspects of behaviour have used certain terms without definition. This has caused confusion in the past and has resulted in many words having vague or various meanings. For this reason an explanation of some such terms used in the present work is now given.

In this study a somewhat artificial distinction had been made between various parts of observed agonistic behaviour. These parts recurred repeatedly and have been described as discrete entities. They have been named behavioural elements or components or responses.

A drive is the complex of factors leading to a given behaviour. Motivation in an animal is a tendency to react to a drive. When two opposing drives are aroused in an individual a conflict situation occurs.

I have used the term subject as meaning the individual under consideration and not as a description of a position in a system of formalised social relationships.

III. RESULTS

1) Activity

The activity patterns of voles and mice adapted to the light regime of 15 hours light / 9 hours dark are shown in Figure 1. Activity has been considered as the time spent outside the nest and is expressed as a percentage of the total time available for activity. The histograms show the combined results from three males and three females of each species over one 24 hour cycle.

It can be seen that *Apodemus* showed a marked nocturnal habit with peaks of activity during the second and last hours of darkness. After dawn, activity decreased until the fourth hour of daylight following which very little activity occurred before the onset of darkness. Day time activity in *Apodemus* represented 17.5% of the total activity. In *Clethrionomys*, however, 43.0% of all observed activity occurred during the hours of daylight. The main peaks of activity in this species also occurred before dawn and soon after the onset of darkness, but were less pronounced. Secondary peaks in vole activity were seen during the day and Figure 1 shows some evidence for a six-hourly periodicity in the activity of this species.

Table 1 indicates that mice spent much more time out of the nest than did voles and yet the latter species were observed to have many more active periods. This is explained by the brevity of vole activity periods (mean = 4.3min) compared with those of mice (mean = 24.6min).

(a) Apodemus

(b) Clethrionomys

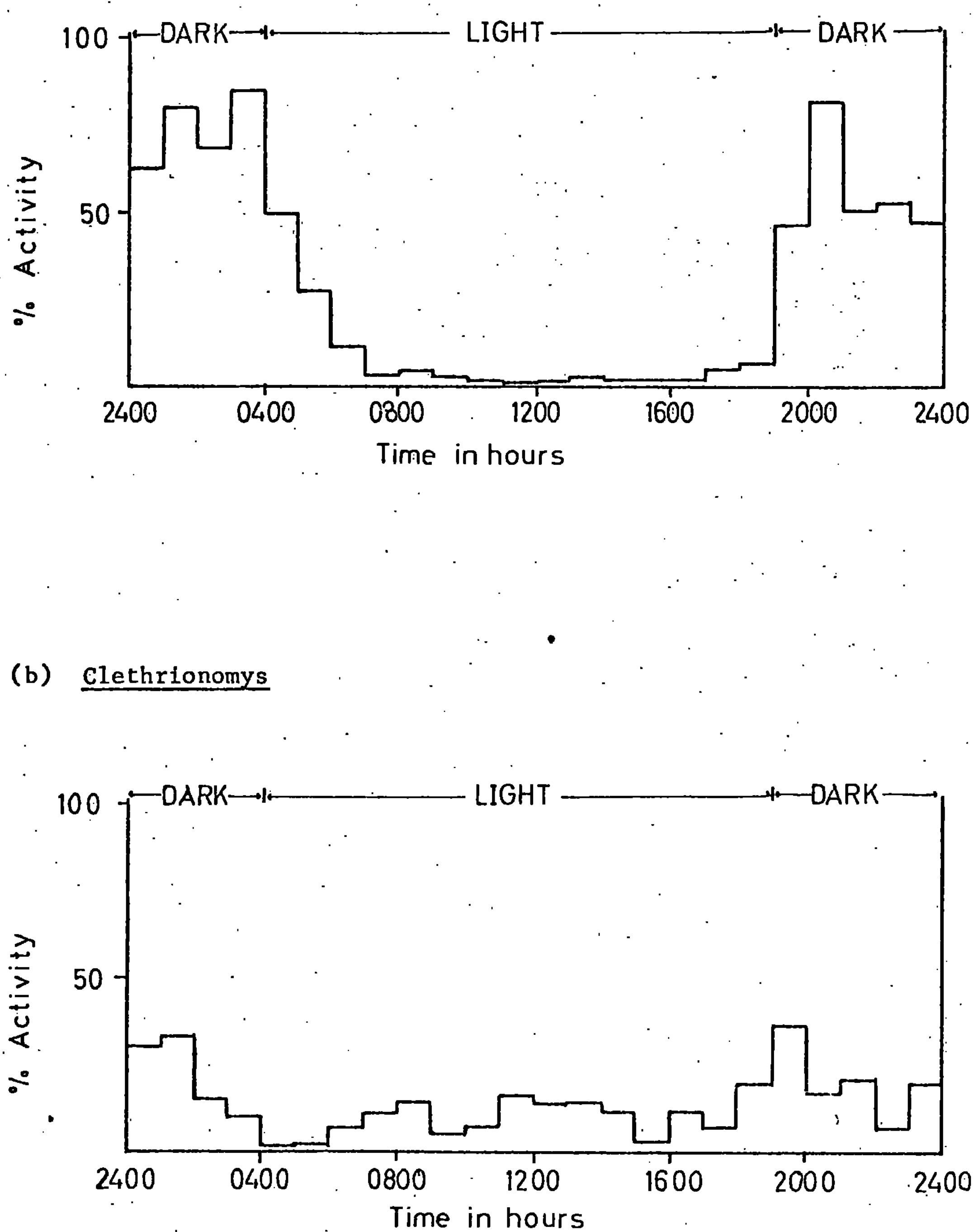


Fig.1. The activity rhythms of Apodemus and Clethrionomys in response to a day-length of fifteen hours.

TABLE 1

The activity of *Apodemus* and *Clethrionomys* adapted to a day-length of 15 hours

	MICE	VOLES
Mean total activity time per individual in 24 hours	422.2 min	198.2 min
Mean number active periods* per individual in 24 hours	17.2	46.0
Mean length of active period	24.6 min	4.3 min

*An active period is a term of activity outside the nest.

2) General Behaviour

The following description of general behaviour in the two species is the result of many periods of observation, usually about an hour in length, of individual animals in the laboratory population.

(i) Exploration

When placed in unfamiliar surroundings the first activity seen in both species is usually of an exploratory nature. Mice will often begin to explore the new environment immediately but voles may remain inactive for a period of time varying individually from a few seconds up to five minutes.

When exploration commences both species behave in a similar manner. The advancing animal's body is tense and extended and the tail is carried rigidly either straight out behind or slightly curved upwards. The ears are directed forwards and the animal looks alert. Movement is slow and hesitant when approaching new objects and more jerky and rapid when withdrawing from the same. This is the elongate approach also seen in encounter behaviour (page 16 & Fig. 2). Voles have a strong tendency to return repeatedly to a familiar spot during initial exploration, which then becomes a series of sorties from that point.

When the new object or new environment has become more familiar the body and tail relax and the animal moves in a less tense manner. Subsequent exploration continues with, in the case of mice, much investigation in a rearing position. The mouse stands on straight hind legs and sniffs the air with small vertical nods of the head. Voles behave similarly but usually take up an upright sitting posture rather than a rearing stance.

It was noted during activity observations that voles occasionally emerged from the nest, explored the cage in a random manner, and then returned to the nest without showing any other behaviour. So far as could be determined, no external stimulus caused this behaviour, and it is suggested that this is similar to the spontaneous "reconnaissance behaviour" of Microtus described by SHILLITO (1963). In contrast, periods of activity showing exclusively exploratory behaviour were not noted in Apodemus, although periods of activity often began with thorough exploration of the cage, feeding and other behaviour being shown afterwards.

There was a marked difference in the behaviour of the two species in their reaction to disturbances such as loud noises outside the cage. Voles immediately took refuge in the nest jars and did not re-emerge until conditions returned to normal. Mice, on the other hand, often vacated the nest jars when disturbed and rarely re-entered while the disturbing conditions persisted.

(ii) <u>Ingestion</u>

Both mice and voles pick pieces of food up in the mouth and then use the front paws for grasping and manipulation while assuming a sitting position. Grain was usually eaten at the food dish if the animals were relaxed. Under disturbed conditions, however, individual grains might be carried in the mouth to a less exposed part of the cage and eaten there. Voles had a tendency to drag pieces of cabbage to the entrance of the nest or even into the nest jar before consuming them.

Refection was seen several times in both male and female voles during the encounter experiments but never in the colonies. No mice were seen to refect.

The animals obtained water from the bottles by placing the tongue in contact with the water inside the drip-feed tubes. Voles drink much more than mice and are also adversely affected by lack of water more rapidly.

(iii) Defaecation and Urination

Individual mice and voles usually used a particular corner of the cage for defaecation. This spot was sometimes changed after a time and other corners were used to some extent, but voles in particular used the same corner with great regularity. Voles also defaecated just outside the nest and both species did so near the food dish. Faeces were excluded from the nest by both species and on several occasions faecal pellets were seen being carried from the nest in the mouth. Urination usually occurred in the same corner as defaecation. In cages where nesting material had been removed from the nest jar, the animals often used the empty jar for eliminatory purposes. Mice and voles will release urine and faeces anywhere when frightened.

(iv) Self Grooming

The body surface is cleaned regularly by both species and the movements involved in washing behaviour are in many ways similar. The toilet is performed in a sitting position and often begins with rapid motions of the front paws in contact with the mouth. The paws are then moved over the fur at the sides of the mouth and brought down towards the nose, one immediately in front of the other (Fig. 3). These strokes are repeated rapidly with each subsequent stroke beginning higher up the face until the head and ears are included. The body fur is then cleaned directly by the mouth using a bobbing head motion accompanied by combing strokes of the forearms and forepaws (Fig. 4).

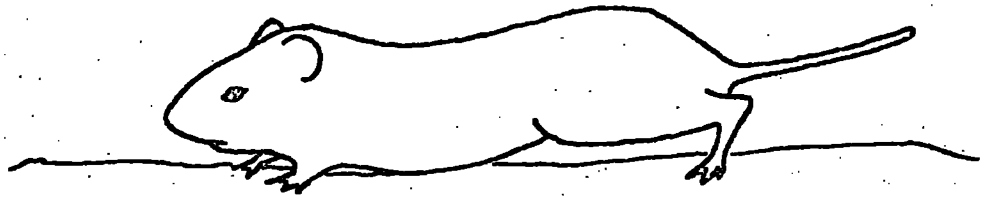


Fig.2. Vole. Elongate posture.

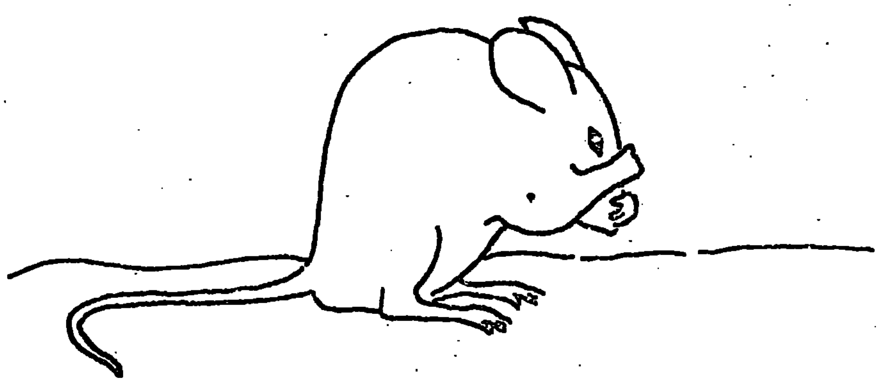


Fig.3. Mouse. Washing face.

Fig.4. Vole. Cleaning body fur.

In mice the long tail is washed last of all by drawing it past the mouth from the base to the tip using the front paws. Voles were not observed holding the tail in this manner.

The complete cleaning of the body surface may or may not occur in the sequence described above, but in any case occurs far less often than partial toilet behaviour involving only the body or the face. Both mice and voles regularly scratch their body fur with the hind feet which are then moved to the mouth and nibbled before repeating the movement. Self grooming behaviour occurs inside and outside the nest and, on the whole, mice perform washing movements more often than voles especially in conflict situations (page 23).

(v) Nest Building

Both sexes of the two species exhibit nest building behaviour. Nests were usually constructed in the jars provided, particularly if a small amount of bedding material had been introduced beforehand. Pieces of nesting material are picked up in the mouth and carried or dragged to the desired site. *Apodemus* may gather the material together before picking it up, an action involving alternate combing movements of the forepaws. Cotton wool is teased apart in the nest using the mouth and front paws and hay is often bitten into short lengths before being incorporated into the structure. Alterations to the structure of the nest are effected by moving the material with the mouth and front paws or by "nosing" it into place.

When nests were constructed on the cage floor instead of in the nest jars, as sometimes occurred in both species, the animals began building by burrowing inside the mass of nesting material and then hollowing out a central chamber. These nests were usually globular structures with two entrances but mice occasionally built simpler cup-shaped forms with little or no roof. Voles showed a preference for cotton wool as nesting material whereas mice used hay, cotton wool and sometimes dessicated cabbage leaves.

3) Agonistic Behaviour

Although both *Clethrionomys* and *Apodemus* bred in the laboratory, sexual, maternal and juvenile behaviour were not closely observed. Agonistic behaviour is defined as any behaviour associated with fighting between two individuals (SCOTT 1956). GRANT & MACKINTOSH (1963), in their study of the social postures of four laboratory rodents, divided the responses involved in adult behaviour into several classes within each of which they assumed motivational similarity. This classification and the terminology used by these authors to describe agonistic elements have been closely adhered to in the present study.

(i) The Acts and Postures

An account of the acts and postures observed during the encounter experiments is given below. It was found that although many individual elements were easily allocated to a particular motivational group, e.g. Attack as a component of aggressive behaviour, others were more difficult to classify. Data abstracted from the encounter score sheets provided a means of analysing the function of several such elements, as shown in Section 3(iii) (page27), thus facilitating their classification.

Introductory Elements : Approach, Nose, Investigate and Sniff

The component Approach is a directed movement towards another animal. In the initial stages of an encounter Approach is performed in the elongate posture already described as part of exploratory behaviour (Fig. 2). Mice soon relax in non-aggressive bouts and thereafter often contact each other without Approach, but in a random way during exploration of the encounter cage. In aggressive contests, however, after preliminary elongate advances, one mouse begins to approach the opponent in a hunched manner with the fur raised on the body and face. This kind of approach usually leads to Aggressive Posture or Attack (see Aggressive Elements). Vole encounters commence similarly although one vole will rarely approach another in a casual way even in the most peaceful bouts, the elongate posture being resumed to a greater or lesser extent by the active vole as it nears the opponent. Voles which do approach others with little hesitation or tenseness are those which are known to have been dominant in a colony. These animals usually move confidently and show bold and relaxed preliminary approaches.

