THE SOCIAL ORGANISATION AND BEHAVIOUR OF THE STRIPED FIELD-MOUSE RHABDOMYS PUMILIO (SPARRMAN 1784): STUDIES IN CAPTIVITY AND IN THE FIELD

by

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ABSTRACT

In Part I of this study, the social organisation and communicative behaviour of the striped field-mouse *Rhabdomys pumilio* was studied in a large outdoor cage. It was found that the social organisation was based on a male dominance hierarchy, with the development of territory in the dominant male and breeding females. The level of testosterone in males was found to be a reliable index of social status. Analysis of spatial relationships and behavioural interactions among individuals showed these factors to be closely related to social status. *Rhabdomys* was found to have a well-developed repertoire of visual displays, to use ultrasonic calls in social interactions, and to be dependent, to a certain extent, on chemical communication.

In Part II, an attempt was made to confirm these findings in the field. Home ranges on the Cape Flats were determined by tracking; testosterone was used as an index of social status. Similarly structured hierarchies were found, as well as indications of territoriality. Home range sizes, distribution and spatial relationships of individuals were determined. *Rhabdomys* was found to prefer habitats of good ground cover.

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INTRODUCTION

Rhabdomys pumilio, the four striped field mouse, is perhaps one of the better known African murid rodents. It has a wide but discontinuous distribution ranging from southern Africa (except the eastern corridor of Northern Zululand, Mocambique, and the lowveld portion of the Kruger National Park) including Angola, Botswana, Rhodesia and Malawi, to East Africa where it has been reported in Kenya, Tanzania and Uganda (Meester and Setzer 1971) and also in the Upemba in Zaire (Misonne 1968).

The southern African range includes a number of biotic zones (Moreau 1952), namely the South-West Cape, the South-West Arid and Southern Savanna. However, Davis (1962) considered Rhabdomys to be primarily a Savanna species, describing it as near-endemic to the Southern Savanna, but having marginal status in the South-West Cape and South-West Arid. Rhabdomys is apparently absent from the montane and subtropical evergreen forest regions distributed within the South-West Cape and Southern Savanna zones.

The single species pumilio is recognised (Meester and Setzer 1971), although there is evidence for subspecific division (Coetzee 1970). The average adult weighs 40-50 grams, although they have been known to reach 70 grams or more (David 1979; personal observation). Roberts (1951) describes the colour as speckled buffy on a dark grey background; there is a certain amount of variation among individuals, ranging from grey to yellowish-brown. The underparts are buffy whitish and the tail dark brown above the buffy beneath. Characteristic are the four dark stripes running longitudinally down the back; these stripes are interspersed by three light stripes, often whitish in colour. The length of the tail tends to vary with climate (Coetzee 1970); this has been used as a taxonomic character at the subspecific level (Roberts 1951).

A number of studies have been carried out on various aspects of Rhabdomys' ecology and behaviour: Choate (1972) as part of a study on Rhodesian rodents in general; Stiemie and Nel (1973) on nest-building behaviour; Brooks (1974) made a detailed study of *Rhabdomys* ecology in the Transvaal with special emphasis on the ecological relationship with *Otomys* the vlei rat; Marais (1974) on the behaviour of a captive colony in relation to increasing population density; and studies by various members of the Zoology Dept. U.C.T. on different aspects of Rhabdomys' ecology on the Cape Flats, in particular a detailed study of population dynamics (Jarvis and David unpublished).

The Cape Flats supports very high numbers of *Rhabdomys*: David (1979) has estimated 200 mice/ha in a peak year. The reason for this is the abundant food supply in the form of seeds of alien vegetation, in particular two species of *Acacia*: *A. seligna* (Port Jackson willow) and *A. cyclops* (Rooikrans). These were imported from Australia in the latter part of the last century in an attempt to control the sand dunes, and have proved so successful that they are now in the process of ousting the indigenous vegetation (Taylor 1972) which is now present as relatively isolated patches of *Metalasia* and *Rhus* dominated stands (Taylor 1972). Apart from food, the abundant vegetation supplies adequate cover, on which Rhabdomys, as a diurnal animal, is particularly dependent (Nel and Rautenbach 1975).

The studies done on *Rhabdomys* indicate that the mouse is diurnal, although Smithers (1971) observed a trend towards crepuscularity; primarily granivorous, but may be herbivorous at times (Brooks 1974; Shelton 1975; King 1976), and its local distribution tends to be limited by the availability of adequate cover (Brooks 1974; Nel and Rautenbach 1975). Behaviour observations show *Rhabdomys* to be aggressive in nature (Choate 1972), establishing clear-cut dominance hierarchies in a laboratory cage (Murray 1974) with the emergence of territorial behaviour in a more spacious environment (Marais 1974). Choate (1972) believes that this intolerance prevents the population erruption that might otherwise occur.

Rhabdomys, by virtue of its abundance and granivorous feeding habits, resulting in attraction to cultivated land and crops, is of economic importance to man; Smithers (1971) in fact reports that it may enter buildings and live as a commensal to man. Delany (1972) has reported extensive damage to stands of wheat and maize in East Africa, and, citing other authors, to oil palms in eastern Nigeria. Damage to conifer plantations has also been observed (Hechter-Schulze 1962). On the brighter side, however, *Rhabdomys*, unlike a number of other African rodents such as *Praomys* and *Tatera*, apparently has no part in the transmission of bubonic plague (Davis 1964).

All the work that has been done on *Rhabdomys* to date has been either purely ecological (e.g. Brooks 1974; David unpubl) or behavioural studies carried out under essentially artifical conditions (e.g. Choate 1972; Marais 1974), and questions arise as to the relevance of the latter findings to the natural situation. Unfortunately the ethologist wishing to study small mammal behaviour is faced with the almost insurmountable problem of not being able to see the animals he wishes to observe: they are either nocturnal or, as is the case with *Rhabdomys*, diurnal, but preferring dense cover as habitat. In an attempt to circumvent this problem, I decided to set up a captive colony of *Rhabdomys* in reasonably natural conditions for detailed observations of behaviour and social organisation, and then to go out into the field and attempt, by the necessarily indirect means of hormone assay as an index of rank and tracking for the determination of home ranges, to confirm the initial findings.

The aim of this project, therefore, is a determination of the social organisation of *Rhabdomys*, by the description of dominance relationships, spatial organisation, including territoriality and individual distance, and, lastly, communication, and its role in the maintenance of the social organisation.

PART 1

STUDIES ON RHABDOMYS IN CAPTIVITY

CHAPTER 1

SOCIAL ORGANISATION

1.1 INTRODUCTION

Social organisations are usually classified into two basic types: those based upon a dominance hierarchy and those based upon territoriality. Both of these are closely related and may, in fact, be considered as the two extremities of a single continuum. The dominance hierarchy has been defined (Wilson 1975) as "the set of sustained aggressive-submissive relations" among a group of animals; a territorial system is one in which members of the group defend areas of ground. Thus the hierarchy may be thought of as a group of aggressively ordered animals coexisting within a common territory (Wilson 1975): the territorial system may be considered as a hierarchy with an added spatial dimension.

Wilson (1975) distinguishes between "absolute" and "relative" hierarchies; in the former, the rank order is maintained wherever the group goes; in the latter, high ranking individuals may yield to those of lower rank when the latter are at or near their sleeping places (Leyhausen 1956). Thus, in the "relative" hierarchy, a spatial dimension is beginning to be added. In this connection, the phenomenon of "individual distance", defined as "the area round a bird, which moves with it, has no topographical reference, and into which no other individual is allowed to come" (Conder 1949) is pertinent; this may in fact be thought of as a "moving territory" which, if at a further point in evolution becomes established in a specific area of space, becomes a territory in the true sense of the word.

The concept of territory is an old one: references may be found in Aristotle and Pliny regarding territorial behaviour in male birds. Early scientific workers include Moffatt (1903) who is credited with the introduction of the word into the scientific literature, Howard (1920) and

Carpenter (1934). Territory may be defined, following Noble's (1937) classic definition, simply as "any defended area". Various types of territories have been observed, especially among birds, e.g. nesting territories, feeding territories and so forth; and much has been written about the adaptive significance of territoriality, especially with reference to population regulation (e.g. Kalela 1954 and especially Wynne-Edwards 1962).

It was perhaps Hediger's (1942) distinction between "distance" and "contact" species that focussed the attention of ethologists on spatial relationships in a non-territorial situation: that of flocks or transient groups. Leyhausen (1950) describes the phenomenon of individual distance rather whimsically in his fable of the porcupines who, huddling together one cold night, discovered that there was a certain minimum distance that has to be maintained between individuals which they called "decency and good manners". Although most studies of individual distance have been done on birds (e.g. Conder 1949; Emlen 1952; Crook 1953), at least two mammalogists have recognised the phenomenon: Lockley (1961) who observed a correlation between greater individual distance and higher social rank in the wild rabbit, and Brown (1966) who described "individual" or "safety" distances in groups of woodmice, Apodemus.

Carpenter (1952) proposed that "the spatial topology of organised groups can be measured and used to indicate strengths and variations (probabilities) of interaction behaviour and the degree of social cohesiveness characterising genera and species". His suggestion was apparently not followed up until the mid-sixties (Quiatt 1966; Kummer 1967). Kummer (1967) used spatial relationships, in terms of age and rank classes as an estimate of the strength of the social bond between them, working on the hamadryas baboon Papio hamadryas. In a later paper Kummer (1971) wrote that "most students of primate behaviour would agree that there are two proven parameters of describing the grouping tendencies of a population: the distribution of individuals in space and the frequencies and types of directed communicative acts among them". Altmann (1965, 1967, 1968) in his series of studies on the rhesus monkey Rhesus macaca, preferred to estimate the interactional probability by the second method, that of observing interactional behaviour itself.

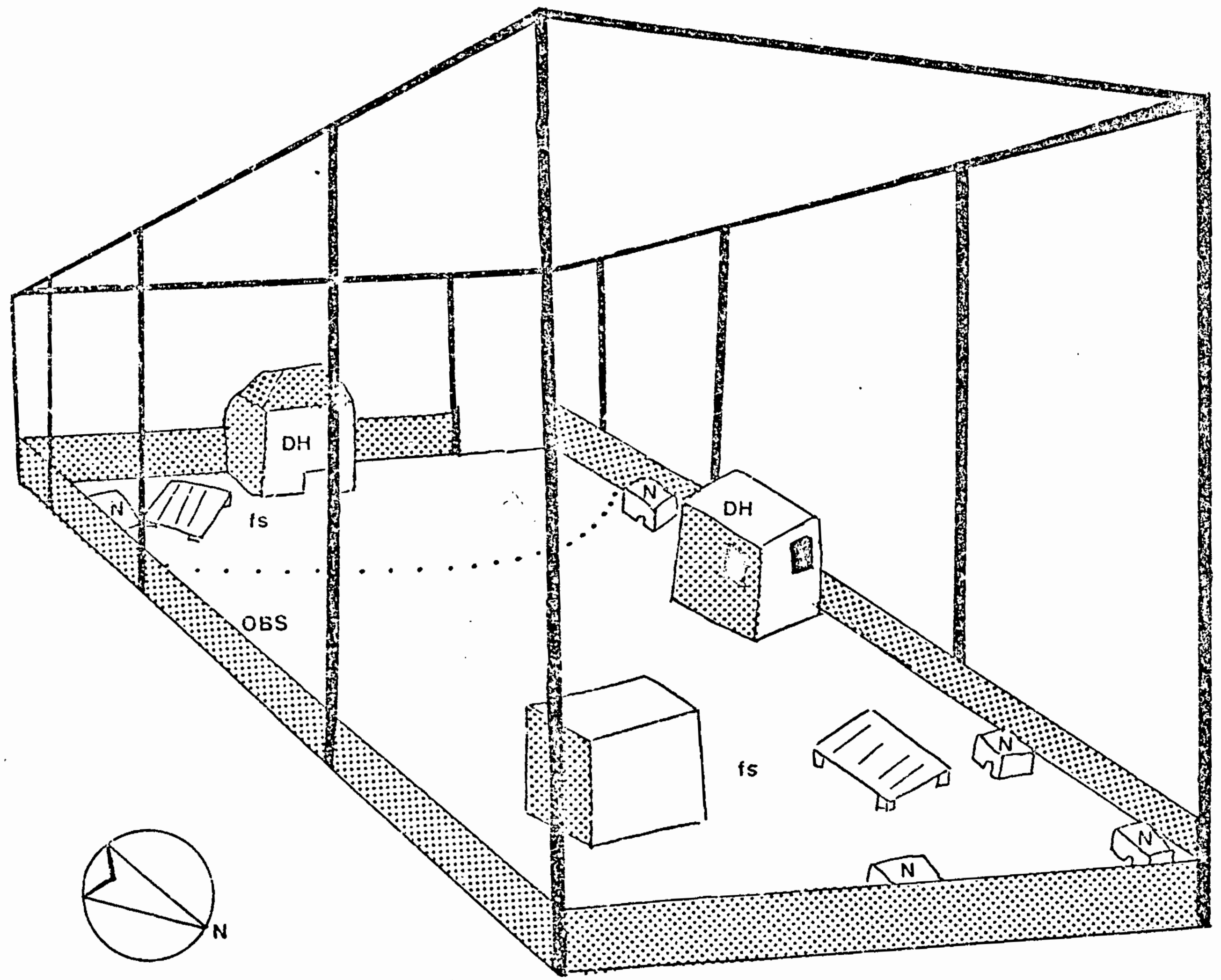
I propose to use both methods to describe the social organisation of Rhabdomys, and to compare the two. The first part of this section is an analysis of the social organisation of the captive colony, in terms of dominance relationships, territorial behaviour and an analysis of spatial relationships between individuals, using an adaptation of Kummer's (1967) method. Although this was devised and used in the study of primate groups, there is no reason why it cannot also be used in the description of a rodent society. I have also included two further aspects that I feel to be of importance here: activity patterns and the utilisation of the environment in terms of nests, burrows and runways. The second part considers interactions between individuals, loosely divided according to visual acoustic and chemical means of communication.

1.1.1 Materials and Methods

Animals were live-trapped on the Cape Flats (on the farm "Delft" near Faure) using trap-lines rather than a grid. After transportation to the Zoology Department, University of Cape Town, they were weighed, sexed and marked by ear-clipping. This technique of clipping small pieces of the outer edge of the pinna, affords easy recognition of animals for observational studies, and appears to be relatively painless for the animal and allows at least a dozen animals to be so marked. Certain animals could also be recognised by abnormalities and the tail; e.g. if it was broken in a particular place, or if part of the tail had been lost.

Observations were carried out in a large outdoor cage, dimensions 10 x 5 m (Figure 1.1). This was constructed of wire mesh (chicken wire) closed at the top with the same material, and had galvanised sheeting running from approximately 0,5 m above ground to about the same depth below. The cage contained two hutches housing dassies (Procavia capensis), a large upturned wooden box and two more wooden structures approximately 0,5 x 0,5 m in size and 15 cm from the ground. Five

FIGURE 1.1. Diagrammatic representation of the cage in which the captive colony was housed.



wooden "nestboxes" (dimension 30 x 30 x 15 cms - with an opening 6 cm high) as well as plenty of cover in the form of branches and small shrubs were placed in the cage.

Observations were always carried out from within the case, against one side. A tape-recorder (battery-run cassette recorder) was used for quantitative observations; the tape was left running throughout the observation time. The tape was then transcribed using 30 second time intervals. Qualitative observations, using a notebook, were also made. Binoculars were used for observation and identification of animals. Food was provided at two sites, one in the south-eastern and one in the north-western side of the cage: the food consisted of sunflower seeds and dried maize as well as, on occasion, fresh vegetables. Water in two drinking troughs was provided in the same places.

Eighteen mice were released into the cage in March and April 1977. A period of 8 weeks was allowed to elapse before quantitative observations were begun: during this period while the animals settled down and established their social relationships, preliminary observations were carried out. The object of these preliminary studies was, firstly, to determine the most efficient sampling procedures, and, secondly, to draw up a provisional catalogue of behaviour patterns. Quantitative observations were begun in June 1977, in the following areas.

Activity Patterns

One day per month was set aside for the assessment of activity patterns. If the weather was bad, the assessment was postponed until the nearest fine day. The technique used was scan sampling at half hour intervals (Altmann 1974): each half hour an assessment was made of the numbers of animals active. Because of the changing numbers in the population throughout the year, these figures were expressed as a percentage. Observations were begun at sunrise (05h30 in summer, and 07h30 in winter) and discontinued at sunset (19h30 in summer and 18h00 in winter).

Observations on dominance and territorial relationships

Observations in this area were carried out simultaneously with observations on behaviour patterns (Part 1, Chapter 2). Using the methods described above, observations were carried out to sample as much of the day's activity as possible.

Testosterone Measurement

Male animals were lightly anaesthetised with ether and about 400 µl bled from the retro-orbital sinus using heparinised haematocrit tubes. The blood was centrifuged and the plasma deep-frozen. Radioimmunoassay for testosterone was done by the Department of Chemical Pathology, Medical School.

Spatial Relationships

These were determined by the nearest-neighbour method, adapted from Kummer (1967) as follows: A "subject individual" is selected at random, his or her sex and rank (alpha, beta or omega male, female) noted, and the three nearest neighbours determined. A contingency table is then drawn up, using "subject individuals" as headings for the columns, and "class of neighbour" as headings for the rows. The total number of times a particular class is nearest-neighbour to a particular class of subject individuals gives the observed frequency for that box in the table. Expected frequencies are determined by calculating the proportion of each class in the colony, e.g. beta males formed 25% of the population, by an hypothesis of random distribution, 25% of the nearest-neighbours of any class of subject individuals (with the exception of beta males) should be beta males. The observed and expected distributions may then be compared by a X^2 test, for significant difference.