Fig.5. Mice. Nose.

Fig.6. Mice. left, Parry; right, Investigate.

Nose, Investigate and Sniff are all acts describing nasal exploration of the opponent and frequently occur after Approach. Nose is the most clearly defined element of the three. In *Apodemus* it involves close naso-nasal contact and may be accompanied by closing the eyes and turning the head on to one side (Fig. 5). This action is also seen during the introductory behaviour of *Peromysus* (EISENBERG 1962). In voles Nose is limited to vibrissal contact.

Exploration of the anogenital area of another animal is referred to as Sniff. The act was only noted once in voles and did not involve close contact. In contrast, Sniff was regularly performed during mouse contests.

Investigate is nasal contact with any other area of an opponent's body (Fig. 6).

Aggressive Elements : Aggressive Posture, Attack, Fight, Wrestle and Chase

Aggressive Posture is in most respects identical in both species. The fur is raised on the head and body making the animal look larger than normal (Figs. 7&13) and erection of hairs on the lower part of the face gives a distinct "Roman-nose" appearance. The posture is usually assumed by an aggressively motivated animal which has approached its opponent with the back arched and taking short steps. The hindquarters are kept close to the ground and the tail is usually relaxed. A vole exhibiting Aggressive Posture has its body positioned towards the other animal in a definite oblique manner. This is probably the "Offensive Sideways Posture"

Fig.7. Mice. left, Aggressive Posture; right, Upright Posture.

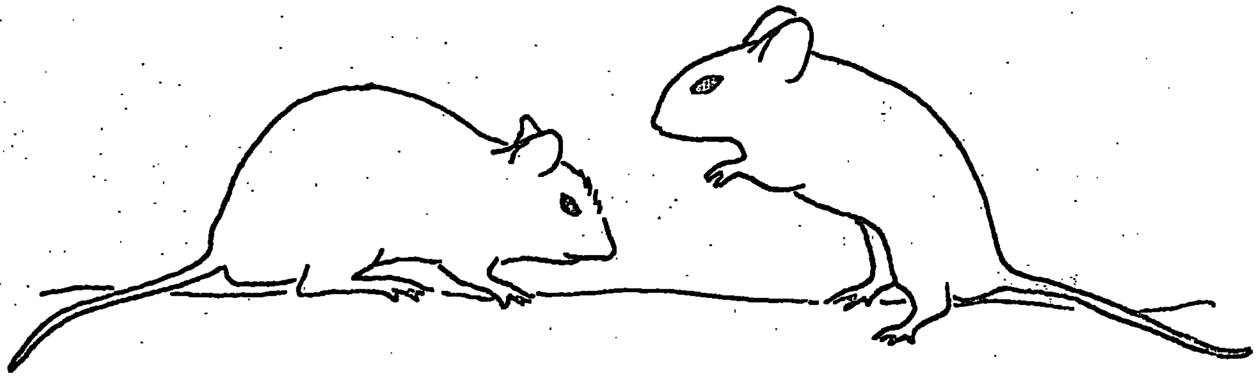


Fig.8. Mice. left, Attack; right, Avoidance leaping.

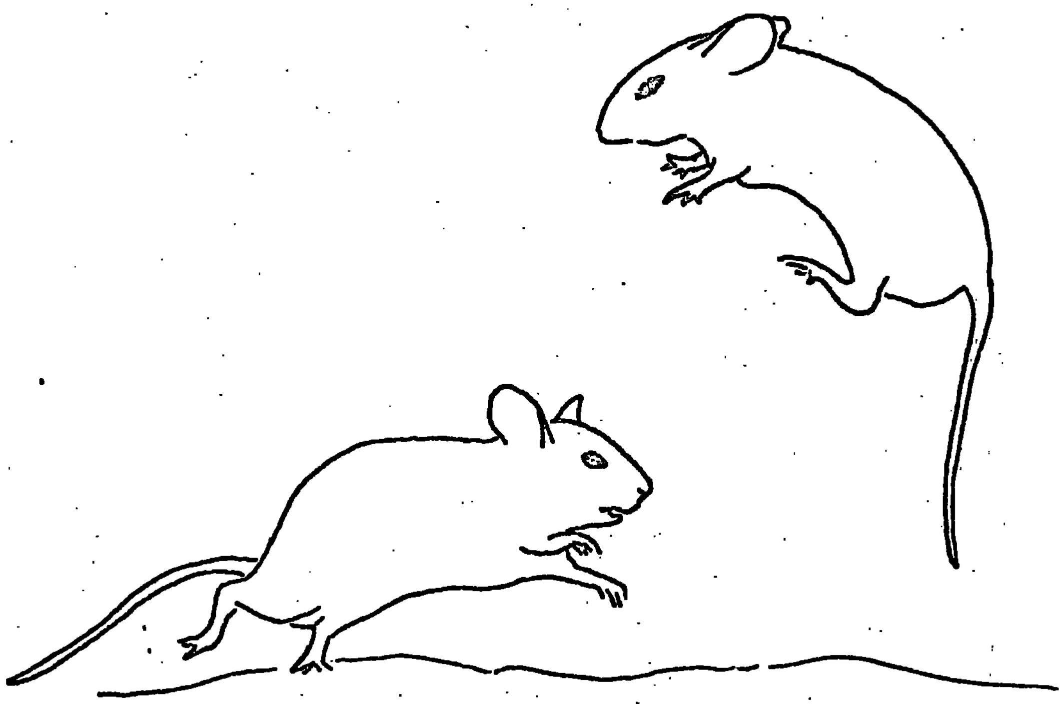


Fig. 9. Voles. Fight.

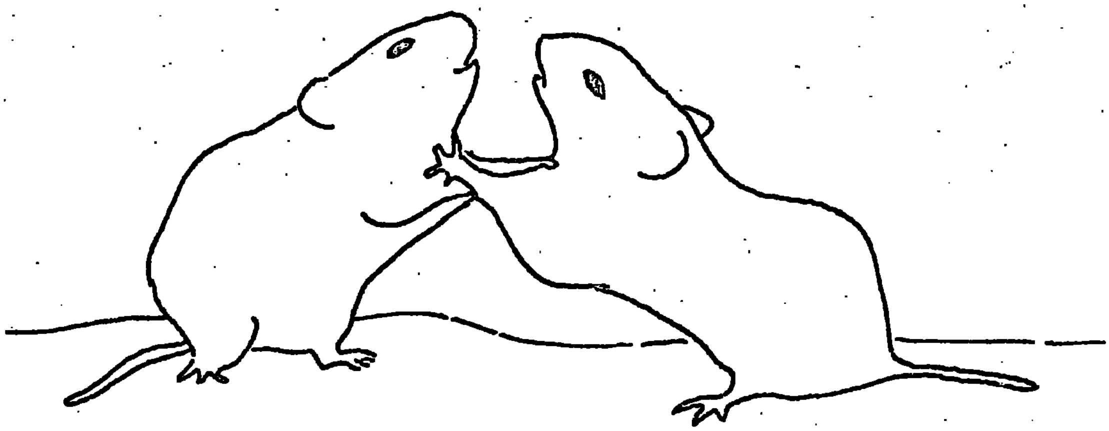
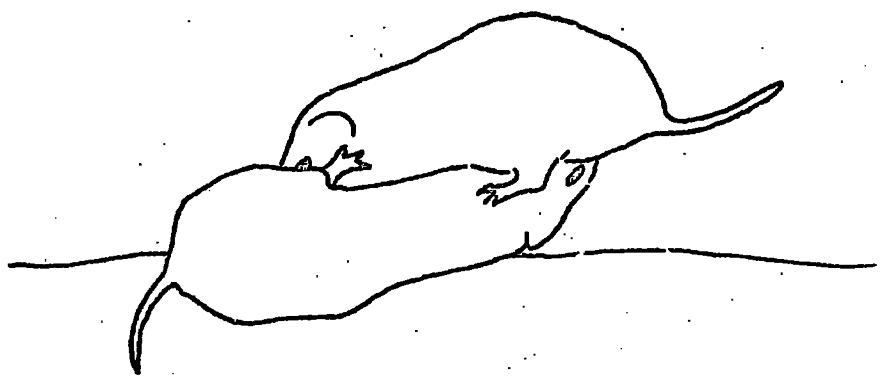


Fig. 10. Voles. Wrestle.



of other rodents described by GRANT & MACKINTOSH (1963) and was less commonly observed in Apodemus.

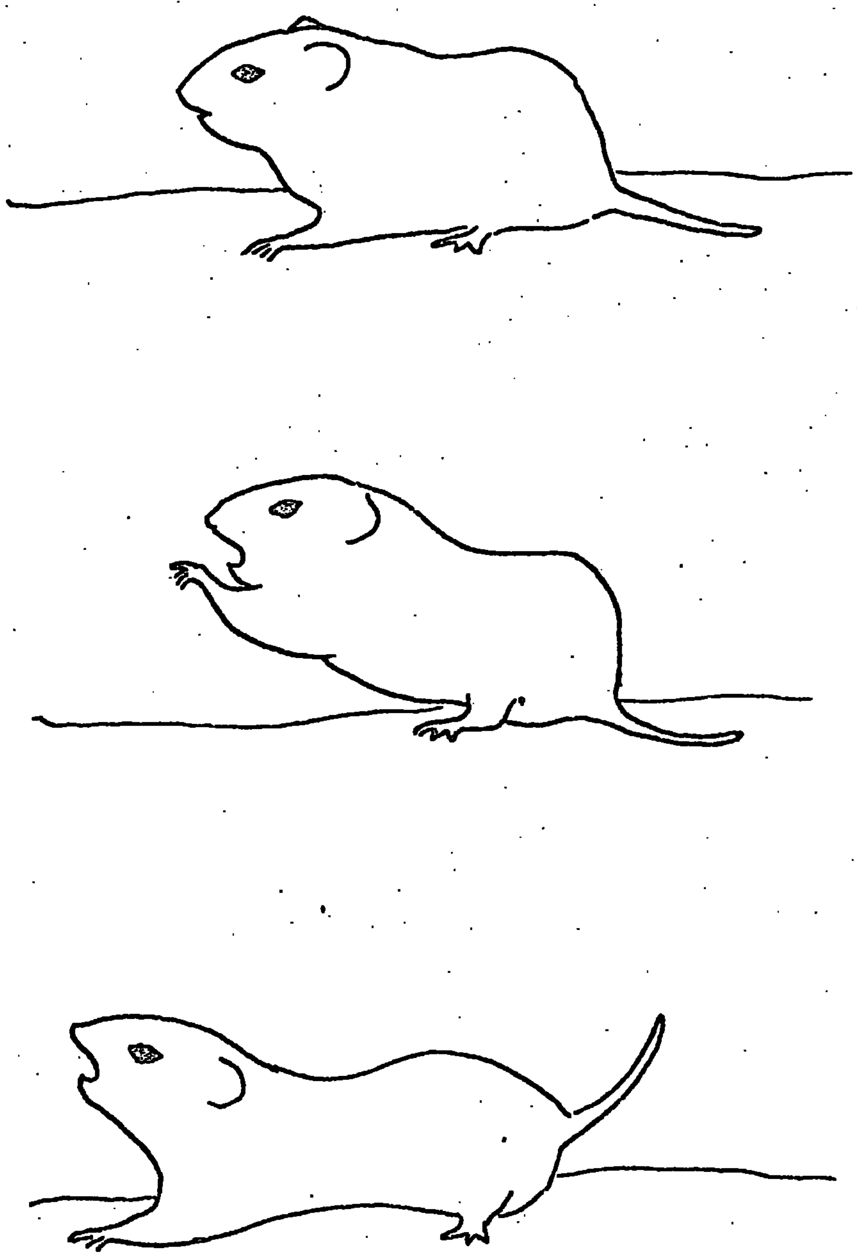
A rapid approach towards an opponent ending in an attempt to bite the latter constitutes Attack. An attacking animal has its mouth open and incisors bared and aims for the side or underparts of the opponent (Fig. 8).

Fight is aggressive contact with an opponent while in an upright position. In both species the contestants stand on their hindlegs and box with the forelimbs with the head directed upwards (Fig. 9). Fight may be succeeded by Wrestle in highly aggressive individuals. The contestants roll about on the floor of the cage while the aggressor attempts to bite its opponent (Fig. 10). It seems probable that some inhibition mechanism is involved in this biting action as damage to the suffering animal is usually less severe than might be expected.

Chase is also an act common to aggressive members of the two species. A chasing animal has its mouth open and shows what appear to be intention movements of biting the opponent (Fig. 12).

Defence Elements : Thrust, and Nest Defence

The response Thrust is seen only in Clethrionomys and covers a range of movements which cannot be clearly separated. In all these the characteristic feature is a directed movement of the head towards the opponent with incisors bared, often accompanied by a biting action. This darting movement of the head may or may not be combined with movement of the rest of the



(a)

(b)

(c)

Fig.11. Vole. (a) - (c). Sequence followed in lunge (Thrust).

body towards the opponent. In the least intense movements the vole assumes a sitting position and shows only a rapid extension and retraction of the forelimbs in the direction of the other animal, whereas in the complete response an obvious lunge at the opponent occurs (Fig. 11). The lunge usually starts from a position on all fours. Then the whole body, excluding the hind limbs, is moved quickly towards the rival animal together with a striking motion of the front paws and a rapid elevation and lowering of the tail. If the opposing vole does not retire it may suffer blows from this forelimb action. At the end of the lunge the animal withdraws to its original position. The interpretation of Thrust as a defensive act is discussed in Section 3(iii).

No response of this kind was observed in Apodemus except by females nursing a litter of young and showing Nest Defence. This act, performed by both species, is displayed at the nest entrance against a strange animal. It takes the form of lunging as described above.

Withdrawal Elements : Retreat, Flee, Defeat

Retreat is the converse of Approach, that is, a directed movement away from an opponent. Although part of withdrawal behaviour, this act is often shown by the more aggressive contestant after a period of offensive activity.

The high intensity form of Retreat is Flee. An animal in flight has its ears back and frequently leaps in the air as it attempts to escape from the rival contestant.

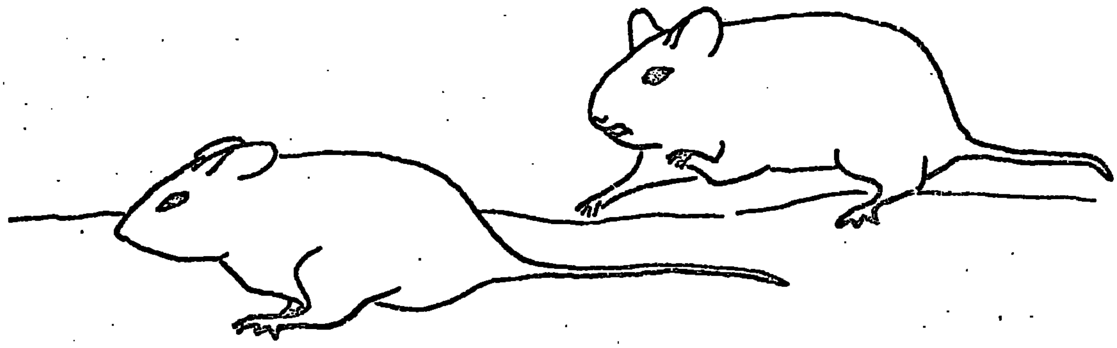


Fig.12. Mice. left, Flee; right, Chase.

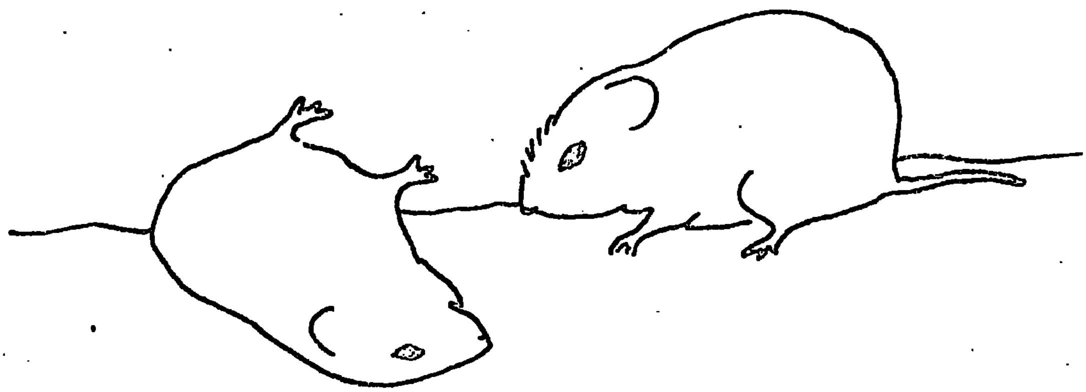


Fig.13. Voles. left, Defeat; right, Aggressive Posture.

This avoidance leaping is especially conspicuous in _Apodemus_ (Fig. 8). Flight in both species often led to the animal taking up a position on the walls of the cage. When this occurred the aggressor usually stopped chasing and lost interest for some minutes. GRANT & MACKINTOSH (1963) noted similar behaviour in other rodents and suggested that by clinging to the bars of the cage in this manner the pursued animal could be preventing the aggressive individual from receiving the necessary stimuli to induce attack.

Defeat is shown by a contestant which has been beaten in fighting or wrestling. The defeated animal lies on its back on the floor or, as was more commonly seen in _Apodemus_, is forced into a corner of the cage (Fig. 13) and exhibits forced immobility with several or all of the limbs extended to ward off the aggressor. This position, like that taken up on the bars of the cage, seems to inhibit further attack by the dominating individual. The Defeat posture may be maintained for up to half a minute in _Clethrionomys_.

Defeat has been classed as a withdrawal element because it occurs in the same situations as Flee, suggesting a similar motivation. The only difference between the two responses is that in the case of Defeat the aggressor cannot be avoided and the individual substitutes immobility for flight action.

Fig. 14. Mice. left, <u>Submit</u>; right, <u>Groom</u>.

Fig. 15. Mice. Crawling over.

Submission : Submit

A vole or mouse shows submission when it is being groomed by an opponent. The submissive animal has its ears back, eyes closed, and shows little other movement (Fig.14). In other situations an animal displaying Submit may appear to be less relaxed and be crouched closer to the ground but with the ears back and the eyes shut in the same manner. This is shown by an individual which is approached by an obvious dominant (the latter may be a stranger or the winner in an aggressive contest) or, in the case of female voles, the act may be exhibited by a stranger when approached by the resident in a home cage encounter.

Contactual Elements : Groom and Crawl

Groom is performed by both male and female mice but was only observed in female voles, and occurs in encounters which show minimal aggression.

The area about the head, ears and shoulders is that usually groomed (Fig. 14). Only one animal grooms in a given encounter, mutual grooming not having been observed. A similar act has been noted in *Peromyscus* (SADLEIR 1965) and other rodents (GRANT & MACKINTOSH 1963) which these authors have called "Aggressive Groom". The name was given because the act was exhibited by a clearly aggressive animal. Such motivation in grooming animals was not apparent in the present encounters and therefore the act has simply been called Groom.

Crawl, describing the acts of creeping over or under the body of an opponent, is only shown by Apodemus. A mouse may crawl over another individual from the front or the rear and usually does so in a diagonal fashion, crossing to the other side of the opponent with slow movements (Fig.15). Crawling under is usually an incomplete act; the animal merely pushes the head and front part of the body under that of the opponent. These crawling movements were observed in Rattus by BARNETT (1958) who described them as "amicable". In his analysis of the social behaviour of the male laboratory rat GRANT (1963) shows evidence that these acts are associated with sexual behaviour. It would be difficult to comment on this in the case of Apodemus when the sexual behaviour of the species had not yet been described. Crawl was seen in the same encounters as those in which Groom was exhibited.

Ambivalent Elements : Upright Posture and Parry

Upright Posture describes a range of stances in both species which vary from an almost crouching position with forepaws just raised off the ground, to a body position which is closer to 90 degrees to the horizontal with forelimbs outstretched towards the opposing animal (Fig.7).

In the mouse only, the upright position may be modified as Parry. The front paws come into contact with the opponent and slight warding off actions are performed (Fig. 6).

The evidence suggesting that Upright Posture and Parry are ambivalent elements is presented in Section 3(iii).

Non-Social Elements : Scratch, Self Groom, Eat, Drink, Dig

A number of activities occurred regularly in the encounters which appear to be irrelevant to agonistic behaviour. However, the form that they assume and the situations in which they were manifest suggest that they may often be displacement activities. These responses were shown with particular regularity by the following types of individual :-

(A) An aggressive animal which had approached an opponent but had not fought or attacked.

(B) An individual which had fought or attacked another and then retreated.

(C) A mouse or vole which had chased an opponent on to the bars of the cage and had subsequently transferred its attention away from that individual.

(D) A male mouse during periods of intense introductory behaviour.

Because the circumstances of the above animals are of the type in which displacement activities might be expected (see page 58), they have been called displacement situations. The responses concerned were not confined to such situations, however, but were seen on other occasions when displacement activity was not suggested. For this reason the elements have been termed non-social rather than displacement.

Scratch was performed only by highly aggressive male mice. The animals walk forward with the back arched and the body high off the ground, at the same time scratching each side of the body alternately with the hind feet.

The Self Grooming behaviour of both species observed during encounters covered the range from the full washing sequence to extremely abbreviated movements of the front paws to the mouth or on the face. These abridged motions were mainly seen in circumstances A, B, C and D described above.

Eating, like Self Groom, was exhibited by both mice and voles in forms ranging from normal eating at the food dish, to the picking up of pieces of sawdust from the cage floor and either dropping them immediately or briefly nibbling them. Again the most curtailed movements occurred in the typical displacement situations already mentioned.

Water was not available to the contestants during most encounters, but on several occasions when the cage did contain a water bottle, the Drinking behaviour shown was abbreviated in form. Sometimes no liquid was taken, the movement being merely an approach to the water bottle and a quick turn of the head to the imbibing position. These incomplete motions strongly suggested displacement behaviour.

Mice and voles both showed digging behaviour during bouts, although not in any specific situations. There is much less evidence to suggest that Dig is a displacement activity than there is for the acts Self Groom and Eat.

Displacement behaviour is further discussed on page 57.

(ii) Associated Behaviour

The above account of acts and postures seen in the agonistic behaviour of mice and voles is not a complete description. Other behaviour patterns were observed during encounters which were either difficult to record sequentially using the present methods, or which occurred too infrequently to be regarded as characteristic of any specific circumstance. For instance, members of both species occasionally showed twitching of the dorso-lumbar fur during social interaction. This was seen frequently in vole encounters and was sometimes accompanied by swallowing motions and yawning in both contestants. In mice, however, fur-twitching was usually shown only by aggressive individuals.

Descent of the testes was often seen in male *Apodemus*. This occurred early in a contest if the individual became aggressive, but at a later stage, or not at all if the encounter was peaceful. EISENBERG (1962) noted a similar response during encounters with male *Peromyscus*.

On a few occasions highly aggressive male voles used a prancing gait between attacks on an opponent. This method of locomotion was characterised by small lateral movements of the forelegs which caused sawdust to be sprayed to the side of the animal as it moved forwards.

Tail vibration was seen in *Apodemus* on three occasions. EIBL-EIBESFELDT (1950) regards this "tail rattling" in the house mouse as part of threat behaviour, but in this study the small number of observations gave no indication of such a function.

Mice and voles were sometimes seen to "freeze" in position during contests with highly aggressive opponents, and on several occasions this seemed to inhibit further offensive activity by the assailant. CLARKE (1956) in his account of the aggressive behaviour of Microtus suggested that, as in the response Defeat, the "freezing" individual prevents the opponent from receiving the correct stimuli for releasing attack.

It is almost certain that auditory and olfactory communication are important in the social behaviour of these two rodent species. Sounds within the range of human hearing were produced by voles in many encounters. Defending voles are particularly vociferous and emit high-pitched chattering and squeaking noises which increase in intensity as an aggressor approaches. A vole which was losing a contest frequently made similar sounds when attacked or while fleeing. During aggressive Clethrionomys contests both animals usually produced faint rattling sounds, apparently by moving the teeth against one another. This has also been described in Microtus by CLARKE (1956) and in Rattus by BARNETT (1958). Both authors suggest that it may subserve threat. The only sounds heard in Apodemus encounters were emitted by submitting females which had been vigorously attacked and then re-approached by an aggressive male.

The noise is best described as a mewing squeak. It is known that high frequency sound communication is employed by both *Apodemus* and *Clethrionomys*, but this could not be detected using the present methods.

An indication that chemical communication may play some part in agonistic behaviour was shown by certain *Apodemus* males which, during aggressive contests, dragged the perineal region over the cage floor or the food dish. It could not be determined whether or not glandular secretion or urination occurred during this activity. Voles did not show this type of behaviour but similar actions have been observed in other rodents (EISENBERG 1962).

(iii) The Motivational Analysis of Four Responses

The classification of certain of the elements of agonistic behaviour described above was hindered by a lack of knowledge of their underlying motivation. The issue was further complicated when, as occurred in Thrust and Upright Posture in *Clethrionomys*, and Upright Posture and Parry in *Apodemus*, the form taken by the act or posture was subject to considerable variation. The position occupied by each of these responses within various agonistic behavioural sequences has therefore been analysed in an attempt to gain further insight into their nature.

Each analysis is based on data abstracted from the encounter score sheets for all-male contests. The analyses did, of course, precede the classification described in Section 3(i).

Table 2

The frequency with which elements preceded and succeeded the component Thrust within 10sec.

No. of observations of Thrust = 152.

	Prec. Elem.		Succ. Elem.		Foll.Elem.
	(i) Sub.	(ii) Opp.	(iii)Sub.	(iv)Opp.	(v)
Approach	9	55	1	1	1
Nose/Inv./Sniff	1	1	-	-	-
Agg. Posture	-	61	1	29	2
Attack	-	-	-	3	1
Fight	-	6	-	11	-
Wrestle	-	-	-	3	-
Chase	-	2	-	-	-
Thrust	-	1	-	1	62
Retreat	-	3	2	79	6
Flee	-	-	1	-	16
Submit	-	-	-	-	1
Up. Posture	9	3	-	7	4
Self Groom/Eat	-	1	-	5	4
None	0		8		65

Prec.Elem. = element immediately preceding Thrust.

Succ.Elem. = element immediately succeeding Thrust.

Foll.Elem. = element shown by subject after Thrust.

Sub. = subject.

Opp. = opponent.

Table 2 shows such an analysis of the act Thrust. Columns (i) and (ii) indicate the frequency with which any behavioural element immediately preceded Thrust and which of the two contesting animals performed that element. Columns (iii) and (iv) show, in the same way, the immediate succeeding element to Thrust. The action taken by the subject after it had exhibited Thrust is shown in column (v). All the responses tabulated occurred within 10 seconds of Thrust, the arbitrary time limit being necessary to ensure that a given act and Thrust were associated. For instance, if the next act shown after Thrust did not occur until, say, one minute later, it would be unlikely that the two were related. When no other behaviour was observed within the 10 second period, then Thrust was considered to have begun or, conversely, to have ended a behavioural sequence.

From Table 2 it is primarily evident that the elements immediately preceding and succeeding Thrust were performed by an opposing animal and rarely by the subject. Hence the act usually occurs within "action-reaction" behaviour sequences. The most commonly observed components of these sequences are shown in Fig. 16 which is a summary of Table 2.

GRANT & MACKINTOSH (1963) described Thrust in four other rodents as an intention movement of aggression, and one of the same authors working with the laboratory rat (GRANT, 1963) showed that the act is usually followed in the subject by aggressive behaviour. EISENBERG (1962) described a similar response in Peromyscus which he said "........ may precede the attacking rush leading to the locked fight". All these authors have stated that the act was primarily one of

Number of observations of Thrust = 152

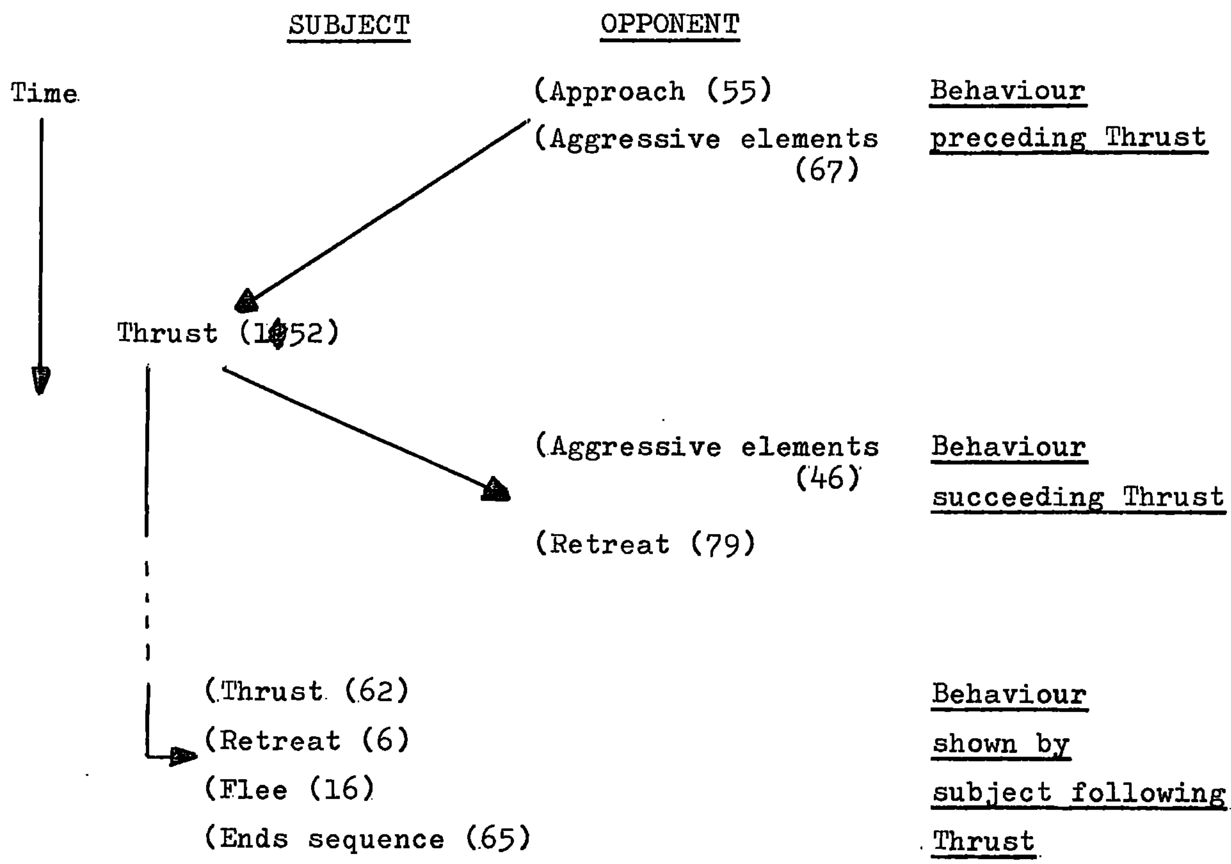


Fig. 16. The position of the element Thrust within agonistic behavioural sequences of Male *Clethrionomys*

threat. The form taken by the response in Clethrionomys is similar to that described in other rodents by the above authors and indeed suggests an intention movement of attack. However, overt aggression by the subject was only once observed after Thrust, whereas the most common derivative elements were Retreat and Flee (Table 2 and Fig. 16). Thrust was mainly performed after an opponent had shown Approach or Aggressive Posture, and stimulated the opponent to either show further aggression or, more frequently, to retreat. In the latter case Thrust often ended a sequence of behaviour in the subject.