1.2 RESULTS AND DISCUSSION

1.2.1 The Colony: An Overview

By June 1977 when observations on the colony were begun, there was a total of 15 mice: 9 males and 6 females, as follows:

Males: M2
3
4
5
6
7
9
10
11

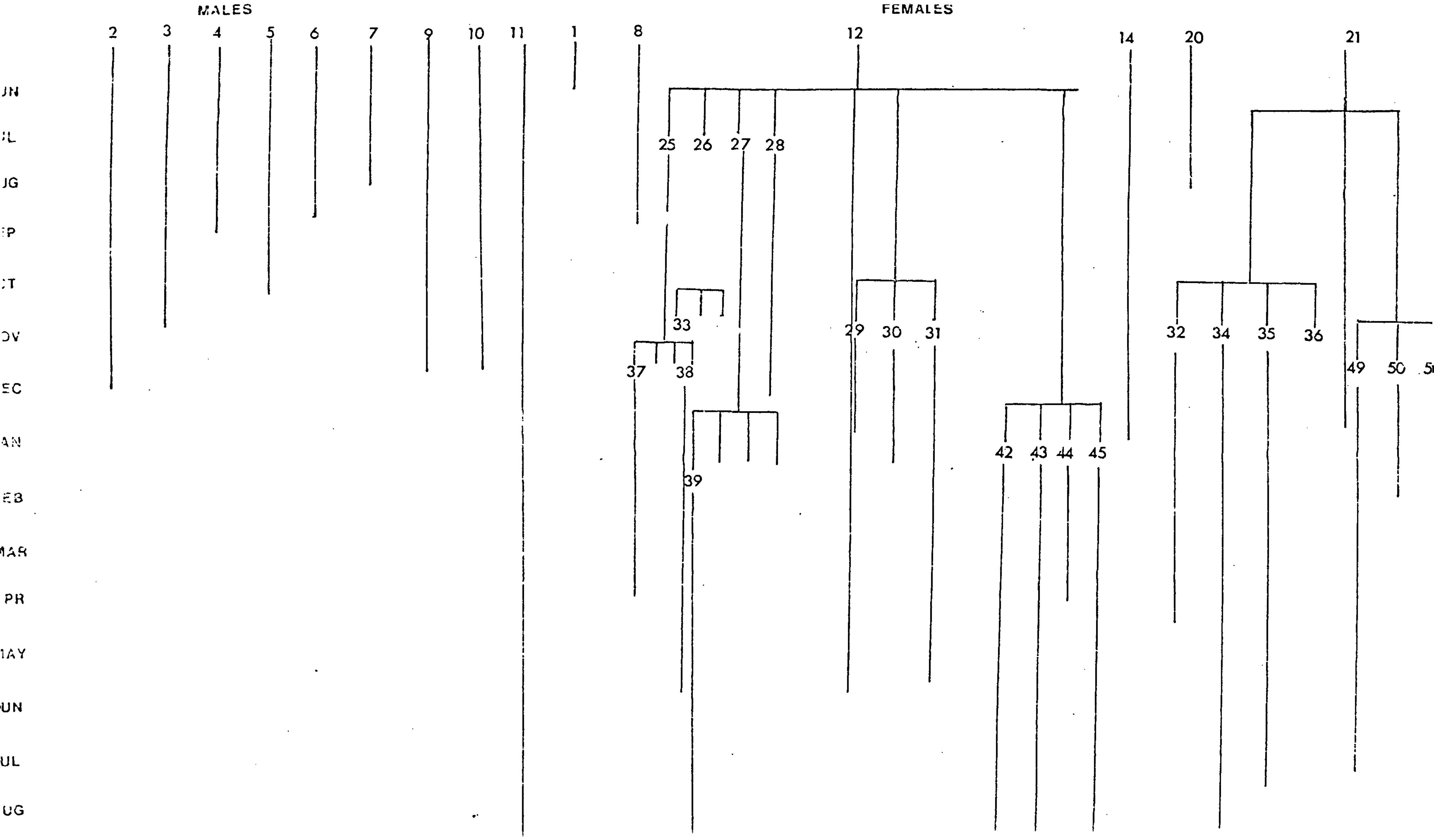
Females: F1
8
12
14
20
21

Figure 1.2 shows a graphical representation of the lifespans and relationships among the colony.

Towards the end of June 1977, M2 and F12, who had established a territory on the south-eastern side of the cage, produced a litter of 4 animals (FF 25,26,27; M28). It is unusual for Rhabdomys to breed at this time of the year, in mid-winter, and it is perhaps significant that the animals concerned were the dominant male, female who were also territorial. Approximately one month later, the same pair produced a second litter. This time of 3 young (M29, F30, M31). All these juveniles lived permanently within the south-eastern territory.

The rest of the colony meanwhile inhabited the north-western part of the cage. Four of the males were relatively dominant (MM 3,7,10 and 11) and were designated beta males; males 4,5,6 and 9 were classed as omegas. Of the betas, M7 died of natural causes in August; in October, when most of the animals were in breeding condition, rivalry ensued between MM 10 and 11, resulting in the death of M10 in late November. Examination of his body showed numerous wounds, particularly on the rump and tail, as a result of fighting. Male 3 was interesting in that he took little part in the social activity of the colony and established his residence inside the dassies' hutch, emerging only to feed: he was often observed sunbathing on a ledge of the hutch. Whether this could be classed as territorial

FIGURE 1.2. Life histories of the members of the captive colony. The length of the line below each animal's number denotes the length of time it was present in the colony.



behaviour is difficult to say; although no actual defence of the hutch was observed, the other mice generally did not enter it; it was also observed that Male 2 always stopped chasing Male 3 at the hutch's entrance. In November 1977 Male 3 disappeared.

Thus by the end of November, M11 was the sole beta of the original batch of males. However, Male 28, one of the recently matured offspring of M2 and F12, assumed beta status at about this time. In mid-December, M2, the dominant, was discovered dead in his nest; after this, a great deal of aggression was observed between the two beta males, M11 and M28. By early January, however, M11 had apparently established himself as the alpha: M28 meanwhile had been badly injured in the fighting (from attacks from the breeding females as well) - his tail was badly broken, requiring it to be carried almost vertical while running and his rump was almost devoid of skin. On 30 January 1978 he was found dead.

Of the four omega males, Male 4 died in early September 1977, while Male 6 vanished at the beginning of October 1977. The two remaining omegas who survived into the breeding season, MM 5 and 9, suffered a great deal at the hands - or teeth - of the other animals. Male 5 disappeared at the beginning of November 1977 leaving M9 as the sole omega. It was not only the other males who displayed aggression, but also the breeding females, in particular F12 and one of her daughters, F27. The unfortunate omega tended to hover on the outskirts of any feeding group, ready to flee at the slightest movement from a dominant animal. At the end of December 1977 M9 disappeared.

Of the four females remaining after the death of F1 and disappearance of F20, two were designated as omegas: FF 8 and 14. Of the other two (FF 12 and 21), F12 was the dominant aggressive consort of the alpha male, M2, inhabiting the south-eastern territory. F21 lived in the north-western area and was often observed in association with M11, the beta male. She produced a litter of 4 (FF 32 and 34 and MM 35 and 36) in November, and another in December. At this time there were large numbers of juveniles in the colony. Only a relatively small proportion reached full maturity as a result of mortality from drowning in the water trough (4 deaths - 2 of these belonged to F12), getting caught in the wire mesh of the cage (3 deaths) or simply disappearing, presumably having escaped from the cage. By December there were five actively breeding females in the colony - FF 12,21,25,26,27. F14, as far as is known, never bred - and it became exceedingly difficult to differentiate the origin of the juveniles. In January F21 disappeared. Of the two omega females, F8 disappeared in September, and F14 was found dead in December. For about 2 weeks prior to her death, her back and tail were badly wounded and after bleeding as a result of bite wounds inflicted primarily by FF 12 and 27, who were particularly aggressive towards her. It is interesting that none of the recently matured juveniles at this time, the offspring of the dominants M2 and F12, assumed omega status: Of the 3 females of the first litter, one (F27) was particularly aggressive, while the other two, FF 25 and 26, lived largely in the south-eastern territory, feeding with their parents and other juveniles, and only establishing separate nests when breeding. F25 died in January 1978, cause unknown, and F26 disappeared in March.

Meanwhile, the new alpha, M11, had established himself in the south-eastern territory with F12. He was now the sole remaining male of the colony founders, and she was the sole surviving female. Of the recently matured juvenile males, Male 39 was the most dominant, in association with two other betas M31 (offspring of F27) and M45 (uncertain parentage, F25 or F26). Two omega males were distinguished: MM 41 and 44 (also uncertain parentage - either F25 or F26). All these animals survived without mishap until June 1978 when observations were discontinued. It was interesting to note that during the non-breeding season, when aggressive behaviour is supposedly at its lowest, the alpha male, M11, and the most dominant of the betas, M39, exhibited a great deal of social interaction, particularly in the form of sunbathing together, a phenomenon that was not observed between Male 2, the previous alpha, and Male 11, then a beta. One might in fact hypothesise that in the absence of much overt aggressive behaviour, that the two males were of equal status; it was unfortunate that observations could not be continued into the following breeding season to see the outcome.

Among the females, the only significant observation made was the absence of omega females. This may have been due to the fact that the breeding season was drawing to a close. F12 died in April 1978, and was not replaced as the consort of the alpha male.

Observations were discontinued in mid-June 1978; the colony was, however, maintained for as long as possible while experiments were being carried out. Unfortunately, building operations in the Department shortly afterwards necessitated the breaking up of the colony and the transfer of the animals indoors to the laboratory.

1.2.2 Activity Patterns

Walker (1968) describes Rhabdomys as diurnal; Smithers (1971) while agreeing with this, observed occasional nocturnal activity with a trend towards crepuscularity. Choate (1972) found that, in the laboratory, Rhabdomys was active mainly at midday, while Christian (1977) in the Namib Desert, observed no tendency towards crepuscularity or nocturnality; the mice, on the contrary, displayed continuous activity throughout the day.

The activity patterns of Rhabdomys under semi-natural conditions are shown in Figure 1.3. These findings appear to confirm the findings of Christian (1977) rather than those of Smithers (1971). These observations are supported, in a qualitative way, by observations on mice kept in captivity. At one time I kept a group of 6 mice at home with me for a period of nearly four weeks. I observed that they woke and began moving about regularly as soon as the room became light in the morning; in the evenings they would retire to the nest, become quiet, presumably sleeping when darkness fell; but if an artificial light was switched on, they would almost immediately become active again. No tendency towards noctural activity was observed at all. From Figure 1.3 it can be seen that, especially during the summer months, November to March, there is a clear trend away from activity in the middle of the day and a consequent tendency for more crepuscular behaviour. This was also found by Berry (1973) on the Cape Flats. Coetzee (pers.comm. in Christian 1977) stressed

FIGURE 1.3. Activity patterns of the captive colony.

1 : 06h00 - 07h00
2 : 07h00 - 08h00
3 : 08h00 - 09h00
4 : 09h00 - 10h00
5 : 10h00 - 11h00
6 : 11h00 - 12h00
7 : 12h00 - 13h00
8 : 13h00 - 14h00
9 : 14h00 - 15h00
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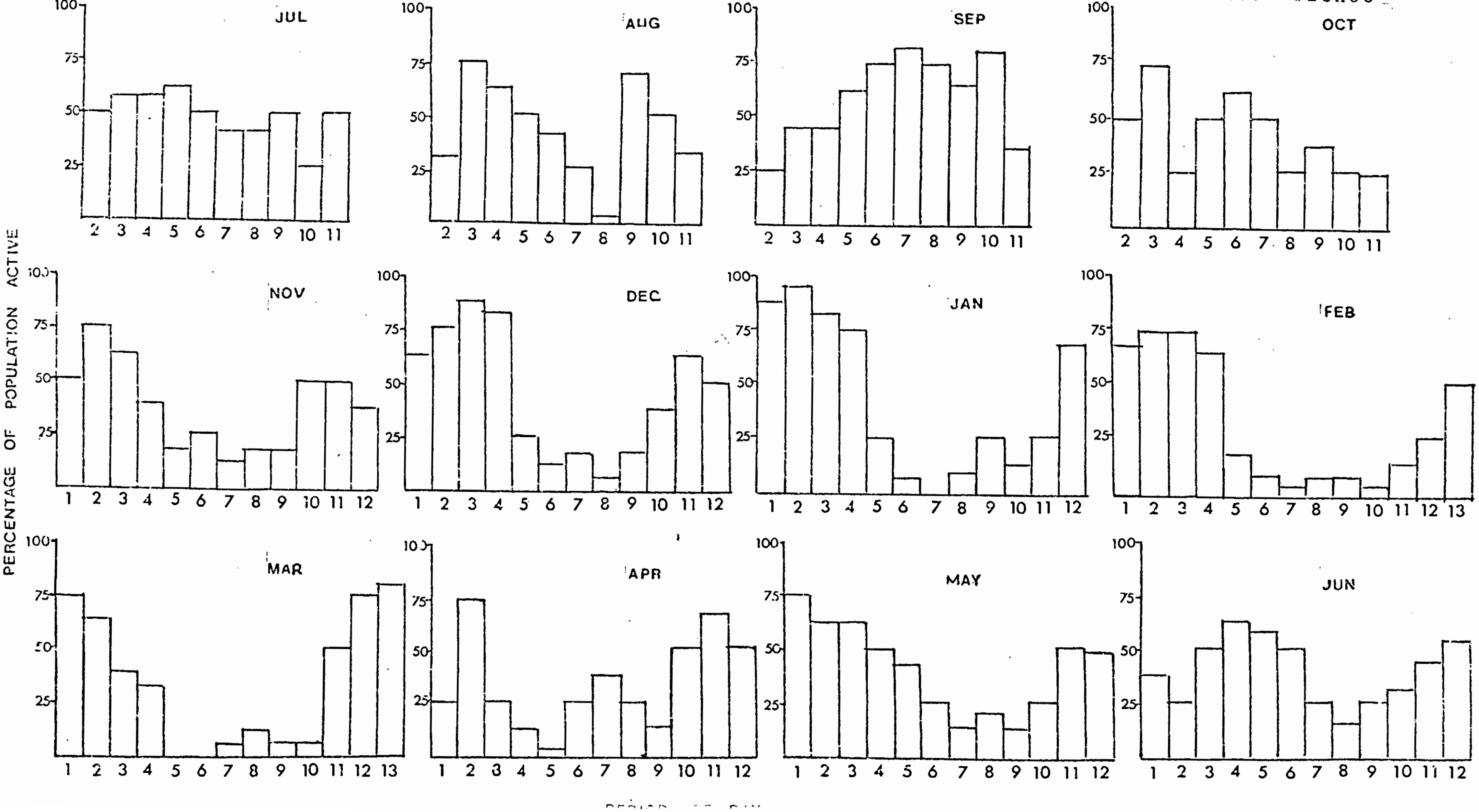
14 : 19h00 - 20h00



the importance of cover in Rhabdomys' activity in South West Africa, suggesting that whereas the mice might be active under cover of large bushes throughout the day, they may emerge out of this cover only in the early morning and late afternoon. Christian (1977) was working in an area where there was plenty of ground cover. In the cage where the colony was kept, however, the cover was rather more sparse, thus it could very well be that the tendency towards crepuscularity observed was a function of the lack of continuous ground cover.

The preference for cover could be due to either of two factors: firstly, camouflage from predators, especially aerial ones, when the bright clear sunlight of midday would make the mice more conspicuous; and, secondly, and perhaps more likely, thermoregulation. Rhabdomys exhibits a greater proportion of sunbathing behaviour in the winter months, throughout the day, and very often in exposed areas, whereas in the summer months, sunbathing activity is confined to the early morning. (The lack of sunbathing in the afternoon was presumably due to the fact that the cage falls into shadow at this time.) Rhabdomys appears to need to sunbathe: whether it is the thermal energy or the ultraviolet radiation that is required is unknown; this might prove an interesting topic for further research. There does, however, appear to be a limit, beyond which the animals seek the coolness and shelter of their nests and burrows.

1.2.3 Utilisation of the Environment: nests, burrows and runways

Rhabdomys is generally regarded as a nest-builder rather than a burrower (Daris 1942); Brooks 1974), although various authors have described burrows: e.g. Shortridge (1934) has observed that the burrow has a starting entrance which is normally at the base of a bush or otherwise in sheltered cover (Smithers 1971). Brooks (1974) did not find Rhabdomys burrows in his study grid, and postulated that this was because the ground tended to become waterlogged easily and that there was ample vegetative cover for nesting above ground. Smithers (1975) gives a detailed description of Rhabdomys burrows in Rhodesia: "These burrows may reach a depth of about half a metre and have a chamber which is lined with soft grass in which they nest and in which the young are born."

In the captive colony, however, both burrows and nests were built: three weeks after the mice had been released into the cage, four burrows were observed - a description of two is as follows:

The first was found with its entrance below a nest-box. It appeared to have originally had two entrances, one fairly old, while the other showed signs of great activity and excavation, with a large pile of sand scattered on top beneath the nest-box. When excavated, the burrow was found to be shallow - at deepest 10 cm. The width was at no place greater than 6 cm: the entrance was long, sloping downwards. No nesting material or caches of food were found.

The second burrow was found beneath a flat piece of asbestos that was lying on the ground. Once the asbestos covering was removed, the whole burrow system lay exposed. It, too, had a shallow sloping entrance, a short passage which divided into two tunnels of more or less equal length, about 20 cm. At no part was the burrow deeper than 6 cm. Again, no nesting material or food caches were observed.

The shallowness of the burrows observed in the cage may have been due to the hardness of the ground: hard closely packed clayish soil. Rhabdomys had been observed to use burrows on the Cape Flats (Jarvis pers. comm.) which are much deeper: it is uncertain, however, whether these burrows were in fact made by Rhabdomys or were abandoned burrows of Tarera afra.

Figure 1.4 shows a diagrammatic representation of the two burrows.

The only times when nesting materials were found in burrows were when the burrow was occupied by a breeding female. The second burrow described above was, in fact, taken over by F27 many months later: it was observed that she lined one chamber with nesting material, in which the litter was placed.

Powell (1925) described large nests and sticks containing family groups of 12-30 Rhabdomys. Shortridge (1934), however, questioned this, on the grounds that Rhabdomys was not know to be communal. Hanney (1965)