The form taken by the act Thrust and the situations in which it is shown by an animal does, therefore, suggest threat. But the reactions of an opponent to Thrust and the way in which the subject then behaves do not indicate high aggressive motivation in the latter. It seems more probable that Thrust is a threatening gesture which serves a defensive function, and is performed by a vole which has its aggressive and flight drives simultaneously activated.

Analyses of behavioural sequences associated with Upright Posture in mice and voles are summarized in Figs.17 & 18 . It can be seen that in both species Upright Posture was performed after an opponent had shown a variety of acts and postures. Many of the same elements were shown by the opponent in reaction to Upright Posture by the subject, indicating that the performance of Upright Posture has little

Number of observations of Upright Posture = 32

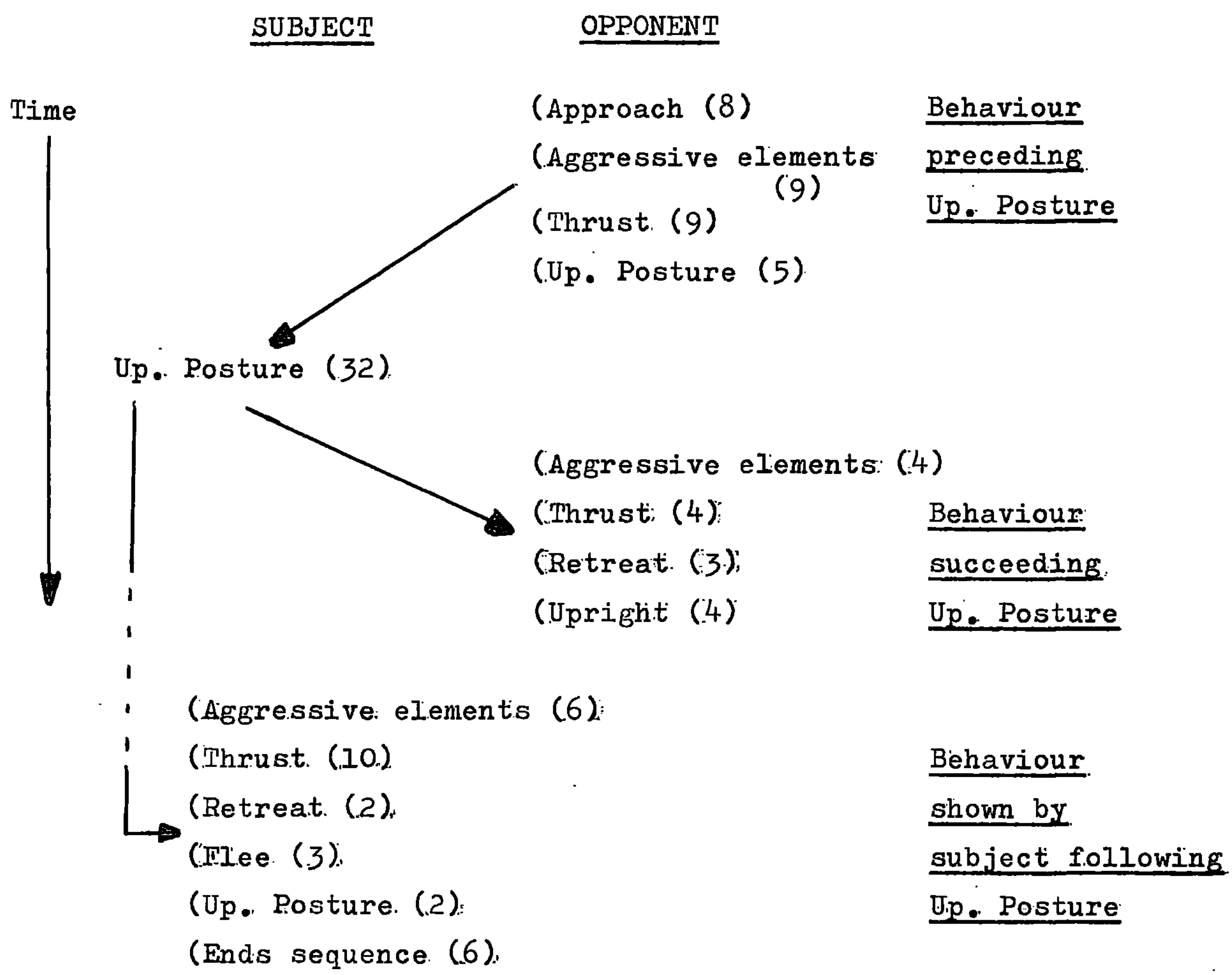


Fig. 17 The position of the element Upright Posture within the agonistic behavioural sequences of Male *Clethrionomys*

Number of observations of Upright Posture = 87

SUBJECT | **OPPONENT**

Time ↓

OPPONENT — **Behaviour preceding Up. Posture**

(Approach (19)
(Nose/Inv./Sniff (29)
(Up. Posture (31)

SUBJECT:

Up. Posture (87)

OPPONENT — **Behaviour succeeding Up. Posture**

(Nose/Inv./Sniff (10)
(Up. Posture (31)
(Parry (6)

SUBJECT — **Behaviour shown by subject following Up. Posture**

(Nose/Inv./Sniff (16)
(Aggressive elements (11)
(Retreat (3)
(Flee (4)
(Up. Posture (9)
(Parry (10)
(Self Groom/Eat (5)
(Ends sequence (17)

Fig. 18 The position of the element *Upright Posture* within the agonistic behavioural sequences of Male Apodemus.

tendency to elicit any specific type of response in another individual.

The subject's behaviour after it had exhibited Upright Posture varied from overt agression to flight without any bias to either extreme. It is therefore suggested that Upright Posture indicates a conflict situation in an individual caused by weak activation of both aggressive and flight drives. Consequently the posture has been classed as ambivalent.

Parry has already been described as similar to Upright Posture in form (Section 3(i)). The evidence that the two responses occur in similar behavioural situations rests with the data in Fig. 19. Accordingly, Parry has also been classed as an ambivalent element.

4) The Colonies

The experimental colonies shown in Table 3 were set up and their progress watched over 10 weeks. In each colony formed the animals were introduced to the cage simultaneously.

In this section "fighting" is used in the general sense and describes the expression of aggressive behaviour patterns.

(i) Aggression and Mortality in Undisturbed Colonies

In unisexual pairs and colonies of *Apodemus* the only fighting seen took place between males on the first day of meeting. In bisexual colonies of *Apodemus* fighting was seen to occur sporadically between males for the first three days, Number of observations of Parry = 16

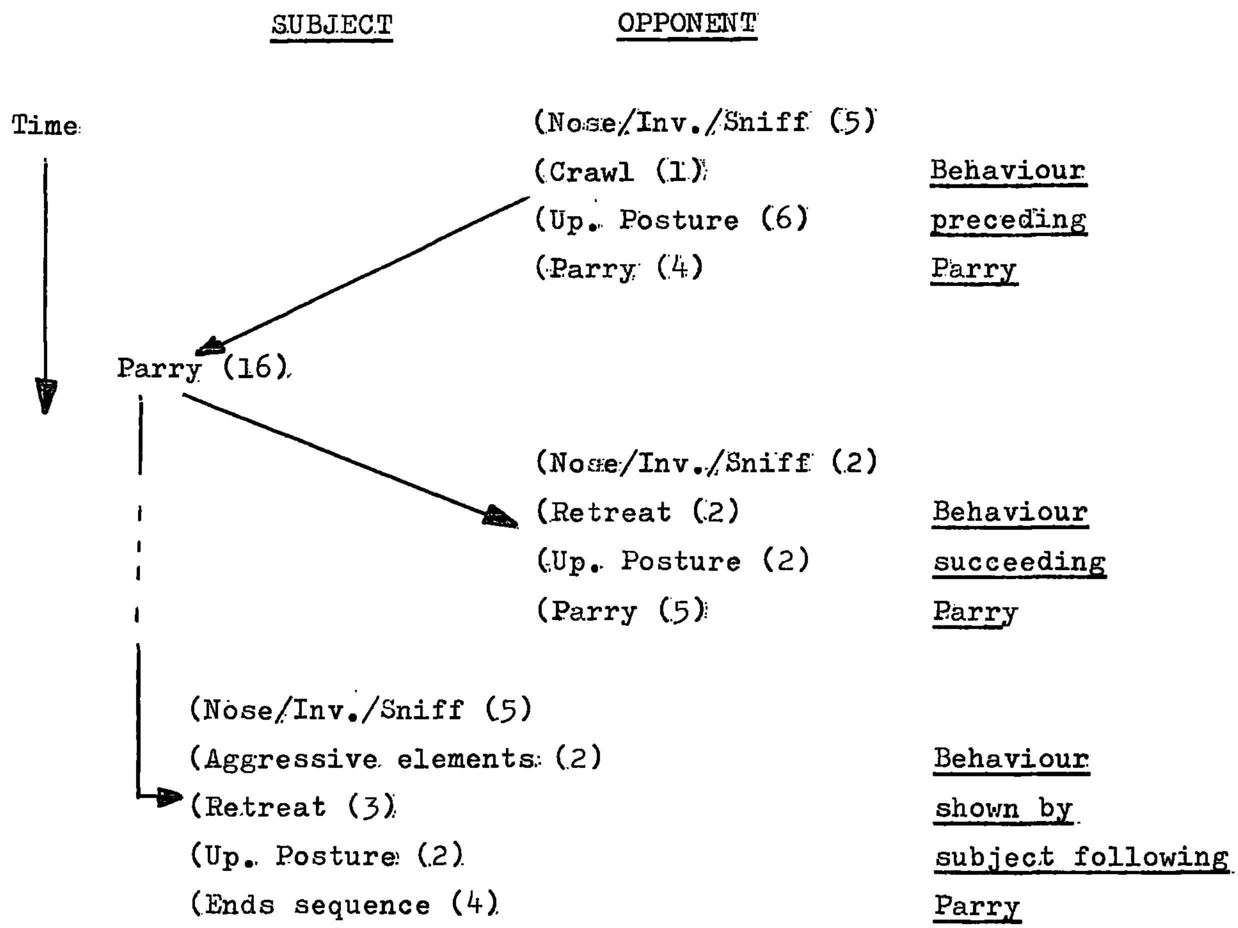


Fig. 19 The position of the element Parry within agonistic behavioural sequences of Male *Apodemus*

but thereafter no aggression was observed. During these first three days male mice were frequently seen chasing females round and round the cage. However, the chasing was not observed to precede or follow other aggressive behaviour patterns and it seems possible that it was in some way connected with sexual behaviour.

In contrast, hostile behaviour was shown by most members of newly formed Clethrionomys colonies. Most voles showed defence when approached by another individual, and the chattering noises emitted by defending or fleeing animals was an indication of the occurrence of friction between colony members. During their first week of existence all the vole colonies, except the bisexual pairs and the colony of litter mates, showed origins of strife and were extremely noisy. After this period the all-female colonies became more pacific and antagonism was usually limited to occasional defence by an approached animal. Members of all-male colonies were more aggressive than animals in the unisexual female colonies. Nevertheless, after the first week the pairs of males (colonies C_6 & C_7) and one of the colonies containing three males (C_4) also settled down. Offensive behaviour continued to be seen in other all-male groups until the fifth week, after which they all appeared to be stable.

TABLE 3

Mortality in undisturbed colonies of *Clethrionomys* and *Apodemus* during 10 weeks

VOLES			MICE		
Colony Number	Members	Deaths	Colony Number	Members	Deaths
C 1*	4♂	1♂	A 1	4♂	0
" 2*	4♂	0	" 2	4♂	0
" 3*	3♂	1♂	" 3	3♂	0
" 4	3♂	1♂	" 4	3♂	0
" 5*	3♂	0	" 5	2♂	0
" 6	2♂	0	" 6	2♂	0
" 7	2♂	1♂			
			" 7	4♀	0
" 8	4♀	1♀	" 8	3♀	0
" 9	4♀	0	" 9	3♀	0
"10	3♀	0	"10	2♀	0
"11	3♀	0	"11	2♀	0
"12	2♀	0			
"13	2♀	0	"12	3♂ 2♀ (litter mates)	0
"14	3♂ 1♀ (litter mates)	0	"13	3♂ 1♀	0
			"14	2♂ 1♀	0
"15	3♂ 2♀	2♂	"15	1♂ 2♀	0
"16	3♂ 1♀	2♂	"16	1♂ 1♀	0
"17*	3♂ 1♀	1♂	"17	1♂ 1♀	1♂
"18	2♂ 1♀	1♂ 1♀			
"19	1♂ 2♀	0			
"20	1♂ 1♀	0			
"21	1♂ 1♀	0			

* Colonies in which dominant individuals were recognised.