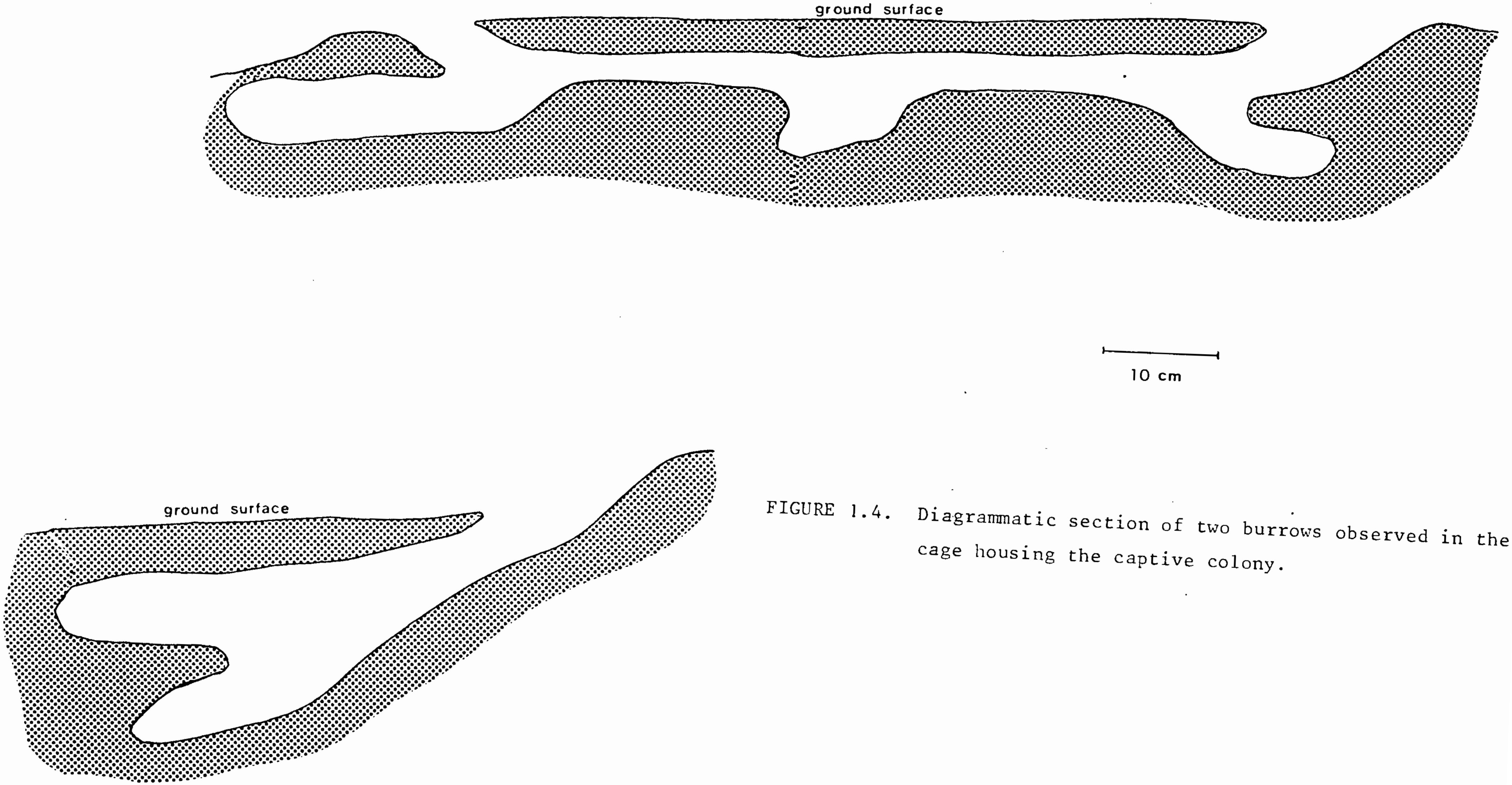
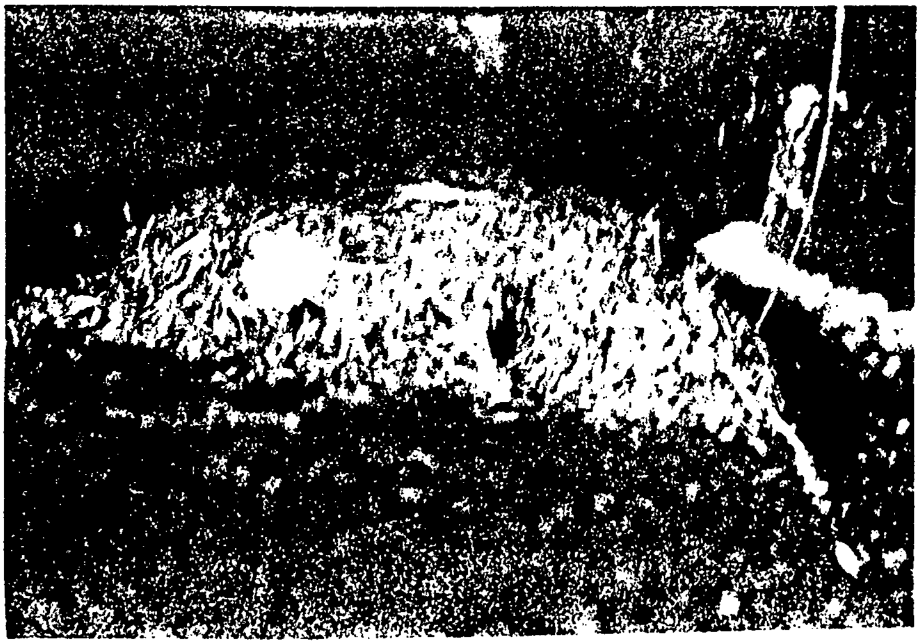


FIGURE 1.4. Diagrammatic section of two burrows observed in the cage housing the captive colony.

PLATE 1.1. *Rhabdomys* nest.



and Stiemie and Nel (1973) in a laboratory study of nest-building behaviour, found that Rhabdomys constructed closed nests which were rounded in shape. Choate (1972) and Brooks (1974) described similar nests in the field.

In the colony, nests were built in two places: beneath one of the dassie's hutches (in the south-eastern territory) and beneath the large wooden box. Plate 1.1 shows a photograph of the tower. Both nests were rounded in shape, constructed of finely shredded grass, and the inner chamber lined with finer grasses. Both were roughly 20 cm in diameter, with a height of about 10 cm; one had a single entrance; the other (under the box) had two.

In both cases, these nests were constructed in sheltered areas; confirming the observations of Choate (1972) who found nests in large grass tussocks or at "the end of a covered runway in deep grass"; Brooks (1974) who found one in a metre-high stand of grass.

Runways are very characteristic of Rhabdomys in the field (e.g. Shortridge 1934; Brooks 1974 and personal observations). In the cage, there was not sufficient cover for them to be apparent as well-defined pathways: however, it was observed that the mice followed definite routes when moving from nests and nest-boxes to the feeding site. These routes tended to include as much cover as possible, especially as stopping places; it is feasible that such "bolt-holes" may exist in the field situation as well. A significant observation is that subordinate mice were never challenged on a runway, even though passing within centimetres of a dominant: challenges occurred only at the feeding site itself or while exploring in the cover, or sunbathing. This finding agrees with Brown's (1962) description of the behaviour of Apodemus on runways: the resident mouse usually had access to the runways of the entire community. Curry-Linhahl (1956) observed that the bank vole, Clethrionomys, which like Rhabdomys, is diurnal, lived in well-protected spots which were relatively separated, and used runways as the common ground between them. Evidence for the presence of runways was also found in the experimental grid on the Cape Flats (Part II).

1.2.4 The Social Order

1.2.4.1 The Dominance Hierarchy

Following van Kreveld's (1970) criterion, overt aggression was used as a measure of rank in the colony. Figure 1.5 shows the relative frequencies of the behaviour pattern "attack" (see Chapter 2 for definition and description) among the three social groupings, designated, according to the classical ethological tradition, as alpha, beta and omega. The frequencies shown in this figure are the pooled scores of 2 alpha males, 7 beta males and 6 omega males divided by the number of animals in each group.

1.2.4.2 Testosterone

It has been known for many years that an increase in aggressive behaviour follows administration of testosterone (e.g. Clark and Birch 1945; Birch and Clark 1946; Beeman 1947). It is only in recent years, however, with the development of such sensitive assay techniques as the radioimmunoassay, that the intrinsic levels of circulating hormone have been measured. Again a correlation between plasma testosterone levels and aggression has been observed: Rose *et al* (1971) found a significant relationship between plasma testosterone and social rank in a group of rhesus monkeys *Rhesus macaca*.

On this basis it was decided to investigate the relationship between plasma testosterone and social rank in *Rhabdomys* with a view to the possibility of using the testosterone concentration as an index of dominance. The literature, however, appears to be somewhat contrary as to the reliability of testosterone levels. Bartke and Dalterio (1973) and Bartke *et al* (1973) found irregular diurnal fluctuation in testosterone levels in the laboratory mouse *Mus musculus*; while other authors e.g. McKinney and Desjardins (1973) on wild *M. musculus* and Rose *et al* (1971) on the rhesus monkey, have reported little individual variation in animals bled on different occasions. In an attempt to avoid a possible serious source of bias, two samples were taken from each Rhabdomys, one in the morning and one in the afternoon of the same day. As may be seen from

FIGURE 1.5. Frequency of the behaviour pattern "Attack" for males in the captive colony.

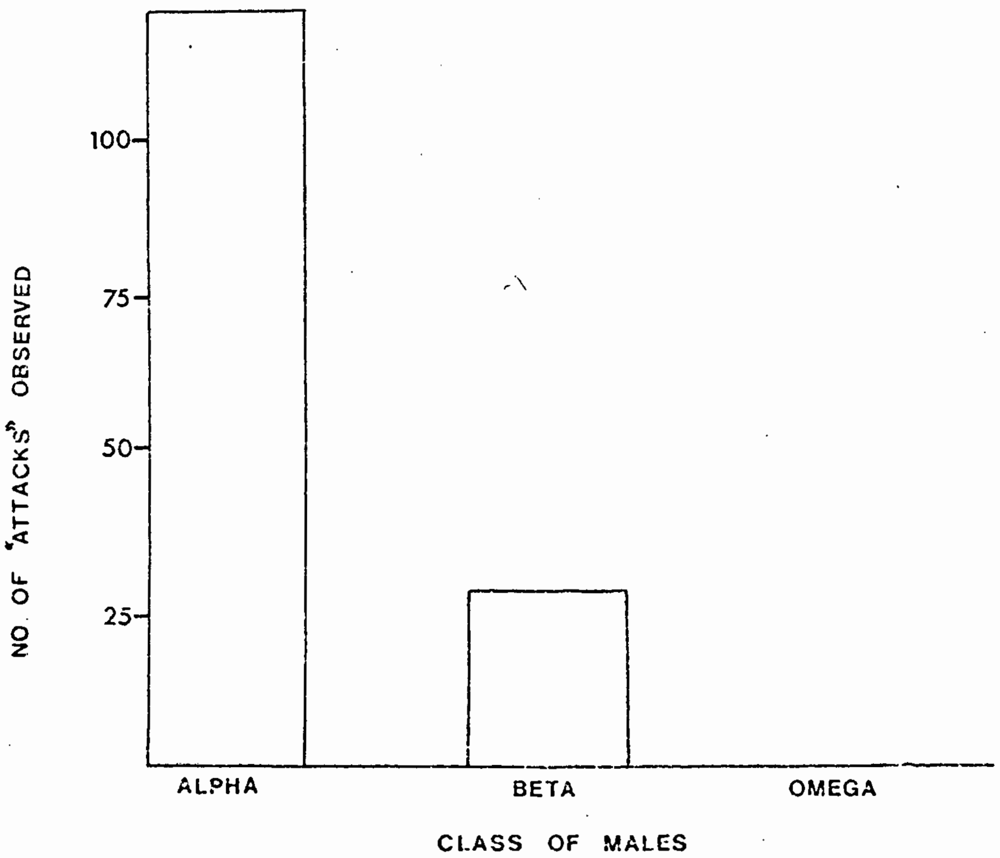


Table 1.1, the differences between the two values are in fact negligible.

Male No.	Rank	Assay 1 (nmde/1)	Assay 2 (nmde/1)	Mean
2	Alpha	23,00	23,60	23,30
11	Beta	18,56	18,30	18,43
28	Beta	16,90	17,21	17,05
8	Omega	2,87	3,15	3,01
9	Omega	1,73	2,05	1,89
6	Omega	2,38	2,72	2,55

TABLE 1.1 Testosterone levels of captive male *Rhabdomys* during the breeding season (December 1977) Blood for Assay 1 was taken in the morning and that for Assay 2 was taken in the afternoon of the same day.

These results confirm the results cited above (McKinney and Desjardins 1973 and Rose et al 1971) of the reliability of testosterone measurement at different times of day. Reasons for the apparent contradiction between these results and those outlined on laboratory stock (e.g. Bartke and Dalterio (1973) are obscure: a possible solution is the suggestion offered, on the basis of the observation that it is apparently only laboratory stock animals that exhibit this variation, by Bartke and Dalterio (1973) that "domestication is associated with pronounced changes in the pattern of testosterone secretion in *Mus musculus*". How and why such a change should occur is unknown: perhaps the result of stress. However, it appears that this diurnal variation is not found in *Rhabdomys*, so that the testosterone values obtained may be considered reliable.

The correlation between plasma testosterone levels and social rank is highly significant ($r = -0,968$). On the basis of these results, it appears that the measurement of testosterone levels might be a good index or predictor of social rank in this species.

The reasons for the higher levels of male hormone in dominant mice probably lies in the so-called "pituitary-adrenal-gonadal pathway" hypothesis. A great deal has been written on this topic, particularly by J.J. Christian and his co-workers (e.g. Christian 1950; 1955 a and b; 1956 a; Christian and Davis 1964). The hypothesis rests on the observation (e.g. Selye 1946) that "stress" produces an increase in adrenocatical activity, and a concomitant decrease in secretion of gonadal hormones. Subordinate animals are presumably more subject to stress than are dominants, resulting in increased adrenocatical activity and lower testosterone values. Dominants, on the other hand, are relatively free of this "restriction" and high testosterone levels are not inhibited.

1.2.4.3 Body Size and Mass

Grant (1970) observed a strong correlation between size and social rank in certain of the

The body weights of male members of the Rhabdomys colony, in relation to their rank, are shown in Table 1.2.

Male Number	Rank	Body Mass (grams)
2	Alpha	101,7
11	Beta	82,3
28	Beta	77,4
6	Omega	74,9
8	Omega	69,8
9	Omega	72,5

TABLE 1.2 Body masses of male members of the Rhabdomys colony in November 1977.

While size may predict the status that the animal might hold, it is impossible to sort out the cause and effect relationships here: one cannot say whether rank is a result of size or size the result of rank. The latter is probably more likely: considering van Kreveld's (1970) definition of dominance as implying "control of access to resources", it is clear that a dominant animal, having freer access to food than his subordinates, might tend to increase his size. Certainly this is borne out by Male 2, the alpha, who, shortly before his death was observed to weigh 101,7 grams, a remarkable achievement for a Rhabdomys who average weight is in the region of 40 to 50 grams. A post-mortem examination of male 2 revealed large layers of subcutaneous adipose tissue.

1.2.4.4 Age

The young male Rhabdomys, on reaching sexual maturity, leaves the parental nest and, if applicable, the territory of the dominant male. He makes his own nest in another area and socially moves into the lowest ranks of the hierarchy. Two examples are as follows:

Male 28's parents were M2 (the alpha and holder of the south-eastern territory) and F12. He was the only male member of a litter of 4 and was born and raised in the south-eastern territory, from which he seldom, as a juvenile, ever ventured. He was tolerated by M2 until he reaced sexual maturity, whereupon he moved out. It is probably, although not certain, that he was driven out of the territory, perhaps as a response to a chemical signal. He established a hom inside the dassies' hutch, and fed in the north-western area, where he was regularly attacked by M11, and was vigorously chased off the south-eastern territory by both M2 and F12. Of the 3 adult males (M2, M11 and M28) he was the lowest-ranking, and by mid-December 1977 showed evidence of bite wounds on the back and tail. At this time, M2 died, and for about 2 weeks there was considerable fighting between M11 and M28, until M11 assumed the dominant position. From this time, M28's condition deteriorated rapidly: his back showed permanent bleeding wounds, and his tail was badly broken. (It should be noted that M11 was not the only aggressor: there were 3 territorial and aggressive breeding females in the colony at this time.) On 30 January 1975, M28 was found dead.

M39 was born in January 1978; his mother was F27, offspring of M2 and F12 and sibling to M28. She was a relatively aggressive female; she lived in the communal nest in the south-eastern territory until she became pregnant and, approaching parturition, she established a nest of her own in the eastern corner of the cage. On 21 January 1978 she produced a litter of 5: 2 males and 3 females. One of the males was drowned in the water trough as a juvenile, the other reached adulthood and was designated M39. Throughout his immature stages he foraged with the rest of the litter near the nest-site, and in the south-eastern territory. Upon reaching maturity, he moved out and joined the ranks of the communal north-eastern territory. At this time, there was only one other male in the cage - the dominant, M11 - so that M39 was able to establish himself without difficulty. He in fact assumed the status of a beta male, which he retained until observations ceased in June 1978.

The above two sample histories indicate that juvenile males are (a) excluded from the home site upon reaching sexual maturity and (b) once they have moved out they assume subordinate status. As the higher-ranking males either die or move up in status, the young subordinate can move up in the hierarchy.

The so-called "age-graded male system" has been described for monkeys and apes (Eisenberg _et al_ 1972) as well as for other species, e.g. the black grouse (Johnsgard 1967). In this system, a single older male tolerates younger males; when the alpha weakens or expires, one of the older lieutenants takes his place. This system is apparently intermediate in evolution between the unimale (or despotic) society, and the multimale (with multiple males enjoying equal status) society (Eisenberg _et al_ 1972).

The ages of the male members of the colony that had died by January 1978, as assessed by tooth-wear (Henschel 1977) are shown in Table 1.3. Hershel's age-classes were, however, calculated for animals living in the wild and under different food conditions to the animals in captivity, so that the age in weeks may not necessarily be correct. The Table should, however, give an indication of the relative ages of the mice: as they were captured at the same time (March / April 1977) and kept under identical conditions in captivity, this variable has been held constant.

The sample size is far too small for any conclusions to be drawn: I decided to include these data simply because they may give an indication of an interesting phenomenon, in that the alpha position is occupied by a relatively young animal, and omega positions occupied by an animal that was known to be young (M28 - born in captivity) and a mouse that was very old indeed (M8). The beta males apparently fall somewhere between these 2 extremes. It could be that when a group of mice that are presumably strangers to one another, are thrown together, it is a relatively young and vigorous animal that comes out on top, while the old and more feeble mouse assumes a subordinate position. Of course, in view of the sample size, this remains mere speculation.

Male No.	Rank	Age class	Est. Age in Weeks
2	Alpha	5	19-26
10	Beta	8	60-70
7	Beta	6	27-37
6	Omega	8+	>75

TABLE 1.3 Estimated ages of males as assessed by tooth wear.

However, when the alpha male, M2, died, one of the beta males, M11, assumed alpha status which he maintained for a further 9½ months until his death, by which time he had reached a ripe old age (considering that he had been captured, as an adult, in April 1977, 9 months prior to his taking over dominant status in January 1978, he must have been at least 19½ months old at the time of his death.

On the basis of these observations, one may conclude that the recently matured juvenile either assumes a subordinate place in the hierarchy, if space is available, or may emigrate (something that could not be observed in the cage). Once he has, if he ever does, attain dominant status, he is able to maintain this position, even though he is in fact less strong and vigorous, purely by metacommunicative means (Altmann 1967) or through ritualised threat and gesture. A detailed discussion of these aspects will be presented.

1.2.4.5 The Female Hierarchy

The female hierarchy is rather more subtle than that of the male, and depends to a large extent on the breeding condition of the female. Pregnant females, shortly before parturition and those already suckling a litter, defend a territory centred around the nest. A female in this condition is extremely aggressive and will attack any intruder with the exceptions of alpha male, and females of equal status. It is not true, however, to say that female status depends entirely on breeding condition: clear differences in rank are observed even during the non-breeding season. For example, F12, the "consort" of the alpha male, M2, was dominant, apparently of equal status to the alpha male. All other animals were kept at a distance, and she assumed joint responsibility with M2 for the defence of the south-eastern territory. At this time (July-Dec.1977) she was the only breeding female in the colony, and the only dominant one. Among the other female members of the colony, F21 showed beta status, while two females, F14 and F8, showed distinct omega behaviour. The latter mouse disappeared, and F14 eventually died, much wounded and bitter, in Dec. 1977; as far as is known, she never bred. F12's female offspring from her first litter, FF 25,26 and 27, as adults, appeared to be of equal status to that of their mother, treated the alpha male as an equal, and beta and omega males as subordinates.

Female rank thus appears to depend partly on breeding condition and partly on another factor or factors. My hypothesis, based upon observation, is that the "alpha" females are those who, by chance or otherwise, manage to establish their nest and territory in a prime position. As the juvenile females, upon reaching maturity, are not excluded from the parental home site as are the males, the young breeding female has access to good nest sites. However, because of this more complicated situation in the female, and the complex nature and interrelationships of the hormones involved in breeding, female dominance relationships cannot be as easily described as those of the males.

1.2.5 Territory

Territorial behaviour has been described in Rhabdomys by a number of authors, e.g. Choate (1972) and Marais (1974) both of whom observed males inhabiting well-separated areas, and assumed territoriality to be the governing measure of social organisation in this species.

By the time the colony had stabilised and observations begun, it was noticed that M2 occupied, together with FF 12 and 20 the south-eastern end of the cage, and vigorously attacked any members of the colony that entered this area. The area enclosed the entire end of the cage, including one dassies' hutch - affording excellent shelter - one nest-box, and one of the two feeding sites. Characteristic alert and nervous behaviour was exhibited by intruders as shown in the following example:

M9 was observed running along the eastern runway into the south-eastern territory: jerky run, stops, sniffs air, twitches ears, freezes (juvenile 30 cm away) runs jerkily, body very elongate, freezes, incipient upright, sniffs air. Male 2 emerges from under dassies' hutch, approaches feeding site, M9 sees him, flees. M2 attends, gives chase. M9 runs to centre of cage, then into north-eastern area. M2 stops chasing near first dassies' hutch, turns, gives perineal drag, walks jerkily back into territory, crawls over stone, perineal drag, then back to feeding site.

A full description and explanation of these behaviour patterns will be given later, however, it should be noted that those of M9 - the jerky run and elongate posture, freezing at any disturbance, alert behaviour such as ear twitching and sniffing air, and the incipient upright, a characteristically defensive posture - all indicate an animal that is unsure of itself, and "expects" to be attacked.

Although no other animals, male or female, were permitted in the south-eastern territory, M2, as well as F12, often ventured into other parts of the cage where their dominant status was maintained.

When the breeding season began, the same situation prevailed in that none of the other males showed territorial behaviour; females, however, shortly before parturition, established themselves in a nest-box or burrow and vigorously defended the area in the immediate vicinity against subordinates. The alpha male and equal-status females were not, however, attacked.

When M2 died, M11 took over the dominant position as well as the south-eastern territory. It is interesting that F12 tolerated this moving in; she remained in the territory and lived quite amicably with the new dominant, as did the juveniles already present. No evidence of M11 killing juveniles was found, as has been reported in certain carnivores (e.g. Schaller 1963) nor was any variation in the territorial boundaries observed. Male 11, also, like his predecessor, would move out of the territory and into the north-western area where he always maintained dominant status.

It is interesting that, although no overt territorial behaviour was observed for the nest and the colony, when a strange mouse was introduced into the cage, he was vigorously attacked, not only by the territorial animals in the south-eastern territory but also by animals in the north-western area. Whether this is evidence of a "group territory" as observed by Eibl-Eibesfeldt (1950) and Crowcroft (1953) in wild _Mus musculus_ and by Frank (1957) in _Microtus_ is difficult to say. Certainly, these observations appear consistent with Frank's (1957) postulation and the "Grossfamilie" whose members vigorously attacked all strange individuals.

1.2.6 Analysis of spatial relationships

Spatial relationships among _Rhabdomys_ as at a feeding site as determined by the nearest-neighbour method of Kummer (1967) are shown in Tables 1.4 (a) for the non-breeding season, and (b) for the breeding season.

Since female rank was determined by breeding condition, females are only designated as "alpha", "beta" and "omega" during the breeding season. For the non-breeding season, I have grouped them all togheter in the "beta" class.

SUBJECT INDIVIDUALS BY CLASS

CLASS OF NEIGHBOURS		ALPHA M	BETA M	OMEGA M	BETA F	JUVENILE
ALPHA M	OBS: EXP: X^2 :	- - -	39 14,45 *41,71	13 5 *12,18	42 12,61 *68,5	6 2,5 4,9
BETA M	OBS: EXP: X^2 :	40 23,17 *11,23	54 29,95 *21,67	20 15 1,67	66 37,7 *12,20	6 7,59 0,33
OMEGA M	OBS: EXP: X^2 :	14 23,7 3,96	21 43 *11,26	4 10 3,6	23 37,72 * 5,74	3 7,59 2,77
BETA F	OBS: EXP: X^2 :	42 39,65 0,139	68 72,3 0,25	28 25 0,36	24 50,46 *14,19	8 12,7 1,74
JUVENILE	OBS: EXP: X^2 :	7 15,8 4,90	6 28,95 *18,19	0 10 *10	9 25,2 0,62	10 2,5 *22,5

TABLE 1.4(a) Spatial relationship according to nearest neighbour method for non breeding season
Values marked* are significant ($p < 0,05$)
The values shown are frequencies (see materials and methods)

SUBJECT INDIVIDUALS BY CLASS

CLASS OF NEIGHBOUR		ALPHA M	BETA M	OMEGA M	ALPHA F	BETA F	OMEGA F	JUVENILE
ALPHA M	OBS:	-	13	1	19	30	8	26
	EXP:	-	5,81	0,32	6,31	12,62	3,19	13,81
	X^2 :	-	* 8,89	1,445	*25,52	*23,94	7,25	*12,59
BETA M	OBS:	13	2	2	15	28	13	20
	EXP:	18,18	11,62	0,94	18,94	18,94	9,56	41,44
	X^2 :	1,76	*44,03	1,19	0,82	* 4,33	1,24	*11,09
OMEGA M	OBS:	1	2	0	0	0	0	2
	EXP:	12,3	11,62	0,32	12,62	25,25	6,37	27,62
	X^2 :	*10,22	*44,03	0,32	*12,62	*25,25	6,37	*23,76
ALPHA F	OBS:	19	14	-	-	26	7	37
	EXP:	6,06	14,45	-	-	12,62	3,19	13,81
	X^2 :	25,49	0,014	-	-	*14,19	* 4,55	*38,94
BETA F	OBS:	29	30	0	25	52	15	52
	EXP:	18,18	17,44	0,94	18,94	25,25	9,56	41,44
	X^2 :	* 6,43	* 9,045	0,94	1,939	*28,34	3,09	2,69
OMEGA F	OBS:	7	13	0	7	14	1	5
	EXP:	12,3	11,62	0,625	12,62	25,25	3,19	27,62
	X^2 :	2,17	0,164	0,625	2,503	* 5,012	1,50	*18,53
JUVENILE	OBS:	28	19	2	35	52	7	78
	EXP:	30,31	29,06	1,56	31,56	63,12	15,93	55,25
	X^2 :	0,25	3,48	1,24	0,375	1,96	* 5,00	* 9,36

TABLE 1.4(b) Spatial relationships according to nearest neighbour method for breeding season.
Units = frequency of occurrence of object individual as nearest neighbour.

An examination of the two tables reveals two main trends; firstly in the association of males with other males, and secondly, in the association of males and females. During the non-breeding season, males are tolerant of each other: in fact, there is a significant male-male attraction. Once the breeding season commences, however, this changes to a highly significant (X^2 for alpha and beta males = 41,71; for beta-beta association association 44,03, and for beta-omega association 44,03) avoidance and other male company. This is presumably due to the rise in testosterone levels at this time and the establishment of a rigid hierarchical and territorial system.

The association of males and females is significant in both seasons: there is, however, a distinct "preference" for higher ranking males. This is probably due not so much to avoidance on the part of the females, as the tendency of low ranking males to avoid as much contact as possible with mice of higher rank and a consequent tendency to remain on the outskirts of groups.

Another trend is that females tend to associate with females. At first this might seem strange, in view of the highly aggressive nature of a female behaviour during the breeding season, but it should be remembered that this behaviour is territorial in context, and these nearest-neighbour relationships have been determined in a non-territorial situation, that of the feeding site, which is essentially neutral.

Lastly, juveniles are associated with most groups, implying tolerance on the part of the adults. The assocaition of juveniles with adult females and the alpha female during the bredding season is perhaps not unexpectedly, highly significant. (X^2 = 38,94)

1.3 CONCLUSIONS

Investigation of activity patterns throughout the year indicates that Rhabdomys is diurnal, with activity beginning at sunrise and ending at sunset. In winter, activity tends to continue throughout the day, while in summer there is a marked tendency for a concentration of activity in the early part of the morning and latter part of the afternoon, with very little occurring over the midday period. Rhabdomys appears to construct both nests and burrows. The nests are always in a sheltered position, are made of finely shredded grass and are rounded in shape. The burrows observed in the cage were shallow, although whether this was due to the hard nature of the soil is uncertain. Runways are characteristic of the colony, with animals always using the same paths to move around; a feature of these is that they are essentially neutral ground, and animals using them are never challenged.

The social structure of the colony consisted of a single dominant or alpha male, two or three middle-ranking or beta males, and rather more low-ranking or omega males. Investigation of their testosterone levels yielded a highly significant correlation between the hormone concentration and social rank. This hierarchical organisation is maintained by aggressive behaviour directed by the dominants to the subordinates, and on analysis of spatial relationships shows significant avoidance of males from other males. The alpha is territorial, and, as shown from the behavioural analysis, does most of the breeding. Presumably by his establishment of a territory and defence of its resources he proves and maintains his fitness for breeding. The beta males are the opportunists: highly active and aggressive animals attempting to breed with the females whenever possible (Chapter 2) and seeking to oust the alpha. The omega males, often newly-matured juveniles, are the "hangers'on"; they do not breed and interact very little with other colony members. Presumably in a natural environment many of these would emigrate: those that remain with the colony would have some of the advantages that accrue from social living, such as protection against predators and increased foraging efficiency, and perhaps an opportunity to move up the hierarchy.

The position of the female Rhabdomys is somewhat different to that of the male. Whereas the young male is driven out of the parental nest by the resident male, the young female remains, only leaving to establish her own nest when breeding, but still often returning with her young to feed. These females do not show rank differences among themselves, but will defend the communal territory and their own breeding territory very aggressively against intruders. Analysis of spatial relationships indicates mutual attraction and tolerance of these females with, however, very little behavioural interaction.

In the colony, a number of low-ranking females were observed, who exhibited similar behaviour to the omega males, living essentially on the outskirts of the group and suffering attack and aggression from higher-ranking animals, both male and female. It is difficult to say whether this class would occur in a natural situation: as previously mentioned, I believe that the status of these animals was determined by their failure to establish a suitable nest site or territory as a result of establishing the colony with animals that were presumably strangers to one another. As the young female Rhabdomys generally does not leave the home site, it is therefore possible that the presence of this class of female is an artefact.

The females therefore might be thought to form the stable breeding nucleus of the colony; the males appear to have a separate and more fluid arrangement, competing among themselves for the alpha position and access to the females and hence to the gene pool of the colony. The fact that the rank relationships of the males can be quantitatively measured by testosterone assay is a significant finding that can be used to measure the social organisation indirectly.

CHAPTER 2

ASPECTS OF COMMUNICATION

2.1 INTRODUCTION

Wilson (1975) defines biological communication as "the action on the part of one organism (or cell) that alters the probability pattern of behaviour in another organism (or cell) in a fashion adaptive to either one or both of the participants". Communication is thus neither the signal emitted by one organism nor the response evoked in another, but the relationship between the two.

There are four sensory channels through which communicative messages can be transmitted: visual, acoustic, chemical, tactile. Of these, visual communication, making use of postures and movements of the animal's body, either augmented by morphological characteristics, has been the most intensively studied, perhaps because this modality is more familiar and accessible to the human observer. Certainly it is this modality that traditional ethologists have emphasised, particularly stereotyped postures and movements, the "display" or "fixed action pattern" (Lorenz 1941). Acoustic communication appears to be rather less widespread among mammals but recent improvements in detecting and recording apparatus have led to a resurgence of interest in this field. The discovery that many mammals make use of ultrasonic frequencies has generated a great deal of interest and research (e.g. Sewell 1969; Sales and Pye 1974). Chemical communication, operating via the olfactory modality, is apparently widespread among mammals: its great advantage is that the signal can operate for relatively long periods of time in the absence of the signaller making this type of transmission especially useful for territorial or solitary animals (Ewer 1968). Chemical communication may be the dominant mode in nocturnal or fossorial animals, where the use of visual signals is virtually useless. In the last two decades, a great deal of interest has been generated on this topic, triggered by the discovery of so-called "primer" pheromones in mice (Parkes and Bruce 1961). The field of tactile communication remains largely unexplored: due to the difficulties involved in studying it, most of the evidence is circumstantial.

The predominant mode of communication used by an animal appears to depend on its ecology rather than on its taxonomy. (Wilson 1975); an animal living in an open environment or one that is diurnal will tend to use visual means of communication, whereas a noctural animal or one living in dense cover might tend to favour chemical means.

Rhabdomys, as described in the previous chapter, is diurnal, favours covered and vegetated environments and displays territoriality; on this basis, one might hypothesise that its communicative repertoire will contain a predominance of visual signals, but that chemical communication may also play a part. This chapter is therefore an attempt to analyse the communication system in Rhabdomys, with special emphasis on how this corresponds to and maintains the social relationships between the animals and the social structure as a whole. The first section deals predominantly with visual communication; in the second, a specialised area of acoustic communication, that of ultrasound, was chosen; while the third section deals with two topics of chemical communication: the role of the preputial glands and the role of the vomeronasal system in chemical communication.

2.2 VISUAL COMMUNICATION

2.2.1 Introduction

Communication by visual means relies upon reflected light, and hence the presence of an adequate source of light. It has reached its greatest development in diurnal, social, species, especially in the Ares, as a class, and among the mammalia, the Primates and certain of the ungulates. Visual communication has been extensively studied by ethologiest and the classical school, who have, indeed, tended to emphasize this aspect of communication above all others.

The publication of Darwin's "The Expression of the Emotions in Animals and Men" (1872) is generally considered as the foundation of modern ethology. In this, he describes various communicative postures in domestic animals and men, and puts forward the famous "Principle of Antithesis", which will be discussed later. Huxley's (1914) study of the great crested grebe and his formulation of the concept of ritualisation was another landmark in ethology. Ritualisation is essentially the emancipation of a behaviour pattern from its original function, to become purely communicative in nature; such a behaviour pattern is then known as a "display" or a "fixed action pattern" (Lorenz 1941). The evolutionary aspects of this phenomenon were discussed in detail, by later ethologists, particularly in a series of papers in the 1950's, e.g. Tinbergen (1952), Daanje (1953), Andrew (1956) and Morris (1957). Displays may arise from three classes of behaviour: displacement activities, intention movements, and autonomic responses. Morphological adaptations may often occur to reinforce or emphasise aspects of the display: distinctive markings and colouration, or exaggerated physical structures are examples of these.

Visual displays have three primary dimensions (Hailman 1977): the orientation of the signaller, or some part of it, to the receiver; the configuration or shape of the animal or relative orientation of its parts, and movement patterns. Signals may depend primarily on one dimension or utilise various combinations.

The visual mode of communication has several advantages of other means of communication; the most important of these is the great diversity of signals and elements of signals that are available, and thus impart a tremendous capacity for information transfer. Secondly, signals may be directed towards specific receivers, in contrast to chemical or even acoustic signals that tend to radiate indiscriminately; and, thirdly, because many visual displays have evolved from intention movements (Daanje 1953) their performance may carry predictive information.

All these factors allow the development of a rich and varied repertoire of communicative acts, particularly favoured if activity occurs during the daylight hours. The majority of rodent species are nocturnal (Eibl-Eibesfeldt 1958) and their visual displays are often somewhat limited and stereotyped (Eibl-Eibesfeldt 1958, Eiserberg 1963); the animals seemingly rely rather more on chemical signals. Rhabdomys is therefore somewhat unusual in its diurnal activity pattern, and an investigation of its visual communicative repertoire should therefore prove both interesting and informative.

2.2.2 Materials and Methods

1. Collection of data. This was described in Chapter 1. All data were obtained from the colony in the outdoor cage.

2. The behavioural catalogue. Preliminary observations were conducted for a period of 2 months; from these observations a provisional catalogue of social behaviour patterns was drawn up. The criterion for the inclusion of a behaviour pattern in the catalogue was that it was social in nature or occured in a social context. The final catalogue contained 25 patterns which were used in this analysis. All behaviours were scored according to who did what to whom and in what order.

3. The influence of sex and social class upon the performance of behaviour. Five sex and social classes were recognised: alpha, beta, omega males, alpha and omega females. Behaviours were scored by who performed the act, and to whom it was directed, e.g. if the alpha male attacked an omega male, this was scored as Attack: αM-ωM.

4. Information theory analysis of communicative behaviour. Information theory was used to determine the constraints of one behaviour pattern upon another. The following methods are adapted from Hazlett and Estabrook (1974 a & b), Steinberg and Conant (1974) and Steinberg (1977). The basic unit of information is the bit (Shannon and Weaver 1949), an abbreviation of binary digit. The bit is defined as the amount of information required to choose between two equiprobable alternatives; if the animal has to choose between four equiprobable alternatives, the amount of information is then equivalent to 4 bits; for n alternatives, $\log_2 n$ bits. Animals, however, do not choose acts from their repertoire with equal probability,

so that the probability of occurrence of an act must be considered when measuring the amount of information.

The information may be calculated from the following formula:

$$H(X) = - \sum_{i=1}^{n} P(i) \log_2 P(i)$$

where X is made up of n categories, and P(i) is the probability of the ith value of X. In practice, however, actual probabilities can rarely be calculated, so that the amount of information can be estimated by the following formula:

$$\hat{H}(X) = \frac{1}{N} (N \log_2 N - \sum_{i=1}^{n} n_i \log_2 n_i)$$

where N = the total number of occurrences of all events and n_i the number of occurrences of event i.

Estabrook (1967) introduced the concept of character analysis into information theory. Briefly, X may be considered as a character, made up of n states (X_i X_2.....X_n). In this analysis, 24 states of each behaviour pattern were used, e.g. Attack: αM-βM; αM-ωM etc. The amount of information per character (behaviour pattern) is calculated by the formula above.

In order to determine the constraints of one behaviour pattern upon another, the multivariable information is calculated:

$$H(X,Y) = - \sum_{j=1}^{n} \sum_{i=1}^{n} P_{ij} \log_2 Pij$$

or the estimated information:

$$\hat{H}(X,Y) = \frac{1}{N} (N \log_2 N - \sum_{j=1}^{n} \sum_{i=1}^{n} n_{ij} \log_2 n_{ij})$$

where X and Y are two behaviour patterns.

The conditional information $H(Y/X)$ is then estimated by: information in character Y, dependent upon the performance of character X.

$$H(Y/X) = H(X,Y) - H(X).$$

The difference between $H(Y)$ and $H(Y/X)$ is the transmission $T(X;Y)$. This is an estimate of relatedness or shared information. The amount by which $T(X;Y)$ exceeds 0 - when there is no shared information - and approaches $H(Y)$ - which indicates complete dependence of Y on X - indicates the constraints between the characters X and Y.

The transmission may be expressed in percentage form (normalised transmission) or percentage uncertainty reduction by the formula

$$t(X;Y) = \frac{T(X;Y)}{H(Y)}$$

This is then an estimate of the percentage uncertainty reduction; if $t = 0$, the uncertainty reduction is nil, and the uncertainty therefore maximal; as t approaches 1,00 or 100%, the uncertainty is reduced, indicating that the performance of behaviour pattern Y is constrained by the preceding performance of X.

2.3 RESULTS AND DISCUSSION

2.3.1 The Ethogram

The following social behaviour patterns were observed in *Rhabdomys*. I have used the term "behaviour pattern" in preference to "display" or "fixed action pattern" as it does not have the correlation of innate or genetic origin. In the naming of the behaviour patterns I have kept as close as possible to the two authorative references on rodent ethology, namely Eibl-Eibesfeldt (1958) and Eisenberg (1967).

Approach Behaviours (Eibl-Eibesfeldt: Annährung; Eisenberg:Approach)

Approach behaviour is defined as directed movement towards another animal. It usually forms the first act of a sequence, so that although it may not be intentionally social per se, it is included in the social context.

Eisenberg (1967) differentiated 3 types of Approach: Slow Approach, Turn toward, and Elongate. The equivalent terms used by Eibl-Ebesfeldt (1958) are, respectively, Vorsichtige Annährung, Zuwendung and Erkünden mit Flüchtomotivation.