The most unsettled colonies of all were the bisexual vole colonies containing more than one male. A great deal of fighting occurred between males in these colonies and, except in the case of colony C_{16}, was followed by the death of all but one male in each group. Males did not fight females in the vole colonies except in colony C_{18} where, after one male had died (8th day), the remaining male vigourously and persistently attacked the female which then also died (15th day). The only bisexual vole colony in which no aggression was seen between males was that composed of litter mates. The members of this colony had lived together since birth and at no time since then had any antagonism been seen or heard in their cage.

The voles which died in all-male colonies C_1 and C_4 did so during the second week, while in colonies C_3 and C_7 deaths were preceded by special circumstances described on page 39 . Deaths in bisexual vole colonies occurred within four weeks of formation of the colonies. In the all-female colony C_8 one female died in the fifth week, at a time when no obvious hostility was being shown. No deaths occurred among animals of either species which existed singly in cages, these being 8 male voles, 6 female voles, 6 male mice and 6 female mice.

Voles assumed a characteristic appearance some time before they died. The eyes closed and the animals seemed to have difficulty in maintaining a normal upright position as they moved about the cage. Their appearance was very similar to that of animals suffering from lack of water, and they usually died within 12 hours of showing such symptoms. No voles were observed to die as a direct result of fighting and, in fact, when in the condition just mentioned they were usually ignored by aggressive individuals. Macroscopic examination of dead animals showed that many had suffered superficial wounds to the limbs and tail, presumably as a result of fighting. However, these lacerations were never infected, nor was there any other evidence to suggest that they were the cause of death. Examination of several vole corpses was incomplete owing to the fact that they had been partially eaten before being discovered.

The only Apodemus to die, the male in colony A_{17}, had looked ill for several days and had not shown symptoms of the kind observed in Clethrionomys. No aggression had been seen in this colony.

(ii) Social Relationships in Established Colonies

In both vole and mouse colonies the component individuals all tended to occupy the same nest jar, even when two were provided in the cage. During active periods outside the nest members of Apodemus colonies frequently showed similar aggregative behaviour, whereas voles seemed to avoid contact with other members of the colony. This mutual avoidance behaviour has also been noted in laboratory colonies of Microtus (SHILLITO 1960). The phenomenon was most marked in all-male Clethrionomys colonies where usually only a single individual was seen out of the nest at any one time. On the occasions when two or more male voles were simultaneously active, and one individual approached another, only rarely was the approaching individual ignored. The vole which was approached usually showed either defensive or aggressive behaviour, or it retreated as the other drew near.

In a number of all-male vole colonies which had become stabilized, one vole was seen to exhibit offensive behaviour more than others in its colony. This individual always won fights, approached other colony members confidently, and was never seen to be attacked by others. These voles were clearly dominant in their colonies. The colonies in which dominance was recognised are indicated in Table 3. No difference in social status could be determined among the subordinates in these colonies.

C_{17} was the only bisexual colony in which more than one male vole survived, and here a particularly clear difference in the status of the males was seen. The subordinate animal spent much of its time alone in a nest which it had built in one corner of the cage. After initial fighting, contact between the two males was rarely observed, but on the occasions when they did meet the subordinate animal either fled or showed a submission posture. The dominant animal occupied one of the nest jars together with the female.

No kind of dominance-subordination relationships were recognised among female voles or in any of the *Apodemus* colonies. All dominant male voles retained their superior status throughout the experimental period.

(iii) Effects of Introducing Males into Established Colonies

At the end of the 10 week experimental period strange males were introduced into several established unisexual and bisexual colonies (Table 4) which were then observed for a further 2 weeks.

In *Apodemus* colonies the interlopers were fought by resident males except in colony A_4 where no aggression was observed. In each case the fighting occurred between the stranger and one particular resident male, although the latter animal had not previously been recognised as dominant over other members of the colony. The initial fighting by resident males usually developed into a Chase-Flee pattern within a few hours. This behaviour was observed more frequently in the bisexual groups than in the all-male colonies, although chasing was rarely seen in any cages after the second day when aggressive behaviour was discontinued.

The introduction of strange males into vole colonies appeared to have a much more adverse effect on the stability of the latter than was the case with mouse colonies. In all-male colonies C_5 and C_3 the intruding animals were repeatedly attacked

TABLE 4

Mortality in colonies after introduction

of strange males

(a) CLETHRIONOMYS

Colony Number	Members	Intruder	Deaths	
			Resident	Intruder
C 5	3♂	1♂	0	1♂
" 3	2♂	1♂	0	0
" 8	2♂	* 1♂	0	0
"15	1♂ 2♀	1♂	1♂	0
"16	1♂ 1♀	1♂	0	1♂
"20	1♂ 1♀	1♂	0	1♂
"21	1♂ 1♀	1♂	0	1♂

(b) APODEMUS

Colony Number	Members	Intruder	Deaths	
			Resident	Intruder
A 3	3♂	1♂	0	0
" 4	3♂	1♂	0	0
" 6	2♂	1♂	0	0
"14	2♂ 1♀	1♂	0	0
"15	1♂ 2♀	1♂	0	0
"16	1♂ 1♀	1♂	0	0

* Individual became dominant.

by the dominant residents, and in colony C_5 the interloper died in the second week. In colony C_3 the stranger survived the 2-week observation period but was never completely accepted in the colony. It usually occupied a separate nest from the other colony members. In colony C_8, however, a different situation was observed in which the introduced male was immediately aggressive to the residents and became dominant in that colony at the end of the 2-week observation period. This intruding male had previously been observed to be abnormally aggressive in other situations (page 44).

Intruding males in bisexual pairs and colonies were immediately assailed by resident males, and fighting occurred regularly during the first two days. Thereafter the strangers were attacked less often, but in each colony were excluded from the nest occupied by the resident male. In colonies C_{16} and C_{20} the interlopers were found dead on the 6th and 3rd days respectively, and the strange male in colony C_{21} died during the second week. The resident male in colony C_{15} also died during the second week, an unexpected occurrence since this individual had been particularly aggressive to the intruder and had defeated the latter on several occasions.

The introduction of strange males into vole colonies not only elicited antagonism between the resident males and the interlopers, but the residents often became more hostile towards each other. Thus in all-male colonies the dominants displayed offensive behaviour more frequently than usual, while the subordinates in the nests were more defensive towards animals re-entering after periods of activity. Increased defensive behaviour was also shown by females in bisexual colonies.

(iv) Other Aspects of Agonistic Behaviour in the Colonies

During the later part of the 10 week experimental period animals from several colonies were used in encounter experiments. It was noted that when a male vole from an all-male colony had participated in an encounter in which much aggressive behaviour had taken place, and then this individual was returned to its original colony, there was often an unexpected increase in hostile behaviour in that colony. When the individual concerned was a dominant animal, then it became offensive towards subordinates in the colony. If, on the other hand, the encountered animal was a subordinate, the following antagonism in the colony did not always involve this animal. It appeared as if the animal had provided the colony with some new stimulus which elicited more defence by the other subordinates and an increase in offensive behaviour on the part of the dominant. It is possible, of course, that the returning individual was being treated as a stranger but, as the period of absence from the colony was rarely more than 45 minutes, this would seem unlikely. The strife situation which was precipitated within the colonies on such occasions was, however, occasionally quite intense and in two all-male colonies (C_3 & C_7) it preceded the deaths of two individuals. In colony C_7 the animal which died had been encountered against another vole and had been defeated several times by the latter. On being returned to the colony it was then attacked by the other resident male with which it had previously lived in harmony for three weeks. This vole died 10 days later. The colony C_3 male which took part in an encounter was the dominant of the colony. After its return to the colony it appeared extremely aggressive and exhibited offensive behaviour towards subordinate voles with which it came into contact. One of these subordinates died after two days of such hostilities.

During observation of the colonies one general difference in the behaviour of Clethrionomys and Apodemus was very noticeable. As was mentioned earlier, voles rarely contacted each other during routine activities outside the nest whereas mice often aggregated in one part of the cage. Often on these occasions individual mice showed submission postures, and contactual behaviour, especially Groom, was sometimes exhibited. On the other hand, observations of such behaviour in Clethrionomys colonies were very rare.

5) The Encounters

One of the first characteristics of agonistic behaviour to be noted in the colony experiments was that interaction only involves two individuals at any one time.

The colony experiments also indicated that not only do mice and voles differ in their behaviour towards other animals of the same species, but that the behaviour exhibited may also vary within the species depending upon certain characteristics of the individuals and circumstances under which they meet. The encounter experiments provided a means of expressing quantitatively such differences in agonistic behaviour.

(i) Categories of Animal and Types of Encounter

The animals which participated in the encounter experiments were divided into several categories, each of which was given the collective name shown underlined. These were :-

a) Adults which normally lived alone - Single males and Single females.

b) Adults as in a) but which were encountered in their home cage - Home Cage males and Home Cage females.

c) Adults from colonies comprising three or more adults of the same sex - Group males and Group females.

d) Adults from bisexual pairs and colonies - Mixed males and Mixed females.

e) Sub-adults aged between 6 and 9 weeks - Juveniles.

f) Lactating adult females with a young litter, encountered in the home cage - Nursing females.

Using these animals the following contests were enacted.

				No. of Bouts	
			Home cage contests	VOLES	MICE
Encounter	type	A.	Single males x Home Cage males	8	4
"	"	B.	Single females x Home Cage females	4	4
			Contests between colony animals and Single animals		
"	"	C.	Single males x Group males	8	6
"	"	E.	Single females x Group females	2	2
"	"	G.	Single males x Mixed males	4	6
"	"	H.	Single females x Mixed females	2	2
			Contests between animals from the same colony		
"	"	D.	Group males x Group males	1	1
"	"	F.	Group females x Group females	1	1
			Contests between colony males and Juveniles		
"	"	I.	Juvenile (male & female) x Mixed Males	4	4
			Contests between Single males and Single females		
"	"	J.	Single males x Single females	2	2
			Contests between lactating females and Single males		
"	"	K.	Single males x Nursing females	1	1

In any one type of encounter each category of each species participating usually behaved in a characteristic and consistent manner. The data from the score sheets of individuals within these species-categories have therefore been grouped and the collective results are shown in Tables 5-7, 9 and 11-14. In these tables the behavioural elements are shown on the left.

The figures in the columns express the relative frequency of occurrence of these responses, the number of times any act was performed by one category of contestant being expressed as a percentage of the total number of behavioural elements seen in that type of encounter.

Tables 8, 10 and 15 contain the results from types of encounters which were only staged once (types G, H & K). The totalled numbers of responses seen in these contests were comparatively small and, as percentages of such small samples could be misleading, in these cases the actual recorded scores have been tabulated.

Tables 5 - 15 demonstrate how the various categories of each species differ in their behaviour in different types of encounter. Aggregated results are, however, only meaningful if the sets of observations which have been grouped together are of the same kind. In vole encounters of type C there were obvious dissimilarities in the behaviour of colony males and the data were grouped in a modified way (Table 7). This and any other differences in the behaviour of animals within one category are described in the next subsection.

(ii) Behaviour During Encounters

It has been seen in the account of agonistic acts and postures that the behavioural repertoires of the two species are basically similar. However, the relative frequencies with which the agonistic behavioural classes occurred in each sex and species

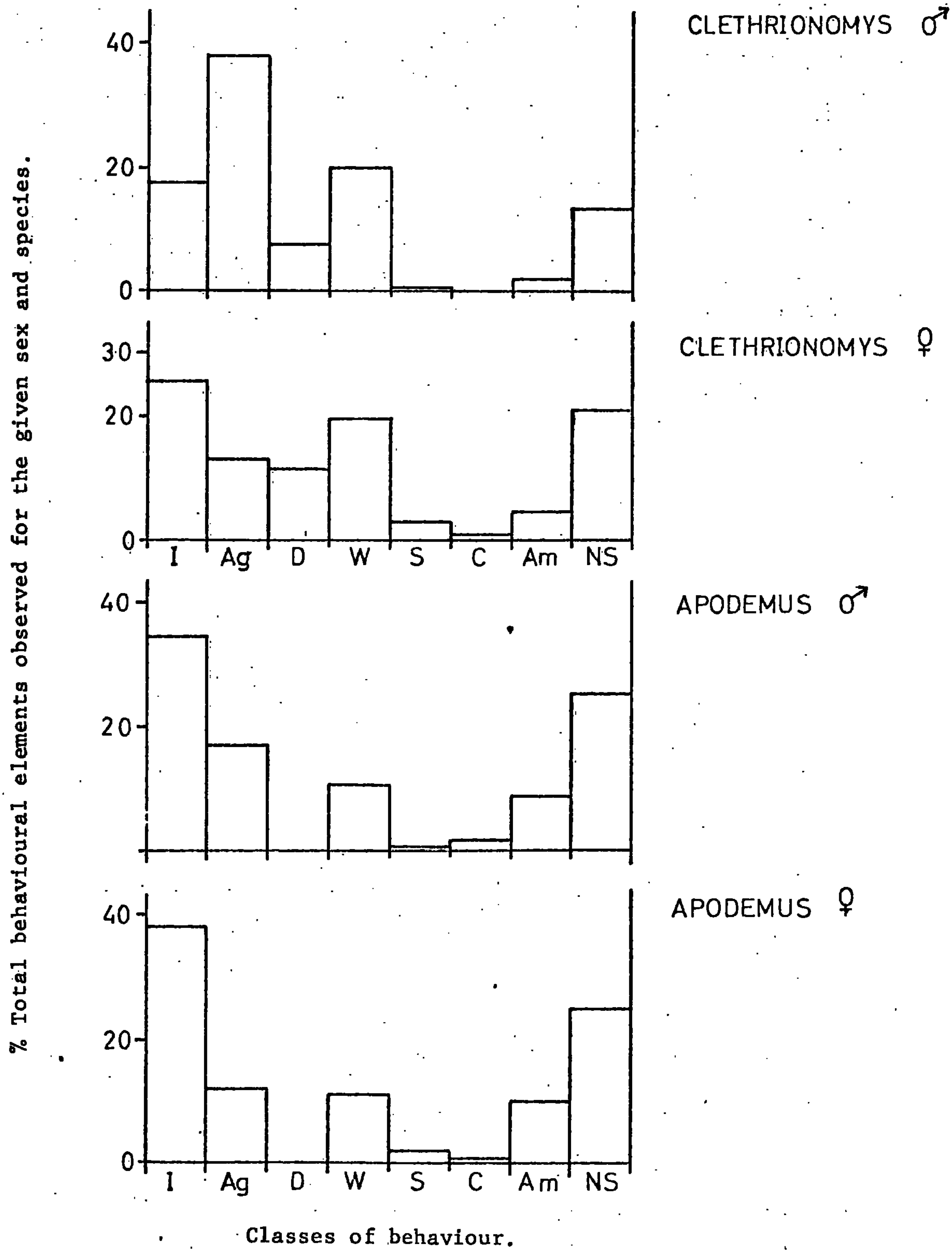


Fig.20. Frequency of occurrence of various classes of behaviour in adult encounters.

differed considerably as shown in Figure 20.