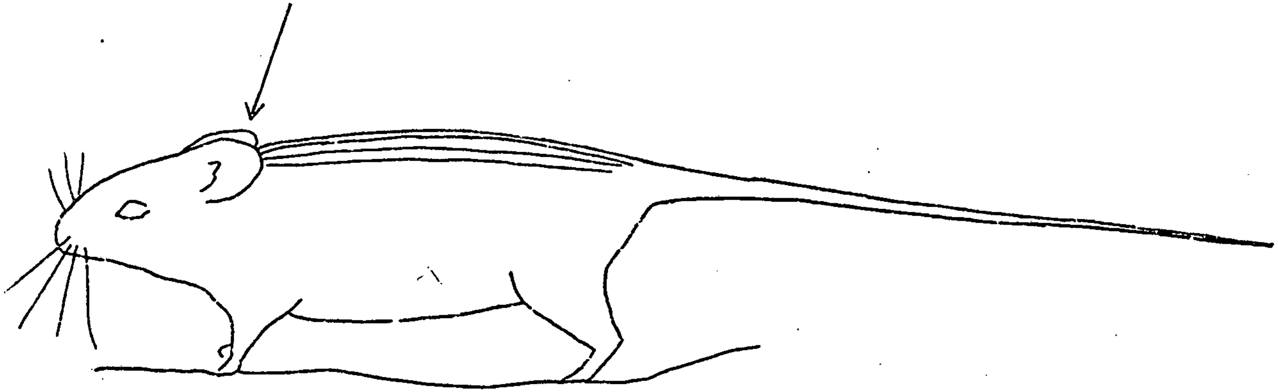
I have retained Turn toward - the definition is obvious by the description - but have amalgamated the two categories of Slow Approach and Elongate into what I have termed Approach Elongate.

The category Approach includes all directed movements toward one animal on the part of another that cannot be included in the category of Approach Elongate. This latter category, unlike that of the ordinary Approach which may or may not have a social motivation but which forms the first act in the sequence, is a distinct display. In this posture (Figure 2.1) the body is extended in an elongate position, the tail usually being held rigid in a horizontal position. The ears are erect, in the initial stages, and the vibrissae are extended. The whole posture conveys a feeling of tension, seen in the rigid tail, the slow deliberate movements and the elongate posture. Eibl-Ebesfeldt's description, Erkünden mit Flüchtomotivation is an excellent one: the posture clearly involves the dual motivation of approach and withdrawal.

One very interesting feature of this behaviour pattern is the fact that ultrasonic squeaks in the region of 40 kHz (see Section (b)) often accompany it. As will be discussed later, the common feature of ultrasonic cries and the behaviours they are associated with is that they are all concerned with the inhibition of aggression.

<u>"Contact-Promoting" Behaviours</u> These include Eisenberg's (1967) categories of Naso-nasal, Naso-anal, Grooming, Head Over, Head Under, Crawling Over and Under, and Circling. Head Over and Head Under and Crawling Over and Under are not seen in <u>Rhabdomys'</u> behaviour outside the

FIGURE 2.1. Approach Elongate. Note the elongated body, flattened ears and horizontally held tail.



nest, and thus could not be observed in the cage. Thus, under "contact-promoting behaviours" I have included the behaviour patterns Naso-nasal, Naso-anal, Allogrooming, Circling, and a fifth category, Sit Close, for which I have found no equivalent in the literature.

Naso-nasal (Figure 2.2a) Eisenberg: Naso-nasal; Eibl-Eibesfeldt: Schnauzen-kontrolle) This behaviour pattern is in many ways similar to Approach Elongate described above. Both the ears and eyelids may be held in a variety of positions - this usually depends upon the relative status of the interacting animals: a subordinate animal will generally show the "submissive" ear and eyelid positions with the ears relatively flattened against the head and the eyes partly or even wholly closed. The dominant, on the other had, usually does not show a change from the normal positions: the ears remain perked and the eyes open. Figure 2.2 shows these postures in two interacting animals. Subordinate mice often tilt the head back slightly, thus partly exposing the throat.

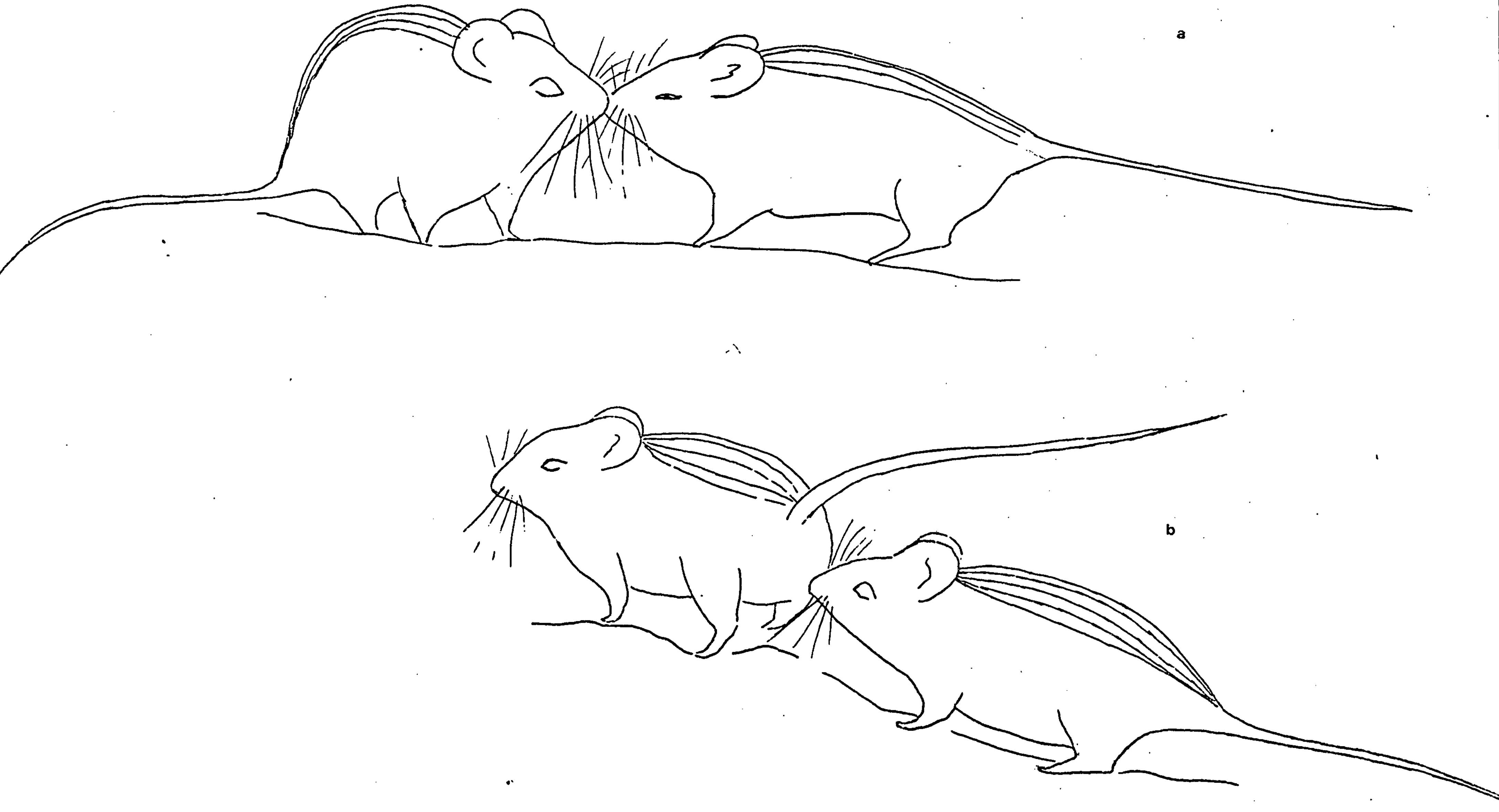
Otherwise, the behaviour pattern is essentially a stationary version of Approach Elongate: the body is held in an extended elongate position often with the hindlegs braced (Figure 2.2a), the tail is also often rigid and may be held horizontally. The noses are brought into contact. Very often the head may be turned so that "the incisors are brought into juxtaposition" (Eisenberg 1967). King (1955) has described this behaviour as "kissing" in the prairie-dog, Cynomys.

Generally, it occurs in two situations: when two animals meet on neutral ground such as on a runway, and secondly, in association with behaviours such as Allogrooming, and Approach Elongate. Thus one might hypothesise that the behaviour is involved in individual recognition; a second function hypothesised from the frequency of the occurrence of Naso-nasal when animals meet on runways, is that of location of food. By the sniffing of another animal's mouth, a mouse might deduce the presence or absence of food in the direction from which the second mouse was moving.

FIGURE 2.2. Sniffing behaviour.

(a) Naso-nasal. Note the submissive posture of the animal on the right.

(b) Naso-anal. The mouse on the left is showing "Crouch" behaviour.



Naso-anal (Figure 2.2b) (Eisenberg: Naso-anal; Eibl-Eibesfeldt) In this behaviour pattern the nose of one animal is brought into contact with the anogenital region of the second. Naso-anal behaviour is common in a sexual context. The animal being sniffed may often exhibit the behaviour pattern Crouch (Eisenberg: Raising Tail; Eible-Eibesfeldt: Präsentieren) in which the tail is raised, the hindlegs braced and the hindquarters "presented" to the animal sniffing.

Allogrooming (Figure 2.3a) (Eisenberg: Grooming; Eibl-Eibesfeldt Soziale Hautflege) I have departed from Eisenberg's terminology as I feel that the term "allogrooming" indicates the social nature of this behaviour and to avoid confusion with Groom Self, in which only a single animal is involved.

This is an elaborate behaviour pattern, and a time-consuming one: in many cases lasting 10 minutes or more. The first animal, often at 90 to the second, puts its paws on its back and commences nibbling at the fur usually on the back of the neck. The nibbling may extend to the face, going up and down from the nose to the ears, often with a break for a Naso-nasal "kiss". Naso-anal contact is also common. The animal being groomed may lower its head below the level of the body. The nibbling behaviour may persist for some minutes; the first animal may then remove his paws from the back of the second and assume the contact position of Sit Close, described below. Often an Incipient Upright 2 or Full Upright posture is assumed (see below). The second animal will then usually turn towards the first, put its paws on the other's back and begin grooming in the same manner. Very often, however, the animals may simply Sit Close, huddled, for many minutes.

The sequence is usually ended by one animal moving off, although sometimes it may return and begin the sequence all over again.

Sit Close (No equivalent in either Eisenberg or Eibl-Eibesfeldt) This is defined as sitting close to or huddling with another animal. I have included this behaviour as I feel it to be definitely communicative in nature, the channel of communication being tactile.

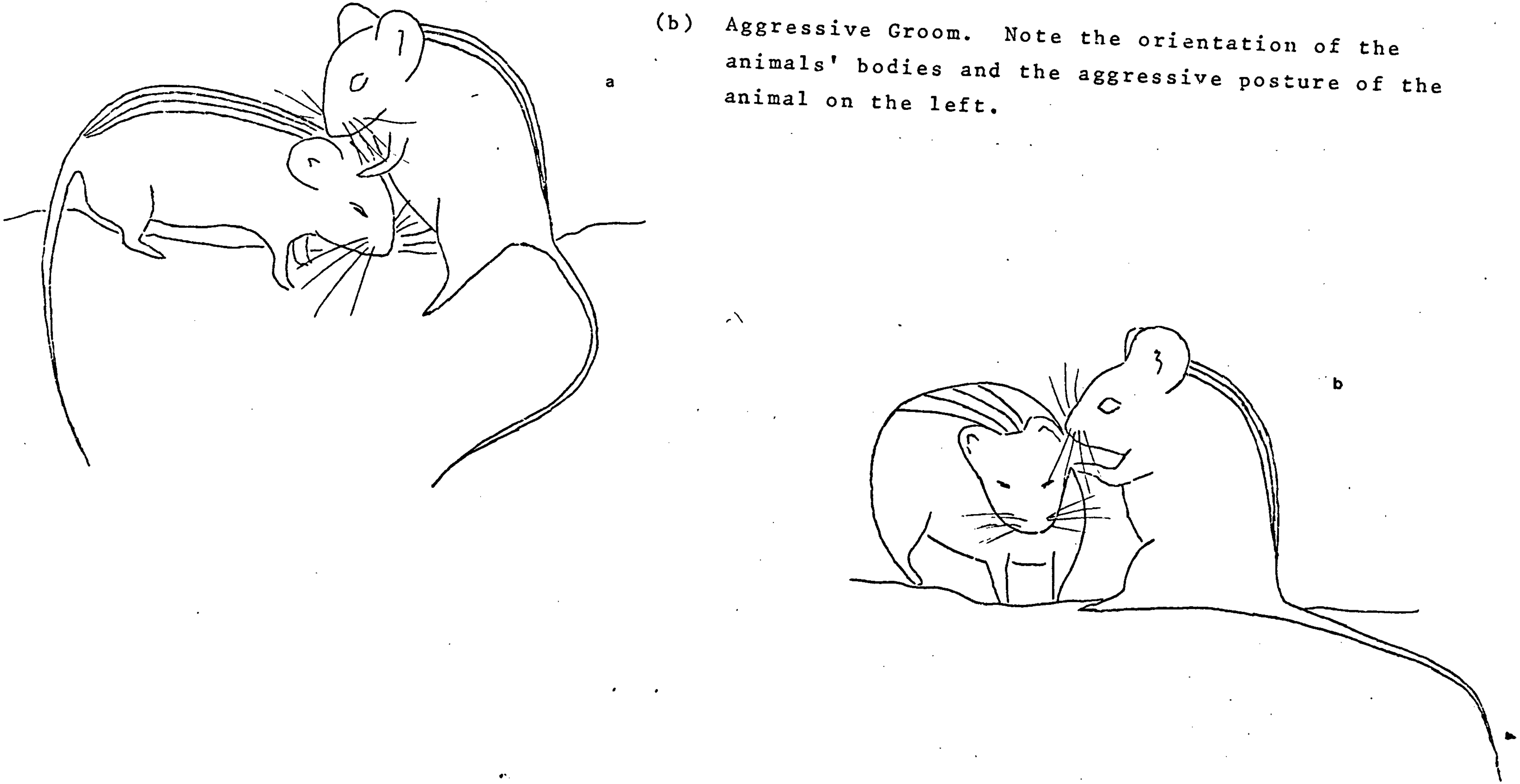


FIGURE 2.3. Grooming behaviour.

(a) Allogrooming. Note the orientation of the animals' bodies.

(b) Aggressive Groom. Note the orientation of the animals' bodies and the aggressive posture of the animal on the left.

Circling (Eisenberg: Circling; Eibl-Eibesfeldt: Kreisen) Circling, or mutual Naso-anal is self-explanatory. This pattern is, like Naso-anal, usually seen in a sexual context. Very often the moving off of one animal (usually the female) leads to the pattern of Follow (Eisenberg: Follow and driving; Eibl-Eibesfeldt: Treiben) on the part of the male. A female, may often, in response to an Attempted Mount, deliver a smart Kick (Eisenberg: Kick; Eibl-Eibesfeldt: Treten) with one hindfoot.

Sexual Patterns Both Eibl-Eibesfeldt and Eisenberg differentiate the male copulatory patterns into sub-components (Mount, Gripping with forelimbs, Attempted Mount, Thrust, Intromission and Ejaculation). While all these patterns occur in Rhabdomys, I feel, for the sake of clarity and ease in manipulating a lengthy sequence (Cane 1977) that two will suffice. Attempted Mount: an attempted, but unsuccessful, mount, and Mount: a successful copulation. In this, the male mounts the female from behind, gripping her abdomen with his forelegs, followed by the patterns of thrust, intromission and ejaculation.

For the female patterns, Eisenberg differentiates Raising Tail and Lordosis. I have described the former above; the latter is the characteristic female rodent copulatory posture in which the back is concavely arched, the rump raised and the tail raised. Assumption of this posture on the part of the female is essential for a successful compulation to take place.

After a successful mount comes the Post-copulatory Wash by both sexes (Eisenberg: Post-copulatory Wash: Eibl-Eibesfeldt: Sich-putzen), not strictly a social pattern. In this, the animal sits in an upright position, lowers its head vertically downwards to the genitals and washes vigorously. The penis of the male may be held in the forepaws. Usually facial washing occurs as well.

Agonistic Behaviour Patterns These may be thought of in terms of a spectrum, ranging from mild threat through to escalated fighting.

Threat (Eisenberg: Threat; Eibl-Eibesfeldt: Drohen) This display is pictured in Figure 2.4. The animal usually remains in a stationary position, directly facing the opponent. The eyes are held wide open in a fixed stare, while the ears are held upright and are often directed forwards. The forelegs are often held apart, the tail often raised and rigid. Piloerection may occur as may Tooth Chatter with the incisors.

Side Display (Eisenberg: Offensive Sideways Posture; Eibl-Eibesfeldt: Breitseitdrohen) (Figure 2.5) In this behaviour pattern, the displaying animal moves towards the opponent in such a way that his body is held sideways on to the latter; in fact moving in an almost crab-like manner (Figure 2.5). This is essentially a "crowding" behaviour. Ears and eyes are held as described above for the ordinary Threat posture. Piloerection almost always occurs. Eisenberg has divided the category into 3 components: Shouldering (Eibl-Eibesfeldt: Schieben), Sidling (Drücken mit der Körperseit and Rumping (Schieben), which I feel to be unnecessary.

The Side Display may lead to the Aggressive Groom (Figure 2.3b) (no equivalent) in which the aggressor approaches the other animal, places its paws on the latter's back, in the same manner as in Allogrooming, and bites the fur on the back. The difference between the Aggressive Groom and Allogrooming lies, firstly, in the vigour with which the grooming in performed - Aggressive Groom is characteristically more rough - and, secondly, the fact that the "groomer" moves up and down the back from neck to rump, rather than concentrating on the head and neck region. Naso-nasal contact almost never occurs in this context, although Naso-anal may. The full Aggressive Groom is more commonly seen in a group of animals in a small laboratory cage where the "groomee" presumably does not have the same opportunities for Retreat or escaping as in an outdoor enclosure. In the latter case, a rather abbreviated form of the Aggressive Groom occurs, in which the aggressor simply puts his paws on the back of the other animal.

If threat behaviour is not heeded, an Attack may result (Eisenberg: Rush; Eibl-Eibesfeldt: Angriff). This is defined as vigorous directed

FIGURE 2.4. Threat. Note the stance, the arched back and tail. the perked ears and wide-open eyes.

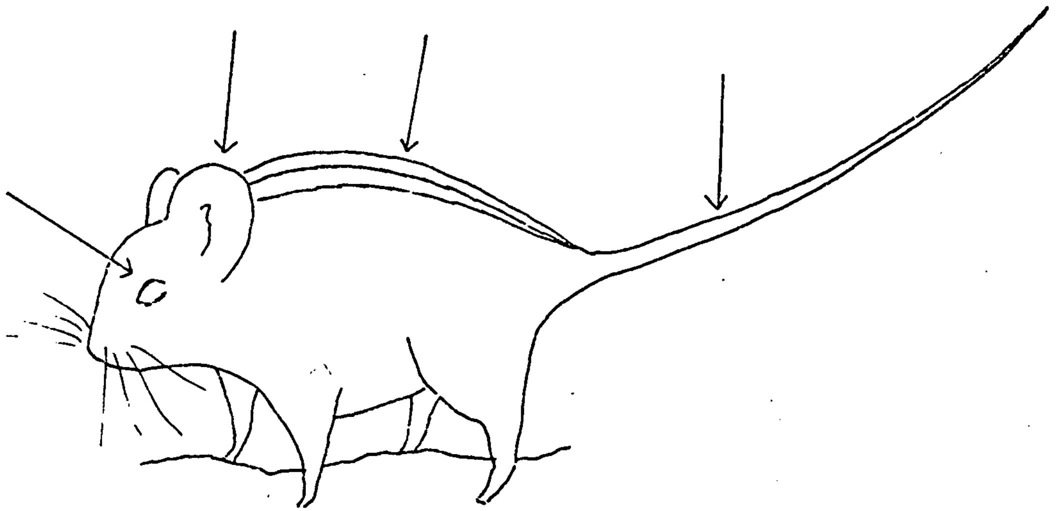
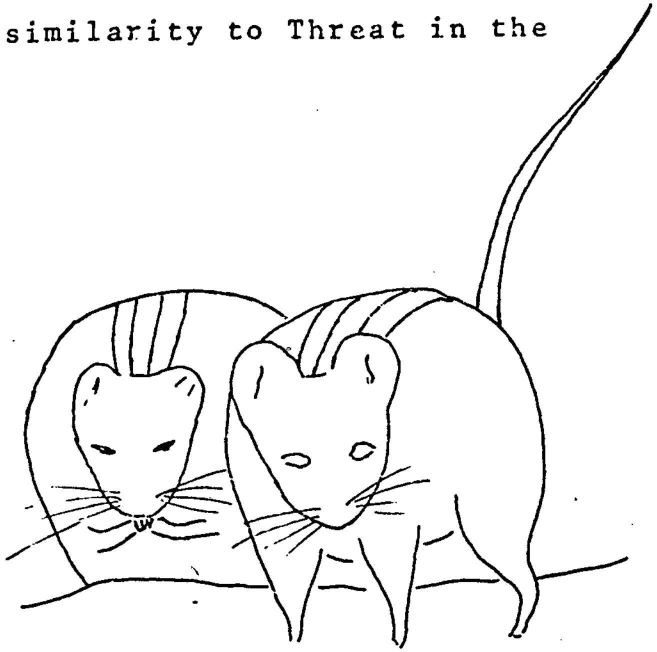


FIGURE 2.5. Side Display. Note the similarity to Threat in the animal on the right.



movement towards another animal.

Retreat (Eisenberg: Move Away; Eibl-Eibesfeldt: Weggehen) and Flight (Eisenberg: Flight; Eibl-Eibesfeldt: Flüchten) are two points on a single continuum of escape behaviour. Retreat may be defined as directed movement away from another animal, while Flight is its high intensity counterpart. Flight as a result of Attack may lead to Chase (Eisenberg: Chase; Eibl-Eibesfeldt: Verfolgen). Other patterns associated with Flight and Chase are patterns involving jumping and leaping (Eisenberg: Escape Leap). Rhabdomys very often shows a vertical jump, which may on some occasions be accompanied by a somersault, with the animal landing back on its feet and continuing the Flight.

Eisenberg differentiates two kinds of Fight: Locked fighting (mutual) and Fight (single). Eibl-Eibesfeldt, however, does not differentiate between the two, nor do I think this is necessary. Fighting in Rhabdomys consists essentially of wrestling, with the object of gaining the upper hand, and biting.

Defensive postures range from the full Defence (Eisenberg: Defence; Eibl-Eibesfeldt: Abwehrstellung) with the animal lying supine on its back exposing the belly and throat, to the Submission Posture (Eibl-Eibesfeldt: Demutstellung) which may be seen in many contexts.

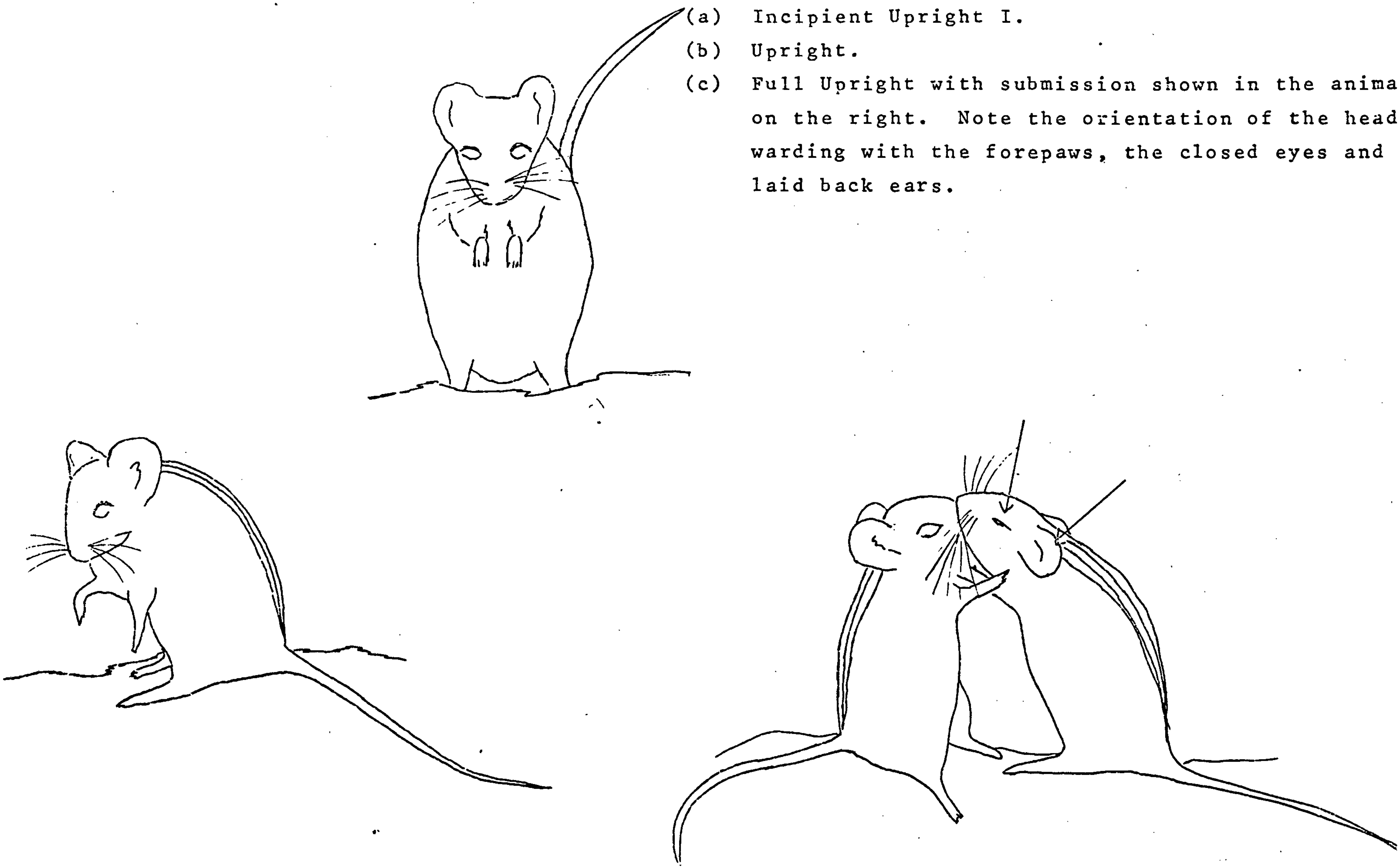
The Submission Posture comprises essentially the antithesis of Threat (cf. Darwin's Principle of Antithesis): in the latter the eyes are wide open with directed gaze, the ears held upright and perked, the forelegs straddled and the fur and tail ruffled and rigid, whereas in the Submission Posture the eyes may be half to fully closed, the head is tilted backwards, exposing the throat, the ears are held flattened against the head and the animal often crouches, with fur unruffled and tail drooping. Long pulses of ultrasonic vocalisation (see section b) may be emitted in this posture. The Submission Posture usually occurs in conjunction with other gross body postures such as the Defensive Uprights (Figure 2.6).

FIGURE 2.6. Defensive postures.

(a) Incipient Upright I.

(b) Upright.

(c) Full Upright with submission shown in the anima on the right. Note the orientation of the head warding with the forepaws, the closed eyes and laid back ears.



Other behaviour patterns that often occur in a defensive context are the Uprights (Eisenberg: Upright; Eibl-Eibesfeldt: Aufrichen) although they may occur in a threatening context as well as recognised by Eibl-Eibesfeldt in his terms Drohstellung and Drohabwehr. I have classed the upright postures into 3: the Incipient Upright I, the Incipient Upright II and the full Upright.

Defensive Incipient Upright I (Eisenberg: Upright, Class 1) occurs very often in a non-social context, usually when the animal is alert thus often occurring in conjunction with or following on from Attention. The posture (Figure 2.6a) consists of the animal either sitting or standing with one of the forepaws raised.

Defensive Incipient Upright II (Eisenberg: Upright, Class II) simply consists of the animal having both forepaws raised off the ground. The body is, however, in the same position as it would be if both paws were still on the ground, in other words the horizontal vertical orientation of the spine has not changed.

In the full Defensive Upright, (Figure 2.6b), the body is extended vertically. This posture may occur in a defensive situation in which the characteristic Submission Posture of half-shut eyes and flattened ears, in conjunction with ultrasound emission, may occur. In this context the motivation may be thought of as withdrawal - the animal drawing itself backwards out of reach of the opponent. Warding with the forepaws may occur in this situation; if both animals are upright, in an aggressive situation, mutual warding (Eibl-Eibesfeldt: Pfottentrommelin). I have not included the latter two patterns in the information theory analysis.

Another very common pattern in association with Attend and Defensive Upright I is pattering with the forepaws. Rather than having a communicative function, this is probably indicative of a state of tension, as it occurs very often in a non-social context.

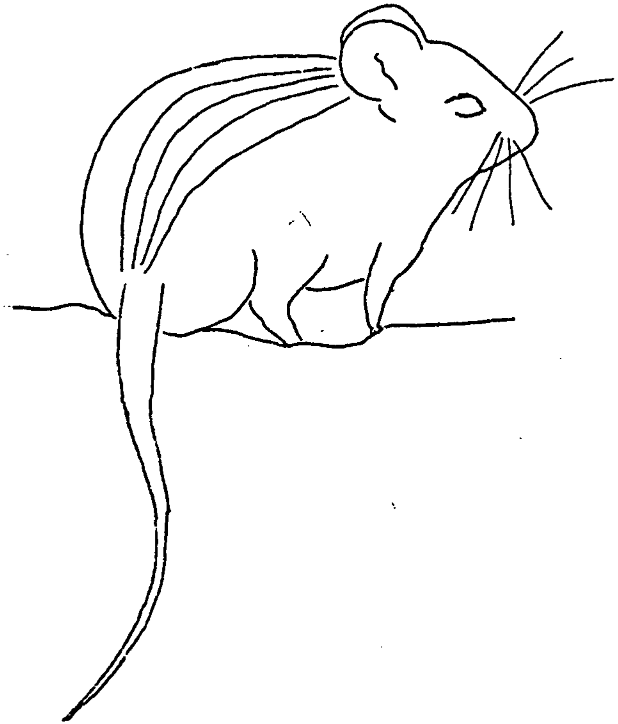
Miscellaneous patterns seen in a social context

Perineal Drag (Figure 2.7) (Eisenberg: Perineal Drag; Eibl-Eibesfeldt: Rutschen auf der Anal region). This behaviour pattern comprises a lowering of the haunches and consequent dragging of the perineal area on the ground, or, as is commonly observed, over an object in the environment, such as a stone, branch, carrot, etc. Examination of the ground surface after the performance of a perineal drag usually shows a small trail of fine droplets of urine. Presumably therefore, this is an example of marking behaviour (Chapter 2.5) in which the preputial glands may play a part. Perineal Drag is shown largely by the males, particularly the dominant; it was also, however, observed on a number of occasions, in a dominent female.

Display Run (no equivalent in either Eisenberg or Eibl-Eibesfeldt) Although not strictly social, this pattern would presumably fall under Altmann's (1962) description of "metacommunicative" behaviour. Metacommunication is communication about the meaning of other acts of communication (Bateson 1955). Altmann (1962) recognised two circumstances in which this type of behaviour may be used in the rhesus monkey: play invitation and status signalling. In the latter, for instance, a dominant monkey may be recognised by his brisk gait, his erect tail and his calm "major-domo" posture. Dominant male Rhabdomys show a similar type of metacommunicative status signalling, which I have termed the Display Run: the animal runs in a slow and somewhat jerky manner, almost prancing, the tail is held rigid and horizontal behind and the fur is ruffled. The whole display creates the impression in the observer of calm and confidence.

Freeze (Eisenberg: Freeze) This is self-explanatory: the animal simply sinks into immobility in whatever posture it finds itself. This usually occurs when the animal is alerted or alarmed, such as by crackling vegetation in the vicinity which might signal the approach of a predator, or at the approach or when catching sign of a dominant.

FIGURE 2.7. Perineal Drag. Note the perineal region lowered onto the ground surface.



Does Nothing (no equivalent) Although scarcely a behaviour pattern it was thought important to insert this category for the purposes of the information theory analysis. The reasons for doing this are discussed under "Methods".

It is one of the tenets of ethology that displays or behaviour patterns have evolved from non-communicative behaviour. The process by which this occurs was called by Huxley (1914) "ritualisation" or emancipation: the behaviour becomes emancipated from its original function and assumes the form of a stereotyped ritual, and the function of being purely communicative. Three types of behaviour have been recognised as being the forerunners of communicative displays: intention movements (Daanje 1950): incomplete or incipient locomotary movements; displacement activities or activities that occur supposedly out of context and with no apparent function; and, lastly, autonomic responses (Morris (1957), in which responses to autonomic arousal, such as piloerection, become incorporated into the pattern.

Charles Darwin is generally credited with the first scientific study on animal communication: "The Expression of the Emotions in animals and men" (1871). In this work, he describes certain principles of communication; the most useful of these is his "Principle of Anthithesis" that may be summarised as follows: when an animal reverses its intentions, it reverses the signal. In other words, patterns such as threat and defence, for instance, should be opposite in appearance.

The visual components of the behaviour patterns described for Rhabdomys fall into two basic categories: postural and locomotory. Postural components include such aspects as the orientation of the animal's head and body, the position of the tail and extension or flexion of the vertebral column, the position of the ears relative to the head and closure of the eyes. As can be seen from the descriptions, an aggressive Rhabdomys (e.g. Threat, Side Display, Attack) tends to make itself appear as large as possible: the body, in Side Display, for instance, is held sideways on to the opponent, or in Threat and Attack, the back is arched. Piloerection often occurs. The head is held down relative to the body, with the eyes wide open and directed in a fixed stare towards the opponent, while the ears are in an upright position.

The postures shown by the defensive or submissive Rhabdomys are, in agreement with Darwin's Principle, almost the exact antithesis. In patterns such as upright and submission, there is no sideways orientation of the body, and no piloerection: the head is tilted slightly (upright) or fully (subm) backwards exposing the throat, the eyes show varying degrees of closure and the ears are held flattened against the head.

Andrew (1972) in a discussion of behaviour patterns in general, differentiates between alert and protective responses. In the former, the ears are up and the eyes wide open, either for the purpose of scanning the environment or concentrating on a particular stimulus. Focussed attention, with its accompanying eduction in effective peripheral vision, may be thought of as a sign of confidence. Protective responses, on the other hand, involving closure of the eyes and flattening of the ears, are thought to be evoked by startling or painful stimuli. An interesting point is the close similarity of a friendly display such as Approach Elongate and a defensive display such as Upright in which postures such as ears flattened against the head are common to both. A friendly display may be assumed by a high status animal to one of lower status and presumably indicates that the subordinate may approach with impunity without the risk of the dominant attacking immediately.

In the consideration of the role of locomotion, one may think of the behaviour of the animal as lying at some point along a continuum from exertion to immobility (Andrew 1972). An animal on the point of attacking is moving toward exertion, while an animal on the defensive, or submitting, is moving toward immobility. In the pattern Attack, or even in the milder Threat, the characteristic arching of the back in the vertical plane has practical value in giving propulsive force to a charge or gallop, producing more powerful and more violent movement. The same arching of the back can be seen in Display Run, although here, where Rhabdomys is not considering an attack or even a chase, it is apparently functionless, and may be thought of as a ritualised response, an intention movement, in fact, that has lost its function. In a friendly display such as Approach Elongate the body is lengthened horizontally and correspondingly reduced in vertical height; the back is in an extended position and a diagonal gait is used again; this is the antithesis of Attack. Movement is slow and cautious. One might almost typify this as approach-withdrawal motivated behaviour; certainly no sharp or violent movements are used that might startle the recipient into attack.

The tail is an extension from the lumbar region of the vertebral column, so that bending of this section is often continued into the tail. This means that the position of the tail can communicate not only the likelihood of locomotion but also its probable intensity. In Attack, for instance, the tail is held rigid and arched, as it is in Display Run: while in Approach Elongate the tail is held horizontally from the body. A defeated animal, one moving toward the immobility end of the continuum, generally shows suppressed locomotion and a drooping tail.

Vocalisations or sounds resulting from respiratory movements may also be thought of in terms of the above continuum. An aggressive Rhabdomys, showing Threat or incipient Attack is tending towards exertion and the rate of ventilation accelerates. Characteristic of a mouse in this situation is a "chattering" sound produced by the throat or teeth. A submissive animal, slowing into immobility, on the other hand, characteristically produces long pulses of ultrasound that are clearly associated with the long slow respiratory movements. (See section 2.4) Respiratory movements incorporated into behaviour patterns may be thought of as ritualised autonomic responses: responses associated with thermoregulation may also be thought of in this category. These responses are evoked by novel or frightening stimuli (Morris 1957) and may take the form of either cooling responses in a mouse preparing for exertion, or warning responses in one preparing for immobility. Piloerection, characteristic of Threat and aggressive behaviour in general falls into the former category, while defensive responses such as upright, including huddling and clasping the limbs against the body, would be an example of the latter.

2.3.2 The influence of sex and status on the performance of behaviour patterns

As was described in Chapter 1, five sex and status classes were differentiated: alpha, beta and omega males, and alpha and omega females.

Inter-Male Behaviour

(a) Dominant male to subordinate males. The behaviour of the alpha male directed to the subordinates, both alpha and omega, is shown in Table 2.1.

Most striking is the high incidence of aggressive behaviour: it is interesting that the frequency of high intensity aggression, as seen in the patterns Attack and Chase, is greater directed to the omega males; behaviour directed to the betas comprises a greater proportion of the "lower intensity" aggression, seen in the various forms of threatening behaviour: Threat, Aggressive Groom and Side Display.

There is a correspondingly complete absence of any form of defensive or submissive behaviour (Flee, Retreat, Upright or Submission) and also a virtual absence of Approach Elongate. There is a very small proportion of conciliatory behaviour (Allogrooming, Sit Close, Put Paws on Back). Behaviour including sniffing is also low, with the exception of Naso-Anal. This might be an indication that this behaviour has aggressive connotations, perhaps in relation to the preputial glands.

(b) Middle-ranking (beta) male to dominant and subordinate males. The behaviour of the beta males is shown in Table 2.2.