The figure suggests that males are more aggressive than females in both species but particularly so in Clethrionomys. Introductory, ambivalent and non-social behaviour seem to be more important in the encounter behaviour of Apodemus than in that of voles. The defence element Thrust, an important component of vole behaviour, was not shown by mice. However, since the histograms were constructed using all the recorded data from adult encounters, and therefore include the results of different types of contest and different numbers of observations, Figure 20 only gives a general indication of the relative importance of the various behavioural classes within each set of animals. In fact, the behaviour of the individuals of each sex and species differed markedly according to their category and to the type of encounter in which they participated, as will now be described.

Home Cage Encounters (Types A, B)

The home cage encounters were the only ones in which individual animals met an opponent more than once. In cases where, for example, male vole "α" met male vole "β" in the home cage of the former, the experiment was later repeated with "β" as the Home Cage male. Then, any differences in the behaviour of the animals on the two occasions could be attributed to the home cage factor. It will be evident that this reversal of roles was not possible in the other types of encounter where the two opponents differed in, for instance, age, sex or social background.

TABLE 5

Occurrence of elements of various classes of behaviour in encounters between Single males and Home Cage males

(Encounter Type A)

		T.E. %			
		VOLES		MICE	
		SM	HCM	SM	HCM
Introductory	(Approach	14.4	0.5	10.2	2.5
	(Nose	0.3	-	5.8	4.7
	(Investigate	-	-	6.6	6.2
	(Sniff	-	-	5.4	3.3
Aggressive	(Agg. Posture	9.4	-	-	-
	(Attack	1.8	0.3	-	-
	(Fight	9.1	-	0.7	0.7
	(Wrestle	7.3	-	-	-
	(Chase	8.6	-	-	-
Defence	(Thrust	0.3	9.7	-	-
Withdrawal	(Retreat	8.4	0.5	0.4	1.8
	(Flee	0.8	11.5	-	-
	(Defeat	-	0.5	-	-
Submission	(Submit	-	-	1.1	2.2
Contactual	(Groom	-	-	2.9	1.8
	(Crawl	-	-	3.6	1.8
Ambivalent	(Up. Posture	0.5	1.3	5.5	7.6
	(Parry	-	-	1.8	2.5
Non Social	(Scratch	-	-	-	-
	(Self Groom	8.1	4.2	13.5	5.5
	(Eat	1.0	-	0.4	1.5
	(Drink	1.6	-	-	-
	(Dig	-	-	-	-
	Total %	71.6	28.5	57.9	42.1
Number of elements observed		274	109	154	112
Number of encounters		8		4	

T.E. total number of behavioural elements performed by both parties to the encounters.
SM Single males. HCM Home Cage males

In encounters of type A (Table 5) the two species behaved very differently. When a Single male vole was introduced into the cage of another (the Home Cage male) the former animal was usually the more active and was first to approach, usually adopting the Elongate Posture. The resident animal would then defend (Thrust) causing the intruder to withdraw (Retreat). This often occurred several times before the Single male became aggressive and attacked the resident. Combat then occurred, the Home Cage male fled and the sequence was repeated, beginning with aggressive approaches by the Single male. Much non-social behaviour was shown by Single males in these contests in typical displacement situations. Although the intruding males all behaved similarly in these encounters, one particular individual was more aggressive than any of the others and was largely responsible for the high values for aggressive behaviour shown in Table 5. This abnormally aggressive individual is also mentioned on pages 37 and 65 .

Apodemus males showed very little aggression in type A encounters. A typical bout began with introductory and ambivalent behaviour by both contestants. Self-grooming often occurred at times of intense introductory activities. The contactual elements, Groom and Crawl, were shown regularly and these two acts were often accompanied by submission in the opponent. In three of the four mouse encounters Groom was exhibited by the introduced male, and in the fourth by the resident.

TABLE 6

Occurrence of elements of various classes of behaviour in encounters between Single females and Home Cage Females

(Encounter Type B)

		T.E. %			
		VOLES		MICE	
		SF	HCF	SF	HCF
Introductory	(Approach	17.4	8.7	9.8	8.2
	(Nose	2.5	1.2	10.2	10.2
	(Investigate	-	2.5	1.6	1.2
	(Sniff	-	0.6	2.0	2.3
Aggressive	(Agg. Posture	-	-	-	-
	(Attack	-	-	-	-
	(Fight	0.6	1.9	0.4	1.2
	(Wrestle	-	1.2	-	0.4
	(Chase	-	1.2	0.4	2.0
Defence	(Thrust	2.5	14.9	-	-
Withdrawal	(Retreat	17.4	4.3	2.7	6.2
	(Flee	1.2	-	2.0	0.8
	(Defeat	-	-	-	-
Submission	(Submit	6.8	-	-	-
Contactual	(Groom	-	1.9	-	0.4
	(Crawl	-	0.4	0.4	-
Ambivalent	(Up. Posture	1.2	2.5	5.5	5.5
	(Parry	-	-	1.2	1.6
Non Social	(Scratch	-	-	-	-
	(Self Groom	5.6	3.1	10.5	7.0
	(Eat	-	0.6	2.3	3.9
	(Drink	-	-	-	-
	(Dig	-	-	0.4	-
	Total %	55.2	45.0	49.4	50.9
Number of elements observed		89	72	126	130
Number of encounters		4		4	

SF Single females. HCF Home Cage females.

Female Clethrionomys in home cage encounters showed much less aggressive activity than did males (Table 6). The sequence of events was initially similar to that observed in male contests but, instead of the intruder becoming aggressive, this animal usually showed submission and was groomed by the resident.

Female mice behaved very much the same as did males of this species in home cage contests but less contactual behaviour was observed. Most aggressive behaviour was shown by resident individuals although, in general, little hostility was seen. Much non-social behaviour was displayed throughout these contests.

Encounters Involving Group Males (Types C, D)

(a) Group Males x Single Males

Group male voles participating in type C contests were not selected from the colonies in a random manner. Observations of behaviour in the colonies had suggested that, among male voles, dominant and subordinate animals existed. Pairs of individuals of each status class were therefore selected from four colonies for encounters against Single males. There was no evidence to suggest a similar difference in status of individuals in male Apodemus colonies, nevertheless pairs of animals from three colonies were chosen so that any differences in their encounter behaviour could be noted. In fact, when meeting Single males, all the Group male mice behaved in a

TABLE 7

Occurrence of elements of various classes of behaviour in encounters between Single males and Group males

(Encounter Type C)

		T.E. %					
		VOLES				MICE	
		SM	GM[1]	SM	GM[2]	SM	GM
Introductory	(Approach	0.3	10.7	15.1	7.9	4.8	9.8
	(Nose	0.3	0.5	-	1.8	7.6	8.4
	(Investigate	-	1.3	-	-	2.8	5.6
	(Sniff	-	-	-	-	1.3	4.1
Aggressive	(Agg. Posture	-	12.5	-	-	-	0.5
	(Attack	-	0.8	0.6	-	-	0.3
	(Fight	-	14.7	0.6	2.4	-	1.0
	(Wrestle	-	9.3	1.2	1.2	-	-
	(Chase	-	9.3	3.0	-	-	1.3
Defence	(Thrust	6.9	-	1.8	11.3	-	-
Withdrawal	(Retreat	0.3	6.9	14.0	5.5	2.8	3.0
	(Flee	9.9	-	-	3.6	1.3	-
	(Defeat	1.6	-	-	-	-	-
Submission	(Submit	1.1	-	-	1.2	0.5	-
Contactual	(Groom	-	-	-	-	-	0.8
	(Crawl	-	-	-	-	-	0.3
Ambivalent	(Up. Posture	1.3	1.6	-	0.6	6.3	6.3
	(Parry	-	-	-	-	1.3	1.0
Non Social	(Scratch	-	-	-	-	-	-
	(Self Groom	0.8	8.0	8.5	7.3	11.1	8.6
	(Eat	-	1.6	3.6	2.4	4.0	5.1
	(Drink	-	-	-	-	-	-
	(Dig	-	0.3	4.8	2.4	-	0.3
	Total %	22.5	77.5	53.2	46.6	43.8	56.4
Number of elements observed		84	291	88	77	172	221
Number of encounters		4		4		6	

SM Single males. GM[1] Dominant group males. GM[2] Subordinate group males.

similar manner and the data from these contests have been aggregated in the usual way (Table 7). The two classes of Group male voles, however, showed differences in behaviour towards Single males and the results of the bouts are presented in a double table (Table 7).

Dominant Group vole contests began with confident approaches by the dominant. The elongate posture was rarely shown by these animals and in three encounters the dominant attacked within the first three minutes. In the fourth bout some preliminary Aggressive Posturing was exhibited by the dominant before combat. This fourth encounter was the least antagonistic, Aggressive Posture and Fight being the only aggressive elements observed. Submission by the Single vole was confined to this encounter, being shown four times during Nose and Investigate by the dominant and before the latter eventually fought.

In the subordinate Group vole encounters aggressive behaviour was shown by both categories of contestant to a similar degree, although no individuals were as offensive as typical dominant males. Non-social behaviour occurred regularly throughout these contests.

The general pattern of Group male mouse encounters of type C was very similar to that seen in home cage encounters. They involved much introductory behaviour which was often associated

TABLE 8

Occurrence of elements of various classes of behaviour in encounters between Group males and Group males

(Encounter Type D)

		Frequency of occurrence			
		VOLES		MICE	
		GMa	GMb	GMc	GMd
Introductory	(Approach	1	17	3	5
	(Nose	-	-	3	2
	(Investigate	-	-	2	-
	(Sniff	-	-	1	1
Aggressive	(Agg. Posture	-	10	-	-
	(Attack	-	-	-	-
	(Fight	-	-	-	-
	(Wrestle	-	-	-	-
	(Chase	-	6	-	-
Defence	(Thrust	-	2	-	-
Withdrawal	(Retreat	3	-	-	3
	(Flee	15	-	-	-
	(Defeat	-	-	-	-
Submission	(Submit	-	-	-	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	-	-	1	1
	(Parry	-	-	-	-
Non Social	(Scratch	-	-	-	-
	(Self Groom	5	4	7	7
	(Eat	3	1	2	3
	(Drink	-	-	-	-
	(Dig	-	-	-	-
Number of elements observed		27	40	19	22
Number of encounters		1		1	

GMa)
GMb)Group males from same vole colony

GMc)
GMd)Group males from same mouse colony

with non-social activities. The bouts were peaceful with slight aggressive activity on the part of the Group males. All animals regularly displayed ambivalent behaviour.

(b) Encounters Between Males from the Same Colony

The two bouts representing encounter type D were staged to test the validity of the observation of dominance which led to the subdivision of the data for vole encounters of type C.

Two voles which seemed to have different status in an all-male colony, and two mice chosen at random from a similar type of colony, were selected for the contests. Each animal was isolated in an unfamiliar cage for 48 hours and then encountered in the neutral cage. The results are shown in Table 8.

Group male b, the vole previously assumed to be a dominant, showed aggressive behaviour and caused flight in the subordinate Group male a. The behaviour of the mice, Group male c and Group male d, was non-aggressive and did not suggest that they occupied different hierarchical positions.

Encounters Involving Group Females (Types E, F)

(a) Group Females x Single Females

This type of contest was totally non-aggressive and comprised almost entirely introductory, ambivalent and non-social behaviour (Table 9). A typically higher proportion of introductory activities was shown by *Apodemus* individuals.

TABLE 9

Occurrence of elements of various classes of behaviour in encounters between Single females and Group females

(Encounter Type E).

		T.E. %			
		VOLES		MICE	
		SF	GF	SF	GF
Introductory	(Approach	15.9	9.1	11.9	8.7
	(Nose	-	-	9.5	10.3
	(Investigate	-	-	4.0	8.7
	(Sniff	-	-	3.2	5.6
Aggressive	(Agg. Posture	-	-	-	-
	(Attack	-	-	-	-
	(Fight	-	-	-	-
	(Wrestle	-	-	-	-
	(Chase	-	-	-	-
Defence	(Thrust	-	2.3	-	-
Withdrawal	(Retreat	11.4	9.1	0.8	4.0
	(Flee	-	2.3	-	-
	(Defeat	-	-	-	-
Submission	(Submit	-	-	-	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	4.5	9.1	4.0	4.0
	(Parry	-	-	2.4	2.4
Non Social	(Scratch	-	-	-	-
	(Self Groom	11.4	13.6	6.3	8.7
	(Eat	9.1	2.3	3.2	1.6
	(Drink	-	-	-	-
	(Dig	-	-	-	0.8
	Total %	52.4	47.8	45.3	54.8
Number of elements observed		23	21	57	69
Number of encounters		2		2	

SF Single females. GF Group females.

TABLE 10

Occurrence of elements of various classes of behaviour in encounters between Group females and Group females

(Encounter Type F)

		Frequency of occurrence			
		VOLES		MICE	
		GFa	GFb	GFc	GFd
Introductory	(Approach	1	1	1	4
	(Nose	-	-	2	4
	(Investigate	-	-	1	-
	(Sniff	-	-	1	2
Aggressive	(Agg. Posture	-	-	-	-
	(Attack	-	-	-	-
	(Fight	-	-	-	-
	(Wrestle	-	-	-	-
	(Chase	-	-	-	-
Defence	(Thrust	-	1	-	-
Withdrawal	(Retreat	1	1	-	-
	(Flee	-	-	-	-
	(Defeat	-	-	-	-
Submission	(Submit	-	-	-	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	-	1	-	-
	(Parry	-	-	-	-
Non Social	(Scratch	-	-	-	-
	(Self Groom	3	2	12	9
	(Eat	-	-	6	4
	(Drink	-	-	-	-
	(Dig	1	-	-	2
Number of elements observed		6	6	23	25
Number of encounters		1		1	

GFa) Group females from same vole colony.
GFb)

GFc) Group females from same mouse colony.
GFd)

(b) Encounters Between Females from the Same Colony

Type F encounters were performed in the same way as were similar male contests (Type D) but, as no formal relationships had been seen among females of either species, pairs of animals were chosen randomly from two colonies.

No behavioural differences were apparent between individuals of either species (Table 10) which further indicated that there was no dominance or subordination among female mice or voles.

Encounters Involving Mixed Animals (Types G, H, I)

(a) Males

Mixed male voles used in encounters of type G and H were those known to have been dominant in their colonies, or were from bisexual pairs and colonies in which they were the only males present. *Apodemus* mixed males were chosen randomly from both pairs and colonies. Table 11 shows the results of such males contested against Single males. The behaviour seen in these bouts was similar in both mice and voles with Mixed males showing high values for offensive activity, and correspondingly high proportions of flight behaviour being observed in Single males.

Encounters of type H involving Juveniles of both sexes and Mixed males followed a similar pattern (Table 12). In these bouts the Mixed males were equally aggressive to male and female Juveniles.

TABLE 11

Occurrence of elements of various classes of behaviour in encounters between Single males and Mixed males

(Encounter Type G)

		T.E. %			
		VOLES		MICE	
		SM	MM	SM	MM
Introductory	(Approach	0.2	10.3	3.3	10.2
	(Nose	0.2	-	0.8	1.4
	(Investigate	-	-	1.9	0.8
	(Sniff	-	-	1.7	1.1
Aggressive	(Agg. Posture	-	16.2	-	8.3
	(Attack	-	2.1	-	5.8
	(Fight	-	9.1	0.6	3.3
	(Wrestle	-	10.7	-	3.3
	(Chase	-	10.5	-	10.0
Defence	(Thrust	11.6	-	-	-
Withdrawal	(Retreat	-	5.7	2.2	2.5
	(Flee	12.1	-	11.1	-
	(Defeat	3.6	-	-	-
Submission	(Submit	0.5	-	-	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	1.4	-	2.5	2.8
	(Parry	-	-	-	-
Non Social	(Scratch	-	-	-	1.7
	(Self Groom	0.9	3.9	5.0	11.6
	(Eat	0.2	0.9	1.4	5.8
	(Drink	-	-	-	-
	(Dig	-	-	0.8	-
	Total %	30.7	69.4	31.3	68.6
Number of elements observed		135	304	113	248
Number of encounters		4		6	

SM Single males. MM Mixed males.

TABLE 12

Occurrence of elements of various classes of behaviour in encounters between Juveniles and Mixed males

(Encounter Type H)

		T.E. %			
		VOLES		MICE	
		J	MM	J	MM
Introductory	(Approach	1.2	23.2	3.7	12.8
	(Nose	0.8	2.0	2.3	4.1
	(Investigate	-	1.2	0.9	1.4
	(Sniff	-	-	-	0.9
Aggressive	(Agg. Posture	-	12.6	-	11.0
	(Attack	-	1.2	-	2.3
	(Fight	-	1.6	-	2.7
	(Wrestle	-	3.7	-	1.4
	(Chase	-	4.9	-	9.6
Defence	(Thrust	12.6	-	-	-
Withdrawal	(Retreat	2.8	8.5	6.4	0.9
	(Flee	6.9	-	12.3	-
	(Defeat	-	-	0.5	-
Submission	(Submit	-	-	0.5	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	1.2	-	-	2.3
	(Parry	-	-	-	-
Non Social	(Scratch	-	-	-	2.3
	(Self Groom	2.4	6.5	3.7	15.1
	(Eat	0.8	5.7	0.5	5.0
	(Drink	-	-	-	-
	(Dig	-	-	-	-
	Total %	28.7	71.1	30.8	69.5
Number of elements observed		71	175	67	152
Number of encounters		4		4	

J Juveniles. MM Mixed males.

TABLE 13

Occurrence of elements of various classes of behaviour in encounters between Single females and Mixed females

(Encounter Type I)

		T.E. %			
		VOLES		MICE	
		SF	MF	SF	MF
Introductory	(Approach	5.3	14.0	12.3	4.9
	(Nose	3.5	1.8	10.7	7.4
	(Investigate	-	-	1.6	4.1
	(Sniff	-	-	4.9	2.5
Aggressive	(Agg. Posture	-	3.5	-	-
	(Attack	-	-	-	-
	(Fight	-	3.5	-	-
	(Wrestle	-	1.8	-	-
	(Chase	-	-	-	-
Defence	(Thrust	7.0	1.8	-	-
Withdrawal	(Retreat	3.5	8.8	5.7	1.6
	(Flee	1.8	1.8	-	-
	(Defeat	-	-	-	-
Submission	(Submit	-	-	-	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	-	-	5.7	4.9
	(Parry	-	-	2.5	2.5
Non Social	(Scratch	-	-	-	-
	(Self Groom	10.5	24.6	13.9	8.2
	(Eat	-	3.5	1.6	4.1
	(Drink	-	-	-	-
	(Dig	3.5	-	0.8	-
	Total %	35.1	65.1	59.7	40.2
Number of elements onserved		20	37	73	49
Number of encounters		2		2	

SF Single females. MF Mixed females.

(b) Females.

Mixed females of both species were selected from the colonies at random and were encountered against Single females in type I contests (Table 13). Mixed female Clethrionomys did show some offensive behaviour towards Single females and defence was exhibited by the latter, but otherwise the two encounters staged for each species were uneventful.

Encounters Between Male and Female Adults (Types J, K)

When Single male voles met Single females (Table 15) no antagonism occurred apart from occasional defence when an opponent approached. However, the reaction of Single male Apodemus to females was very different. These males fought and chased the females intermittently throughout the encounters. They exhibited much typical displacement activity and, after periods of aggressive behaviour, dragged their perineal region over the food dish and cage floor.

Nursing females were extremely aggressive towards intruding males (Table 16) and the encounter pattern observed was the same in both species. Hostilities began when the males approached the nest. The females at first showed Nest Defence but then emerged and attacked the intruders. Between periods of attack the females usually returned to the nest. They appeared to be intensely aggressively motivated and performed extremely abbreviated self-grooming, eating and, in the mouse only, drinking activities. In the Clethrionomys encounter of this type

TABLE 14

Occurrence of elements of various classes of behaviour in encounters between Single males and Single females

(Encounter Type J)

		T.E. %			
		VOLES		MICE	
		SM	SF	SM	SF
Introductory	(Approach	4.8	9.5	15.8	0.5
	(Nose	2.4	4.8	3.2	-
	(Investigate	-	-	3.6	-
	(Sniff	-	-	3.2	0.5
Aggressive	(Agg. Posture	-	-	5.9	-
	(Attack	-	-	2.7	-
	(Fight	-	-	9.0	0.5
	(Wrestle	-	-	0.5	-
	(Chase	-	-	5.9	-
Defence	(Thrust	7.1	2.4	-	-
Withdrawal	(Retreat	2.4	9.5	8.6	0.9
	(Flee	-	-	-	6.8
	(Defeat	-	-	-	8.1
Submission	(Submit	-	-	-	6.3
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	7.1	2.4	1.4	0.5
	(Parry	-	-	-	-
Non Social	(Scratch	-	-	-	-
	(Self Groom	14.3	28.6	6.3	2.3
	(Eat	-	4.8	5.4	0.9
	(Drink	-	-	-	-
	(Dig	-	-	0.9	0.5
	Total %	38.1	62.0	72.4	27.8
Number of elements observed		16	26	160	61
Number of encounters		2		2	

SM Single males. SF Single females

<u>TABLE 15</u>

Occurrence of elements of various classes of behaviour in encounters between Single males and Nursing females

(Encounter Type K)

		Frequency of occurrence			
		VOLES		MICE	
		SM	NF	SM	NF
Introductory	(Approach	4	4	1	1
	(Nose	-	-	-	-
	(Investigate	-	-	-	-
	(Sniff	-	-	-	-
Aggressive	(Agg. Posture	-	-	-	2
	(Attack	-	4	-	18
	(Fight	-	20	-	8
	(Wrestle	-	7	-	14
	(Chase	-	1	-	31
Defence	(Thrust	-	1	-	-
Withdrawal	(Retreat	1	6	-	-
	(Flee	1	-	34	-
	(Defeat	-	-	7	-
Submission	(Submit	-	-	-	-
Contactual	(Groom	-	-	-	-
	(Crawl	-	-	-	-
Ambivalent	(Up. Posture	7	2	-	-
	(Parry	-	-	-	-
Non Social	(Scratch	-	-	-	-
	(Self Groom	1	-	-	5
	(Eat	1	-	-	2
	(Drink	-	-	-	9
	(Dig	-	-	-	-
	Nest Defence	-	4	-	2
Number of elements observed		15	49	42	92
Number of encounters		1		1	

SM Single male. NF Nursing female.

an infant, which had been attached to its mother's teat, became detached and remained on the cage floor when the female returned to the nest. Later, between periods of offence by the female, the intruding male turned its attention to this young vole and attacked and bit it several times.

(iii) Injury During Encounters

The only *Apodemus* to suffer visible injury during the encounters was the male which had been attacked by the lactating female. This animal received cuts on the face, tail and lower area of the limbs. Wounding occurred more often in *Clethrionomys* encounters and several individuals which had been assailed by aggressive opponents were cut in the region of the nose, lips and, less frequently, on the limbs, tail and underside of the body.

(iv) The Aggression Index

An aggression index was constructed as a means of grading male animals according to their aggressiveness at the time they were encountered. Each individual was given a value equal to the total number of aggressive elements it had shown during an encounter. For each species the mean weight of the most aggressive 50% was then compared with that of the least aggressive 50% using a "Student-t" test for small samples (BAILEY 1966). No significant difference was shown for either species ($P > 0.1$) indicating that aggressiveness is not directly related to body weight.

No similar comparison could be made of females because of the extremely small numbers of aggressive members of this sex in both species.

IV. DISCUSSION

1) Diel Activity and General Behaviour

The activity rhythms shown by mice and voles in this study are very similar to those observed by MILLER (1955) in these species in response to a 16 hour day-length. He did not record the total time that his animals were active, but measured the number of "activity periods" per 24 hours. These he defined as "sustained bursts of activity" of less than 30 minutes in length. His study showed the same kind of nocturnal preference in mice (71.9%) and voles (51.4%) as the present experiments. Although the actual number of sorties from the nest is not treated quantitatively in his work, he mentions that they often only lasted for a few minutes.

Field studies have shown that the distribution of *Clethrionomys* in woodland is closely related to ground cover (KIKKAWA 1964, ASHBY 1967) whereas this does not seem to be an important factor affecting the distribution of *Apodemus*. Absence of cover in the open feeding area of the cages may therefore have disturbed the natural activity of the voles in these experiments, and indeed, during observation periods, the voles seemed particularly active inside the nests. Voles did not show any tendency to increase the length of their active periods under the cover of darkness. However, it has not yet been conclusively shown that *Clethrionomys* is insensitive to red illumination (SOUTHERN 1964) and it may be that the observation lights also affected their natural activity.

Field observations of active voles and mice at trapping points by KIKKAWA (1964) and, in the same study, indirect observation methods using radioactive rings and a Geiger-Muller counter have shown that, as might be expected, their activity periods are much longer under natural conditions than in the laboratory. The radioactive tracer study, in which activity periods were measured as time spent away from the nest, showed a period length of 45 minutes to 2.5 hours in voles, and of 1.0 hours to 2.75 hours in mice.

It is suggested that future laboratory studies of activity might benefit by maintaining the animals in an environment which simulates that of the field as closely as possible. An illumination system which provides dawn and dusk conditions should also be used, as gradual changes in light intensity may be important stimuli in the activity rhythms of these species.

Other aspects of the general behaviour of Apodemus and Clethrionomys were obviously affected by laboratory conditions and certain behaviour patterns were not shown at all. For instance, both species are known to spend a considerable amount of their time in nests below ground (SOUTHERN 1964) but the metal cage floors prevented any expression of normal digging or tunnelling behaviour. Much of the behaviour seen in the laboratory is thus unnatural to some extent, and studies made other than in the wild always suffer from limitations imposed by this artificial environment. However, as long as this fact is recognised and taken into consideration, it need not detract from the potential usefulness of the results of such studies.

2) Agonistic Behaviour

(i) Recording and Description

When reading the description of agonistic acts and postures it must be borne in mind that these are not always fixed entities but are often shown as part of a spectrum of activity. Thus, during mutual investigation, one individual may have approached confidently with ears forward whereas the opponent may show definite signs of withdrawal. In this case both animals would have been recorded as performing the act Investigate, even though they were not behaving in an identical manner. Hence, there may be considerable variation within each described response. The naming and classifying of the behavioural elements, while necessary, is therefore somewhat artificial and the transitions involved must be understood.

Further difficulties arose in describing encounter behaviour when the two contestants were engaged in the activities named as Nose, Fight and Wrestle. By their nature these acts required participation by both individuals. But if, for example, Wrestle had been recorded for both animals, each time the act occurred, no indication would have been given as to which of the two was the aggressor. In such a situation, therefore, Wrestle was only recorded for the animal initiating the act.

Again, this is an artificial description of behaviour as obviously the second animal was not doing nothing. It may, for instance, have been attempting to escape or, alternatively, trying to defend. However, these could not usually be distinguished as different behaviour patterns and were observed only as the response Wrestle. The acts Fight and Nose presented similar problems of definition and were recorded only for individuals initiating the act. Of course, on the occasions when both contestants were similarly motivated and both seemed to initiate such behaviour, the act was recorded for each individual.

The use of a portable radio to provide a constant level of background sound during the encounters reduced the reactions of the contestants to noises outside the cage but did not, as far as could be ascertained, affect the behaviour of the animals in any other way.

(ii) Analysis and Interpretation

The elucidation of the underlying motivation of four behavioural elements aided in their classification and confirmed the subjective interpretations of these responses which had been made at the time the encounters were staged.

Nevertheless, the method used, that of calculating the number of times another element preceded or succeeded the response in question, only serves to indicate the likelihood with which one response will follow another. It does not show the degree of motivational association between two responses for which a much more complex analysis, similar to that made by GRANT (1963) on the behaviour of the laboratory rat, would be necessary.

The analyses in section III 3/(iii) used only data from all-male contests because these provided more information than did all-female encounters which, in general, were non-aggressive. Data from encounters between males and females were not used so that behaviour patterns complicated by sexual motivation would be excluded as far as possible.

(iii) Nasils

Various authors have described behaviour patterns in rodents which seem to inhibit or reduce aggression in encounters between two individuals. CLARKE (1956) observed that *Microtus* may adopt a supine posture in response to aggression and this he called "appeasement". In the present study, Submit is similar to the submission posture of *Peromyscus* (EISENBERG 1962). The equivalent response in *Rattus* seems to be "lying down" (BARNETT 1958).

BARNETT (1964) maintains that other responses have a similar function to submission and in these he includes the contactual elements Crawl and Groom. He calls all these movements

"Nasils" which he defines as social signals which tend to inhibit conflict, or which are made during amicable (but non-sexual) encounters between two members of the same species.

It has already been mentioned that in the colonies much more contactual and submissive behaviour was observed among mice than between Clethrionomys individuals, although this difference was not emphasized in encounter experiments.

(iv) Displacement Behaviour

TINBERGEN (1952) defines a displacement activity as follows :

> "A displacement activity is an activity belonging to an executive motor pattern of an instinct other than the instinct(s) activated. .... A displacement activity seems to appear when an activated drive is denied discharge through its own consummatory act(s)."

It is evident, therefore, that one of the main characteristics of displacement behaviour is that it appears irrelevant to the situation in which it occurs. Four elements were described earlier which may have been displacement activities on certain occasions, and the typical displacement situations in which they were often shown have also been mentioned.