There is a high proportion of high intensity aggressive behaviour (Attack, Chase) directed towards the omega, while much less aggression is

TABLE 2.1 Behaviour Patterns directed by the dominant male towards subordinate males

	α - β	α - ω	Total	Rel.Freq.	Info.
Approach	48	24	72	0,126	307,9
App.Elongate	-	-	0	0	0
Naso-Nasal	6	3	9	0,016	19,78
Naso-Anal	25	14	39	0,068	142,88
Sniff Cheek	10	13	23	0,040	72,12
Allogroom	5	-	5	0,008	8,05
Sit Close	4	-	4	0,007	5,55
PPBack	6	2	8	0,014	16,64
Att.Mount	-	-	0	-	-
Mount	-	-	0	-	-
Follow	-	-	0	-	-
Chase	62	79	141	0,2460	697,78
Fight	4	9	13	0,023	33,34
Flee	-	-	0	0	-
Threat	20	3	23	0,040	72,12
Side Display	27	4	31	0,054	106,45
Attack	75	97	172	0,300	885,37
Agg.Groom	15	-	15	0,026	40,62
Retreat	-	-	0	-	-
Upright	-	-	0	-	-
Move On	13	1	14	0,024	36,95
Does Nothing	-	1	4	0,007	5,55
Groom Self	-	-	0	-	-
Totals	320	253	573		2451,1
					= 2,073 bits

TABLE 2.2 . Behaviour Patterns directed by middle-ranking (beta) males to other males

	β - α	β - β	β - ω	Total	Rel.Freq.	Info.
Approach	34	13	35	82	0,1446	361,35
App.Elongate	20	4	-	24	0,0423	76,27
Naso-Nasal	3	13	4	20	0,0353	59,91
Naso-Anal	1	9	21	31	0,0547	106,45
Sniff Cheek	5	15	10	30	0,0529	102,04
Allogroom	2	-	-	2	0,0035	1,39
Sit Close	2	-	-	2	0,0035	1,39
PPBack	1	3	2	6	0,0106	10,75
Chase	o	2	2	79	0,1393	345,19
Fight	0	-	1	1	0,0018	-
Flee	74	11	8	93	0,1640	421,53
Threat	0	1	17	18	0,0317	52,03
Side Display	0	1	15	16	0,0282	44,36
Attack	0	1	85	87	0,1534	388,53
Agg.Groom	0	2	3	7	0,0123	13,62
Retreat	19	4	-	20	0,0353	59,91
Upright	10	1	-	12	0,0212	29,82
Move on	9	2	8	28	0,0493	93,30
Croom Self	6	11	-	6	0,0106	10,75
Submission	3	-	-	6	0,0053	3,29
Totals	189	93	286	567		3246,6
					=	0,6144 bits

TABLE 2.3 Behaviour Patterns directed by subordinate (omega) males to other males

	$\omega - \alpha$	$\omega - \beta$	$\omega - \omega$	Total	Rel.Freq.	Info
Approach	20	22	2	44	0,1317	166,50
App.Elongate	20	17	19	56	0,1677	225,42
Naso-Nasal	2	5	3	10	0,0299	23,03
Naso-Anal	-	-	-	0	0	0
Sniff Cheek	0	1	0	1	0,0029	-
Allogroom	0	7	0	7	0,0209	13,62
Sit Close	0	0	0	0	0	0
PPBack	0	0	0	0	0	0
Chase	0	0	0	0	0	0
Flight	0	0	0	0	0	0
Flee	96	64	1	161	0,4820	818,11
Threat	0	0	0	0	0	0
Side Display	0	0	0	0	0	0
Attack	0	0	0	0	0	0
Retreat	10	12	0	25	0,7485	80,47
Upright	2	18	-	20	0,0598	59,91
Move On	2	2	1	5	0,0149	8,05
Submission	1	4	0	5	0,0149	8,05
Totals				334		1403,16 = 1,6102 bits.

directed to animals of the same rank and almost none at all to the alpha. Low intensity aggression (Threat, Side Display, Aggressive Groom) show a similar pattern.

Submissive or defensive behaviour is directed largely towards the alpha male, a much smaller proportion to same-status animals, and none to subordinates.

Very little conciliatory behaviour (Allogrooming, etc.) is shown at all. There is a high prportion of naso-nasal and sniff cheek, while naso-anal is largely directed to subordinates, a similar distribution to that seen in the alpha's behaviour.

(c) Subordinate male to dominants. The behaviour of the omega males towards the alpha and beta males, as well as towards males of the same status, is shown in Table 2.3.

Firstly, there is a reduction in the number of actions (from 573 for alpha males and 567 for beta males to 334). Secondly, one sees a complete absence of aggressive behaviour of any description.

Apart from Approach, the greater proportion of the omega male's behaviour appears to consist of defensive (Upright, Retreat and Flee) or submissive (Submission) behaviour directed to the dominants. While the frequency of Retreat is much the same when directed to either alpha or beta males, it is interesting that low intensity defensive behaviour, Upright, is directed largely toward the beta male, while high intensity defence is directed largely towards the alpha (half again as much as that to the beta).

The only form of conciliatory behaviour seen in Allogroom, directed toward the beta male. There is a very small proportion of sniffing behaviour, and a complete absence of Naso-Anal.

An interesting point is that there is very little behaviour at all directed toward males of the same status.

Inter-female behaviour

(a) Dominant female. Table 2.4 shows the behaviour of the alpha female toward other alpha females and to the omega females.

It can be seen that the number of actions is drastically reduced (166 as opposed to 573 for the alpha male and 334 for omega male).

There is a high proportion of high intensity aggression, directed towards subordinate females, with a smaller proportion directed to females of the same status. There is a correspondingly almost complete absence of low intensity aggression, as well as of any defensive or submissive behaviour.

Conciliatory behaviour is relatively rare, as is Approach Elongate. As far as sniffing behaviour is concerned, Naso-Anal is absent; only Naso-Nasal and Sniff Cheek are present.

(b) Subordinate female behaviour. The behaviour of the subordinate (omega) female toward other females is shown in Table 2.5.

The distribution of acts is very similar to that shown by the omega male: there is a complete absence of aggressive behaviour of any form, and a correspondingly high proportion of defensive behaviour: high intensity defense (Flee) directed to the alpha female, and a relative lack of low intensity defence.

The frequency of conciliatory behaviour is very low, although Approach Elongate shows a high freqency directed to the alpha female. Similarly, there is an almost complete absence of sniffing behaviour.

Male-Female Behaviour

This is shown in Table 2.6.

Clearly, there is an absence of aggressive behaviour, in both its high and low intensity forms. On the other hand, there is a relatively high

TABLE 2.4 Behaviour patterns directed by dominant (alpha) females to other females

	$\alpha - \alpha$	$\alpha - \omega$	Total	Rel.Freq.	Info
Approach	19	21	40	0,2409	147,55
App.Elongate	0	3	3	0,0181	3,29
Naso-Nasal	3	4	7	0,0423	13,62
Naso-Anal	0	0	0	0	0
Sniff Cheek	2	5	7	0,0423	13,62
Allogroom	0	0	0	0	-
Sit Close	1	0	1	0,0060	-
PPBack	2	1	3	0,0181	3,29
Chase	10	44	54	0,3354	215,41
Fight	0	8	8	0,0482	16,64
Flee	0	0	0	0	0
Threat	0	0	0	0	0
Side Display	0	0	0	0	0
Attack	3	39	42	0,2530	156,98
Agg.Groom	-	-	0	0	0
Retreat	0	1	1	0,0060	-
Totals	40	126	166		570,4 = 1,6758 bits

proportion of high intensity defensive behaviour (Flee) shown by males away from the alpha female only; this is seen in all classes of males but is highest among the omega males. Presumably this is reaction to the aggressive behaviour shown by the breeding female.

Of conciliatory behaviour, the same proportion of Approach Elongate is shown by both alpha and beta males; the porportion is higher for omega males. There is a relatively high frequency of other conciliatory behaviours (Put paws on back, Sit Close, Allogroom); most notable of which is the frequency of these shown by omega males to omega females.

There is a relatively uniform distribution of Sniff Cheek and Naso-Nasal, and a high proportion of Naso-Anal; it is interesting that most of the alpha male's behaviour in this direction is shown towards the alpha female, while those of the betas and omegas are directed largely to the omega females. There is a relatively high frequency of Follow shown by the alpha male in particular. Presumably therefore both these patterns are sexual in this context.

Of sexual behaviour itself, it is very interesting that virtually no sexual behaviour (apart from sniffing) is shown by the omega males. However, for the alpha and beta males, there is a relatively even distribution of successful mounts. A possible reason for this difference will be dealt with in the Discussion.

Female-Male Behaviour

This is shown in Table 2.7.

There is a high frequency of high intensity aggressive behaviour, in terms of Attack and Chase directed by the alpha females to males of all classes, but particularly to the omega males. In comparison, there is a small proportion of low intensity aggressive behaviour (Threat, Side Display and Aggressive Groom). Aggressive Groom, in fact, seems to be the prerogative of the dominant males.

TABLE 2.6 Behaviour patterns directed by males to females

	αM-αF	αM-ωF	βM-αF	βM-ωF	ωM-αF	ωM-ωF	Total	Rel.Freq.	Info.
Approach	68	58	98	52	24	42	342	0,2852	1995,50
App.Elongate	16	2	15	0	37	4	74	0,0617	318,50
Naso-Nasal	5	1	5	1	5	9	26	0,0300	84,71
Naso-Anal	43	16	13	26	0	21	119	0,0992	588,72
Sniff Cheek	14	5	12	15	3	16	65	0,0542	1132,66
Allogroom	6	1	2	10	0	25	44	0,0367	166,50
Sit Close	15	3	5	10	0	25	58	0,0484	235,50
PPBack	9	5	3	2	0	2	21	0,0175	63,93
AM	9	31	21	9	0	1	71	0,0592	302,65
Mount	11	15	9	11	0	0	46	0,0384	176,11
Follow	25	18	19	10	0	0	72	0,0607	307,92
Chase	5	10	3	9	0	0	27	0,0225	88,98
Fight	0	0	0	1	0	0	1	0,0008	–
Flee	12	0	48	0	101	3	164	0,1368	836,38
Threat	0	0	0	0	0	0	0	0	–
Side Display	0	1	0	0	0	0	1	0,0008	–
Attack	0	2	0	5	0	0	7	0,0058	13,62
Retreat	0	0	7	0	11	1	19	0,0158	55,94
Upright	0	0	0	0	1	2	3	0,0025	3,29
Move On	0	0	3	0	1	0	4	0,0033	5,55
Does nothing	4	0	0	0	0	0	4	0,0033	5,55
Groom Self	4	2	6	9	3	7	31	0,0259	106,45
Totals	246	170	269	170	186	158	1199		6488,46 = 1,6777 bits

TABLE 2.7 Behaviour patterns directed by females to males

	αF-αM	αF-βM	αF-ωM	ωF-αM	ωF-βM	ωF-ωM	Total	Rel.Freq.	Info.
Approach	8	30	30	18	17	12	115	0,1213	545,67
App.Elongate	12	5	0	15	26	2	60	0,0633	245,66
Naso-Nasal	8	6	1	0	4	2	21	0,0222	63,93
Naso-Anal	5	23	0	0	2	4	34	0,0358	119,89
Sniff Cheek	16	7	3	0	1	8	35	0,0369	124,44
Allogroom	4	2	0	5	13	20	44	0,0464	166,50
Sit Close	21	6	0	5	8	21	61	0,0643	250,76
PPBack	4	5	0	0	2	10	21	0,0222	63,93
Chase	24	29	64	3	5	2	127	0,1339	615,21
Fight	8	2	10	0	0	0	20	0,0211	59,91
Flee	2	0	0	16	5	0	23	0,0243	72,12
Threat	3	4	6	0	0	0	13	0,0137	33,34
Side Display	0	4	8	0	0	0	12	0,0127	29,82
Attack	26	51	79	0	0	0	156	0,1646	787,78
Agg.Groom	0	0	0	0	0	0	0	0	-
Retreat	44	38	1	38	31	3	155	0,1635	781,73
Upright	5	3	0	7	2	0	17	0,0179	48,16
Move on	5	7	1	5	4	0	22	0,0232	68,00
Groom Self	0	6	0	0	0	3	6	0,0063	10,75
Crouch	4	0	0	0	2	0	6	0,0063	10,75
	199	228	203	112	122	87	948		4098,36
									= 2,5312 bits

A high frequency of Retreat is shown by both dominant and subordinate females to alpha and beta males, but not to omegas. The reason for this is that this behaviour occurs in a sexual context. Retreat is shown by a non-receptive female. The distribution of this behaviour towards the males ties in with the previously observed fact that sexual behaviour is shown largely by the alpha and beta males, and vitually none at all by the omegas.

There is a relatively even distribution of conciliatory behaviour, except that of the omega females' behaviour toward the beta and especially the omega males; this is seen in the high frequencies of Allogroom and Sit Close.

Sniffing behaviour is also evenly distributed. Naso-Anal is particularly high for the category alpha female - beta male; perhaps a further indication of its aggressive correlation.

It appears, therefore, that there is a clear hierarchical organisation in the Rhabdomys colony; this is evident, amongst other things, from the organisation of aggressive behaviour. The alpha dominates both beta and omega, but directs more aggression to the omega than to the beta; the beta shows aggression to the omega, but none to the alpha, while the omega shows no aggression at all.

An observation that is perhaps significant is the type of aggression shown by the alpha male to his two classes of subordinates - beta males tend to receive a porportionately greater share of lower intensity agression (Threat, etc.) while omega males tend to receive high intensity aggression. This, I feel, ties up with the spatial relationships among the animals, and particularly the distances at which animals are tolerated - as shown in Chapter 1, an alpha male tolerates a beta at a shorter distance than he does an omega. So that, assuming a beta and an omega male approach an alpha to the same distance, the presence of the omega will tend to evoke a stronger response from the alpha, seen in the preponderance of high

Defensive behaviour, essentially the reciprocal of aggression, shows the same picture in reverse: omega males show a high frequency of high intensity defensive behaviour (Flee) toward the alpha male, and a correspondingly lower frequency of the same behaviour towards the beta males, to whom a significant proportion of directed defensive behaviour consists of lower intensity defence, such as Upright or Retreat. This indicates not only a greater avoidance of the alpha, but also an increased relative tolerance of the betas.

On the performance of aggressive acts, an alpha female may be ranked with an alpha male. This may also be seen from the frequency of defensive actions on the part of the subordinates. It is interesting, however, that while the alpha male tends to show threat behavour, in the form of Threat, Aggressive Groom and Side Display, the proportion of these acts in the alpha female's repertoire is much lower. A possible reason for this could lie in the fact that while the dominant male wandered all over the cage, often feeding at the north-western feeding site, which did not fall within his territory, the dominant female tended to remain on the territory and closer to the nest-site. While a stranger entering the territory would elicit violent aggression on the part of the territory holder, a subordinate approaching too close to a dominant at a communal feeding site would not represent the same threat, and therefore would not elicit the same degree of aggression: an importunate beta or omega male could easily be put in his rightful place by a Threat exhibition, or if the occasion required, an Aggressive Groom.

It is interesting too, that the incidence of female-female behaviour, whether the animals concerned are of the same of of differing status, is relatively low compared to male-male or inter-sex behaviour. The subordinate female almost never reacts with the dominant female except to take defensive action against the attacks which form the bulk of the latter's behaviour. Males on the contrary, show a wide range of behaviour to the other males, ranging from the full gamut of aggressive behaviour to conciliatory behaviour such as Allogrooming and Sit Close, to sniffing behaviour such as Naso-Nasal. Females, on the other hand, do exhibit these behaviours towards males, as do males to females. One might, on this basis, assume that the social organisation is fundamentally patriarchal, with the male hierarchy forming the backbone of the structure. The females apparently have a more fluid structure, status being determined either by breeding condition or association with a dominant male M12 association with F2, Chapter 1), and this structure being therefore dependent and interrelated with the male hierarchy.

A further point of interest is the relative lack of social interaction of the subordinate animals. These animals could in fact be thought of as outcasts, moving on the periphery of the society, who would, in a natural environment, presumably emigrate. The very high frequencies of conciliatory behaviour in these animals is perhaps significant in view of this: perhaps it is an attempt to establish bonds within the society; a view that may be supported by the incidence of this behaviour higher up the social scale: beta males to alphas, and omega females to beta males.

2.3.3 Information theory analysis and sequences

It is very tempting to assume from merely observing one animal displaying to another that it is communicating. This assumption is, however, totally unjustified unless one can provide a quantitative measure that the behaviour of one animal is in fact affecting the behaviour of another.

The information theory analysis of behaviour sequences is shown in Table 2.8. The high linkages obtained indicate that these patterns are in fact affecting the performance of another, in short that communication between the signaller and the respondent is occurring.

The percentage uncertainty reductions obtained for Approach-initiated sequences are high (99% for Approach-Attack) indicating very strong linkages between Approach and the behaviour patterns Attack, Flee and Retreat. Threat shows a lower linkage.

TABLE 2.8 Information theory analysis of behaviour sequences.
The top figure is the actual frequency of the sequence.
The lower figure is the percentage uncertainty reduction.

	Naso-Nasal	Naso-Anal	Sniff Cheek	Allog	Sit Close	PP Back	Threat	Attack	Chase	Upright	Subm	Retreat	Flee	Move On	Groom Self	Att. Mount	Mount
Approach							54 ,3049	311 ,9955					118 ,9338				
App.Elongate	66 ,5643	9 ,3369	82 ,4304	4 ,4982	53 ,4573	15 ,6488											
Naso-Nasal		10 ,8946	15 ,8648		94 ,8504									30 8147			
Naso-Anal		33 ,7073	2 -	9 ,7418	18 ,7264	5 ,7843				4 ,8370		86 ,7204			15 ,8147	38 ,7740	8 ,7448
Sniff Cheek	9 ,7083	31 ,7329	26 ,7155	14 ,7365										53 7232			
Allogroom	24 ,6469	7 ,6887		10 ,6855	27 ,6754	19 ,6926										5 ,0700	
Sit Close	8 ,6772			84 ,7809		36 ,7239											
PPBack	3 ,2059			8 ,6433	21 ,6933					3 ,7938					25 ,7757		
Threat										16 ,5481		32 ,5378	6 ,6111				
Side Display										10 ,5225	2 ,6882	48 ,4899					
Agg.Groom										10 ,3087	6 ,3802	22 ,3148					
Attack													464 ,6378				
Fight								25 ,8092									
Retreat									99 ,7075								
Flee									333 ,6655								

Approach Elongate gives rise to a number of behaviour patterns - all the category of conciliatory or sniffing behaviour (Naso-Nasal, Sniff Cheek, Allogroom, etc.), indicating that the motivation behind this pattern is friendly and conciliatory. The uncertainty reduction is somewhat less than for Approach-initiated behaviours, an indication that a number of different behaviour patterns may follow on from Approach Elongate.

Sniffing behaviours and conciliatory behaviours are linked - an interesting observation is the linkage between Sniff Cheek and Move On (72,32%) and Naso-Nasal-Move On (77,57%), an indication that these patterns are investigatory in nature, and do not lead to further reaction. It was observed that these 2 patterns usually occurred on neutral ground, such as a runway. Naso-Anal shows high linkages with defensive behaviours (Upright: 83,70% and Retreat: 72,04%) and displacement activities (Groom Self: 81,47%), a confirmation of the previously mooted speculation that this pattern does have aggressive correlations.