TINBERGEN (1952) postulates that there are at least two causes of displacement activity, namely, when there is conflict between two antagonistic drives, and when there is an absence of indispensable releasing stimuli for a highly activated drive. One of these two circumstances might apply to each of the displacement situations described on page 23 Thus, if an aggressive animal which had approached another but not fought or attacked was in a condition where its aggressive and flight drives were simultaneously highly activated, then discharge of drive could be effected through displacement behaviour. Such conflict of activated aggressive and flight drives might also have occurred in two of the other displacement situations; i.e. when an individual had fought or attacked but then retreated, and when a male Apodemus was exhibiting intense introductory behaviour. Alternatively the latter situation may have given rise to conflict between the exploratory and flight drives. The fourth displacement situation, where an individual had chased an opponent on to the bars of the cage and then transferred its attention away from the latter, may have involved the second kind of causation. In this case the chasing individual may have shown a displacement activity because the animal on the cage bars did not provide adequate stimuli for the discharge of the former's highly activated aggressive drive.

The elements Self-groom, Eat, Drink and Dig have all been described as possible displacement activities in other rodent species, notably in Microtus (CLARKE 1956), the house mouse (EIBL-EIBESFELDT 1950), the rat (BARNETT 1958), and laboratory strains of Rattus, Mus, Cavia and Mesocricetus (GRANT & MACKINTOSH 1963). In the present study, however, non-social behaviour was not confined to typical displacement situations but was sometimes shown in circumstances where it did not appear to be irrelevant. Neither were these elements always abbreviated in form, although this was another characteristic of obvious displacement activities. Hence it was often very difficult to interpret any particular response as autochthonous or allochthonous discharge. Further study is definitely necessary for a more complete understanding of displacement behaviour in these species.

The incident described on page 50, in which an intruding male vole attacked a resident infant, was a particularly interesting case of abnormal aggressive behaviour for which two explanations can be advanced. Firstly, it is possible that the male, which was at intervals persistently attacked by the female, was in a condition of high flight motivation but was physically prevented from performing the consummatory act, i.e. flight. If this interpretation is correct then this thwarting of the flight drive could lead to displacement behaviour, i.e. attacking the young vole.

There are, however, several reasons for rejecting this explanation. For instance, at no time did attack by the male show the same abbreviated form as do most displacement acts. Also TINBERGEN (1952) has shown that a displacement activity is likely to be that act which has the lowest activation threshold in any particular set of innate behaviour patterns caused by a single drive. If, therefore, thwarting of the flight drive did cause displacement aggression it might be expected that Aggressive Posture would be performed rather than full-scale Attack with biting.

A third reason for not accepting the displacement theory is that such behaviour would be expected to have been shown at the time when frustration of the activated flight drive was most intense, i.e. during attacks by the infant's parent. In fact this was not observed to be so, and most offensive activity towards the young vole was shown after the female had retired.

If, then, attacking the young vole was not displacement, it follows that it was an autochthonous activity and therefore the male must have been aggressively motivated. However, during normal behaviour such attacks would not be expected, presumably because an infant does not usually provide the correct stimulus for this act. In this instance the male may have been showing behaviour similar to "re-direction activity". This term was proposed by BASTOCK, MORRIS & MOYNIHAN (1953) to describe movements performed by an animal which are appropriate to the situation but are directed towards an appropriate object. Re-directed aggression in Rattus has been described by BARNETT (1958).

3) Mortality in Clethrionomys Colonies

Although injuries suffered by fighting voles did not appear to be directly instrumental in the deaths of certain individuals, the colony experiments strongly indicate that the deaths occurred in some way as a result of aggressive activity. The most acceptable explanation of this mortality is that it was a sympton of artificially produced social stress in the populations. This is the view taken by BARNETT (1964) to explain circumstantially similar, but rather more spectacular deaths in his laboratory populations of Rattus.

Nevertheless there still remains the crucial question; how does a physically non-lethal attack affect the physiology of an opponent, so bringing about its death? This has not yet been satisfactorily answered by any researcher in this field of study. However, it was mentioned earlier that voles occasionally showed symptoms of apparent shock when placed in an unfamiliar environment such as a new cage, and this supports the view that the species may be particularly susceptible to the adverse effects of stress conditions. But, as detailed post mortem examinations of dead animals were not made in the present study, this must be regarded as speculation which will only be proved correct or otherwise after further research into the nature of social stress and how it affects this species.

4) Causes of Fighting and Factors Governing Agonistic Behaviour

The encounters and colony experiments have shown that in neither species was aggressive behaviour an automatic consequence of a confrontation between two animals which were strangers to one another. On the contrary, the extent to which different agonistic behaviour patterns were shown varied according to the conditions under which the individuals met. It has been shown on page 50 that, in male animals at least, aggression is not related directly to body weight and it therefore seems probable that physical size is not an important factor governing aggression. The encounters and colony experiments were designed to indicate how animals reacted to others under different circumstances. Precisely how these circumstances affect the agonistic behaviour of mice and voles will now be discussed.

Various authors have shown that in several rodent species fighting is mainly territorial (e.g. BARNETT 1958, EISENBERG 1962, FRANK 1954), where territory is defined as an area defended (BURT 1943). Indeed, BARNETT (1964), speaking about avian and mammalian species in general, says :

> "......... it seems that some form of antagonistic behaviour has often evolved as a result of the advantage it confers by inducing dispersion."

Any evidence of territoriality of mice and voles in the laboratory would be expected to be shown in the home cage encounters. In fact very little aggressive behaviour was displayed by resident animals and this was especially marked in the males of the two species. There is a possibility that removal of the nests from the home cages a short time before the encounters began altered the familiar environment so that the residents were no longer stimulated to defend the home area. However, it was noticeable that in male Apodemus home cage encounters contactual behaviour was very much in evidence, and this is perhaps an example of inhibition of aggression by the exhibition of nasils in a potentially hostile situation. On the other hand, no satisfactory explanation can be given of the offensive activity of intruding Single male voles in these contests.

The formation of unisexual colonies showed how individuals behaved when confined with others of the same sex. It was observed that in both species aggression occurred readily between males, but that females were comparatively non-hostile towards each other. In Apodemus male colonies this period of aggression was short-lived, but among male voles fighting was more prolonged and preceded deaths in four colonies. Simple dominance-subordination relationships were established in several all-male vole colonies and later encounter experiments showed that dominants were much more aggressive towards unfamiliar males than were subordinates. After the initial period of aggression little fighting was seen in undisturbed male colonies. The introduction of a strange male, however, was nearly always followed by attacks on this interloper. Hence, it would seem that in neither species does crowding per se cause antagonism between males, but that aggressive behaviour is stimulated by the presence of an unfamiliar male.

BARNETT (1958) suggests that in male rats fighting depends on the following two conditions; being in a familiar place and encountering a stranger. He also claims that strangeness is only important in the context of a territorial situation. Now, although both these factors may play their part in determining aggression in Clethrionomys and Apodemus, the present study indicates that strangeness alone is sufficient to stimulate offensive activity in males. It might be thought that a colony male assaulting an intruder is showing territoriality, but the same male attacks just as vehemently when confronted with a stranger in a neutral cage encounter, i.e. in totally unfamiliar surroundings. More detailed experiments designed to establish the importance of territoriality in these two species would greatly add to an understanding of this agonistic behaviour.

Among male voles it seems that previous experience of fighting probably has some influence on an animal's aggressive activities. In the home cage encounters, for instance, an intruding Clethrionomys male which had fought in trial encounters early in the study was particularly aggressive (page 44). When this individual was later introduced to a cage containing a pair of males, colony C_8, it was most aggressive and became dominant in the colony (page 37). It is possible that experience of fighting is also an important factor in maintaining a dominant's status in his colony.

Whatever the underlying causes of fighting in voles and mice, in both species the aggression of males is exacerbated by association with females. This was shown during the establishment of bisexual colonies, in the bisexual colony introduction experiment and in Mixed male encounters. BARNETT (1958) found that male wild rats showed similar excessive fighting in colonies containing females. In the present study the only bisexual colonies containing more than one male which were completely harmonious were those comprising litter mates in which, obviously, no animal was "strange" to any other.

The way in which the sex of the opponent influenced agonistic behaviour was demonstrated in male-female encounter experiments and during the formation of bisexual pairs and colonies. Neither male nor female voles were aggressive towards members of the opposite sex, although defence was initially shown against any approaching unfamiliar animal. Similarly, female Apodemus were not aggressive towards males, but the converse is not true. Male mice did seem to be hostile towards strange females but, as mentioned earlier, it is possible that sexual behaviour was somehow involved. Unfortunately the scope of this study was too limited to provide any additional information on this subject.

The breeding activity of the animals is almost certain to affect the frequency with which various behaviour patterns are shown in the social behaviour of the two species. All the adults studied were in breeding condition and so variations in behaviour due to seasonal changes in gonadal activity remain unknown. The encounters with females were too few to demonstrate how individuals behave at different times during the oestrus cycle. Encounter experiments using lactating females did, however, show that these were most aggressive towards strange males near the nest, a phenomenon which has been recorded in other rodents (e.g. CLARKE 1956, EISENBERG 1962).

5) A Comparison of the Social Behaviour of the Two Species

When mice and voles are compared with respect to their social behaviour, several differences are immediately apparent. Apodemus is the more tolerant species, showing less aggression, and quickly adapts its behaviour to a change in the social environment enabling the formation of large stable colonies. In the laboratory experiments fighting never resulted in deaths and little injury was inflicted. The species in general spends a considerable amount of time in exploration of the physical environment and of other animals of the same species (introductory activities). Contactual behaviour was observed in mice much more frequently than in voles and it seems that this may play some part in reducing or inhibiting intraspecific fighting.

Clethrionomys are, on the whole, more aggressive and artificial crowding of individuals resulted in the death of several male animals. Colonies of male voles often appeared to achieve stability by the formation of a system of formalised social relationships in which one animal was dominant over subordinate males. However, even in these colonies any slight disturbance of the social structure markedly affected the stability of the system.

What, then, is the likelihood that these differences in the laboratory behaviour of the two species reflect similar differences in natural populations? Direct observations of mice and voles at trapping points in the field led KIKKAWA (1964) to suggest the existence of a social hierarchy in *Clethrionomys*, where he recognised dominant males, but not in *Apodemus*. He also reported that voles were frequently aggressive towards others whereas he did not observe fighting among mice. BROWN (1966), however, has claimed that certain male *Apodemus* hold the positions of "powerful dominants" in field populations and that these animals control large territories. She further maintains that :

> "During the main breeding season the adult male *Apodemus* .... will kill or drive away all who might interfere with his activities."

Unfortunately she gives no evidence of any such mortality nor does she provide details of behaviour actually observed in the field. CLARKE (1955) working with open-air confined colonies of *Microtus* reported signs of differing social status among males. The agonistic behaviour of this species was studied by the same author (1956) and is in many respects similar to that of *Clethrionomys* seen in the present study.

Laboratory studies, by their very nature, cannot be expected to provide comprehensive information about field behaviour. Nevertheless, major species contrasts in behaviour observed in artificial populations do represent the different ways in which those populations adapt to the new environment. Hence it is reasonable to suppose that under crowded conditions in the field some kind of dominance - subordination relationships may exist between *Clethrionomys* individuals living in close proximity, and that this might be a means of reducing intraspecific conflict. It is similarly possible that *Apodemus*, being a more tolerant species, achieves stability by using a system of nasils which probably includes submission and contactual behaviour.

As a field population builds up, the frequency with which an individual meets others will increase. The present colony experiments suggest that, whereas mice would quickly adapt to the changing social structure of the population, Clethrionomys individuals would become more antagonistic as they met an increasing number of strangers. It was mentioned earlier that previous experience of aggression may also augment the offensiveness of male voles. Hence we see here a kind of positive-feedback system, with a high population density being accompanied by an "aggression build-up" in the male vole population. Such an occurrence might well lead to a situation where the social stress factor becomes important within the population which could be one cause of the crash phase in the population cycles in this species (ASHBY 1967). From his studies of confined populations of Microtus CLARKE (1955) postulated that intraspecific strife is a primary cause of population cycles in that species. The whole subject of social stress as a factor in population regulation has been reviewed by BARNETT (1964).

One of the main facts established by the present study is that, in both species, aggression is shown mainly by adult males in breeding condition. The importance of such aggression in the population regulation of Peromyscus has been shown by SADLEIR (1965) and HEALEY (1966) who found that high juvenile mortality in the summer breeding season was correlated with an increase of aggressiveness of the males. There is some evidence that low recruitment of juveniles in the early part of the breeding season also occurs in Apodemus (ASHBY 1967). In the present study males of both species which have been living with females are intolerant of juveniles of both sexes. If similar behaviour occurs in the field this hostility would aid in dispersal of juveniles during the breeding season and may thus be a regulatory factor in the population dynamics of the two species.

It will be evident that much of the discussion in this last subsection has been speculative. This is mainly due to the fact that very little information is available about the behaviour of these and similar species under natural conditions. Although the problems involved in observing the behaviour of small nocturnal mammals in the field are great, such studies are of primary importance in gaining any real insight into the role of social behaviour in the population ecology of these species.

V. SUMMARY

Wild *Apodemus* and *Clethrionomys* were trapped and brought into the laboratory where they were kept in cages alone, in pairs and in groups. These were watched over a period of ten weeks. The animals were individually identified and their general behaviour was studied. Details of fighting and mortality in the colonies were recorded.

The activity of the two species was examined. The diel rhythms observed agreed closely with other laboratory studies. *Apodemus* was found to be the more nocturnal species.

Intraspecific encounters between two individuals were staged and the resulting agonistic behaviour described.

A simple analysis was carried out of behavioural sequences containing certain responses in order to elucidate the motivational basis of the latter.

Variation in behaviour shown during bouts is explained by differences in age, sex, breeding condition, social background and previous fighting experience of the contestants, and the circumstances under which they met.

Males are more aggressive than females in both species although voles are generally more antagonistic than mice. The main stimulus for fighting in males appears to be the presence of another strange male. Aggression in males is exacerbated by the presence of, or recent contact with, females.

Conflict between the sexes was not observed in voles. Male mice, however, fought and chased females when they first met but it is thought that sexual motivation may be involved. Lactating females were extremely aggressive to unfamiliar males in both species.

Territorial activities were not convincingly demonstrated in mice or voles. Previous experience of fighting may be important in determining the aggressive behaviour of male Clethrionomys.

Dominance-subordination relationships between male voles were seen in several colonies. There was never more than a single dominant in each colony. No difference in status was recognised between other members of these colonies, between female voles, or in Apodemus.

Mortality in Clethrionomys colonies seemed to be associated with fighting. One cause of these deaths may have been the effects of social stress.

The suggestion is made that, after stability has been reached, each species suppresses potential hostility in the colonies in a different way; in Clethrionomys by the development of a system of dominance-subordination relationships, and in Apodemus by using a specific set of social releasers (nasils). The effects that such behaviour might lead to under field conditions is discussed, bearing in mind current theories about the regulation of population density in these two species.

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