Low intensity aggression tends to lead to low intensity defensive action, seen in the linkage between Threat, Side Display, Aggressive Groom and Upright, Submission and Retreat. High intensity aggression, not surprisingly, leads to high intensity defence: Attack-Flee, Flee-Chase.

Information theory thus appears to be a useful measure of the constraints of one behaviour pattern upon another. Its major disadvantage is the lack of the traditional confidence limits and significance levels that are usual in statistical analysis. Hazlett and Estabrook (1974a) however, do not consider this a serious drawback, since, as there is no concern about a priori distribution characteristics, one can treat data without making (perhaps false) assumptions about distributions; this may in fact be an important advantage as behavioural act frequencies do not generally fit any standard statistical pattern such as the bivariate or removal distribution (Hazlett and Estabrook 1974a). In conclusion, Steinberg (1977): "..these methods of analysis are not without drawbacks, 1971 a,b) found a relationship between ultrasound emission and the development of homiothermy in albino mice (Mus Musculus); the calls appeared to be in response to two situations: cold stress and handling. In the latter situation, the calls produced tended to be somewhat louder and continued until a later age (Noirot 1968; Sewell 1968, 1969). The function of these calls is thought to be a signal to the mother to retrieve the pups if outside the nest or to inhibit maternal "aggression" caused by rough handling (Ralls 1967).

In the adult rodent, ultrasonic calls have been observed in conjunction with aggressive behaviour in a number of species (Sewell 1967, 1969), both on the part of the aggressor who, in the rat Rattus norvegicus, emits short sharp calls in the region 45-70 kHz, and in the loser, who, in association with the submissive posture, emits long calls of slightly lower frequency in the region of 20-70 kHz. Sewell (1969) found ultrasound to be statistically associated with the mating behaviour of male mice (Mus musculus), especially with the behaviour patterns of nosing the female, sniffing her anogenital region and mounting. Barfield and Geyer (1972) described the so-called "post-ejaculatory song" of the male rat: consisting of long calls in the region of 22-25 kHz. The function of all these calls would appear to be the inhibition of aggression.

Other situations in which ultrasound has been observed are during lactation in the female wood-mouse (Apodemus (Sewell 1969) and during exploratory behaviour in both sexes of the same species (Sales 1972 b).

It thus appears that all species of myomorph rodents studied make use of ultrasound; ultrasonic cries in infant rodents appear to be universal, while those of the adults tend to vary from species to species. It therefore seemed likely that Rhabdomys would also use this form of communication and that an investigation of the animal's ultrasonic behaviour would be a worthwhile addition to the other studies on communication.

2.4.2 Materials and Methods

For the detection of ultrasound a portable "Mini-Bat Detector" (QMC Instruments Ltd.) was used. This instrument, operating on a heterodyne circuit, produces an audible analogue of the ultrasound by tuning the detector to the required frequency; it is calibrated from 10-180 kHz. Once tuned, the detector is capable of picking up sound at the calibrated frequency and 10 kHz higher. The exact frequency of the sound may then be determined by recording the sound (the audible analogue of the ultrasound) and analysing it by means of an oscilloscope. The frequency shown on the oscilloscope trace is then added to the calibrated frequency shown on the detector dial; the sum of these two values gives the actual frequency of the sound produced. The detector is capable of picking up sounds to a distance of roughly 3 metres.

Observations were carried out initially on the caged population; detailed observations and recordings were made in the laboratory because of the high incidence of background noise in the open. Ten mice were used: 5 males (of various ranks) and 5 females, as well as observations on infant mice. All adults were established individually in glass terraria (61 x 30,5 x 30,5 cm) containing sand, nesting material and food.

Male-Male Interactions: Each male was introduced into the cage of another male. This allowed 16 pairings.

Female-Female Interactions: As above.

Male-Female Interactions: To test for sexual behaviour, each female was injected with 0,1 mg oestrogen as oestradiol benzoate 48 hours prior to testing, in order to induce oestrus.

Recordings of behaviour were made on a Sony casette recorder using 2 channels; one for the calls and one for speech, thus allowing an exact description of the posture and behaviour of the animal at the time of the call. The tapes were played through a storage oscilloscope (Tektronix Ltd.) which has the facility of displaying the entire call on the screen at any one time. Photographs using a Minolta 101b camera on time exposure were taken of the display and tracings using clear transparent cellophane were made of selected parts of the calls.

Unfortunately the method of ultrasound detection - the bat detector transforms the ultrasonic and therefore inaudible call into an audible analogue, which is then recorded on tape, thus losing its ultrasonic component - does not permit the replaying of calls to the animals.

2.4.3 Results

Ultrasound was observed in association with the following behaviour patterns:

Approach Elongate: These calls are in the region of 40-43 kHz in frequency, a short duration - about 12 msecs (Figure 2.8) and sound essentially like a "chirrup". They appear to occur regularly in association with this behaviour pattern. Approach Elongate, as described earlier, occurs largely when a subordinate mouse approaches a dominant: it is essentially an appeasement posture; thus ultrasound in this category is produced by subordinate, rather than dominant, mice. It occurs slightly more often in females rather than subordinate males, and in the dominant male not at all. There is no audible component to these calls.

Flee: Ultrasonic cries were only observed in association with this behaviour pattern in the case of one particular female (F45) fleeing from a male. The sound was essentially the same as that heard in conjunction with Approach Elongate (Figure 2.8). Again, there was no audible component.

Submission: This is a rare behaviour pattern and, unfortunately, no recordings were obtained of its ultrasonic component. Observations indicate, however, that the sound is of slightly lower frequency than those described above, being in the region of 25-30 kHz, as indicated by tuning the bat detector, and is also much longer in duration. Close observations of the animal concerned showed a close relationship between the emission and the ultrasound and respiratory movements. The change in respiration rate in association with behaviour and motivation has been discussed elsewhere (section 2.3.1); briefly, the submissive animal tends to breathe in a slow and shallow manner, and the ultrasonic calls correlated with exhalation.

Infant Rhabdomys calls were observed in response to both isolation from the nest and handling. It can be seen that the cries in response to handling show a higher rate, and also continue for some days after the eyes open. These calls also tend to be louder than those associated with isolation, confirming Sewell's (1968, 1969) observations on this behaviour in infant mice (Mus musculus). Smith (1972) found that handling may elicit a different type of call in mice: no evidence was found for this is Rhabdomys.

No ultrasonic cries were heard in association with aggressive courtship or mating behaviour in Rhabdomys.

The physical structure of the calls. Figure 2.8 shows a call recorded in association with the behaviour pattern Approach Elongate. The detector was tuned to 40 kHz. An examination of the structure of the call shows both frequency and amplitude modulation: the initial part of the call is of a higher frequency than the rest, while the greatest amplitude occurs towards the middle portion. The amplitude increases sharply towards this mid portion, and then decreases more gradually. The average frequency of this call is 43 kHz, and the duration is 10 milliseconds.

Figures 2.9 and 2.10 show recordings obtained from infant Rhabdomys. The calls are essentially the same as that shown in Figure 2.8 above; again, there are frequency and amplitude changes, although here the frequency is greater in the second half of the call. Again, the amplitude increases sharply in the initial stages and decreases more slowly in the latter stages.

FIGURE 2.8. Oscilloscope trace of ultrasonic call associated with the behaviour pattern Approach Elongate.

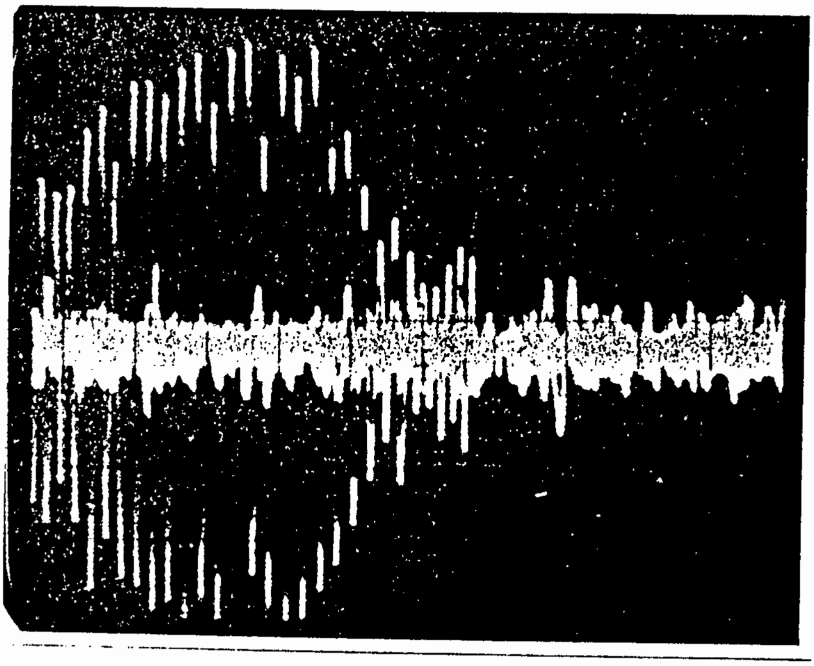


FIGURE 2.9. Oscilloscope trace of ultrasonic call produced by infant <u>Rhabdomys</u>.

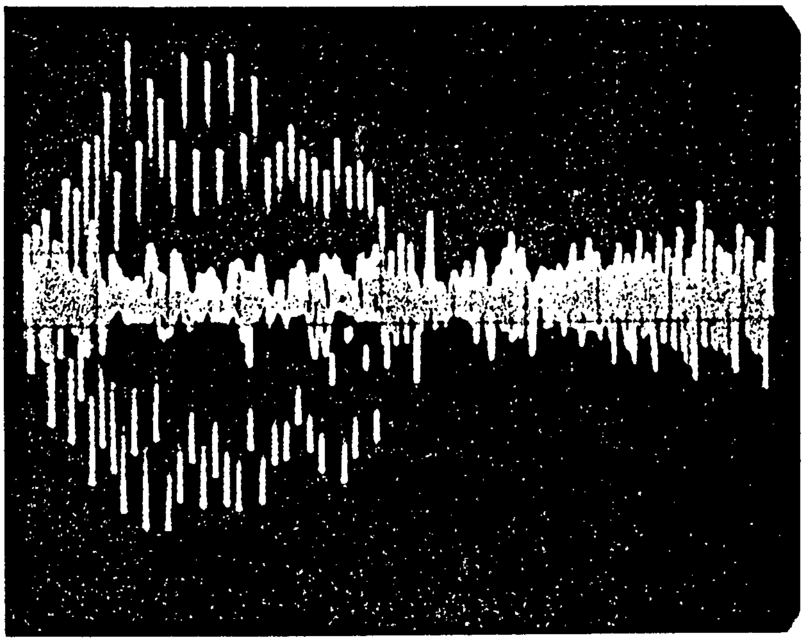
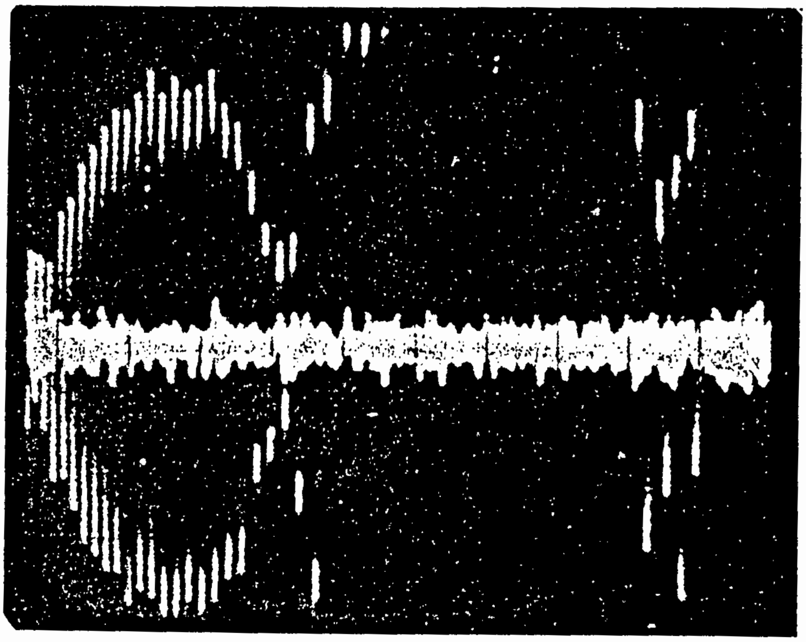


FIGURE 2.10. Oscilloscope trace of ultrasonic call produced by infant *Rhabdomys*.



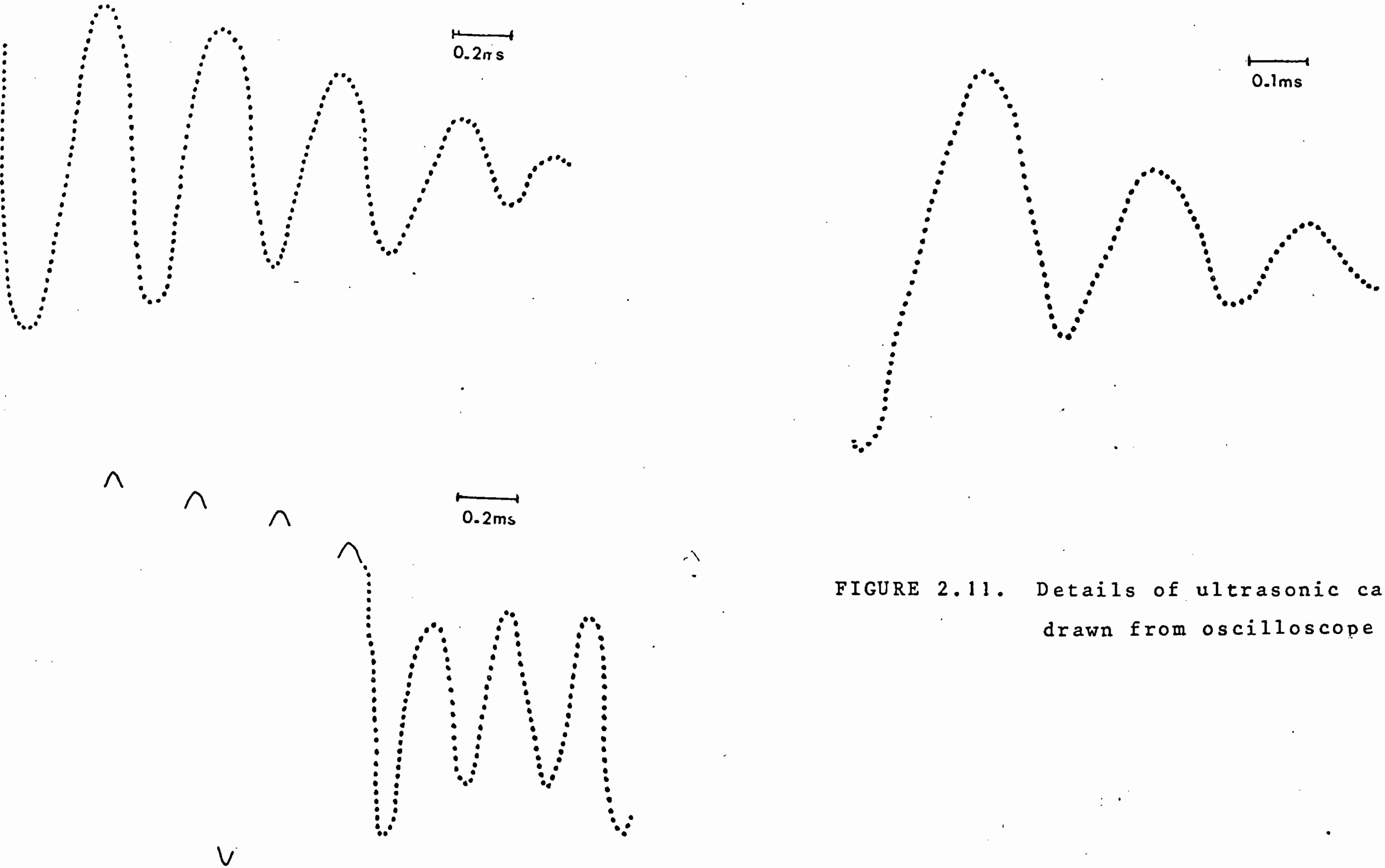


FIGURE 2.11. Details of ultrasonic calls, drawn from oscilloscope trace.

The average frequency of both these calls is 43 Khz; the duration of the call shown in Figure 2.9 is 6 milliseconds, and that shown if Figure 2.10 is 12 milliseconds.

Figure 2.10 shows an interesting phenomenon: two calls following on immediately from one another. The initial call is very loud (much greater amplitude) and of slightly lower frequency (42,4 kHz). These calls are produced both when an infant mouse is isolated from the nest, and when handled. The calls are the same in physical structure, except that in the latter case, of a great amplitude.

Figure 2.11 shows details of the above calls. These traces show regular frequency, but clear amplitude modulation. This steadily decreasing amplitude with constant frequency is a good example of a damped oscillation.

2.4.4 Discussion

There are two methods available for the detection of ultrasound. The first is by recording the sound on tape running at very high speed, which can then be re-played at a lower speed, thus reducing the fequency of the sounds to the audible range. The second is by producing an audible analogue of the sound, thus giving a more direct and immediate indication of the presence of ultrasound. The former method requires the use of highly sophisticated equipment, and has the advantage of retaining the call in its original form, allowing it to be replayed to the animals. This method was tried, without success, largely due to technical problems involved in transporting the animals some distance to the acoustics laboratory for relatively short periods of time, which appeared to stress the animals considerably and consequently affected their behaviour: they simply huddled together and would not respond. It was unfortunately not possible to transport the equipment. Thus it was decided to use the bat detector, which, while it does not allow the replaying of the calls to the animals, has the supreme advantage of being portable and being able to be used in the field, or in this case, in the cage, with no interference at all with the animals or their behaviour.

Ultrasound as a communicative device is effective only over very short distances; due to the high frequency and correspondingly short wavelengths, the sound waves are easily reflected from objects and alternate rapidly in air: it is these characteristics that make it effective in echolocation. One would therefore expect ultrasound to be used in close-range communication: this appears to be the case in its association with the behaviour patterns Approach Elongate, Flee and Submission, as well as the behaviour of infant Rhabdomys. As far as function is concerned, Noirot (1966) postulated that the function of the cries of infant rodents is to inhibit aggression and initiate retrieval and comfort behaviour on the part of the mother. There is no reason to dispute this hypothesis for infant Rhabdomys - it is also not uncommon for adult animals to "mimic" juvenile behaviour when seeking to conciliate or pacify a conspecific (Ewer 1968); as Rhabdomys uses ultrasound in behaviour patterns that are essentially designed to inhibit aggression (Approach Elongate, Flee and Submission), this could very well be an imitation of juvenile behaviour. As adult animals rarely attack juveniles (Ewer 1968), particularly their own offspring, mimicry of a juvenile could very well serve as a device for inhibiting aggression.

Rhabdomys apparently does not use ultrasound in association with aggressive and mating behaviour, but does in conjunction with Approach Elongate, which has never been observed in other rodents investigated (Sales and Pye 1974). It is interesting to speculate on possible reasons for this difference: probably the most likely explanation lies in the fact that Rhabdomys is diurnal: to the best of my knowledge in contrast to all the other rodent species investigated. This means that visual communication plays a larger role - the importance of vision, and in particular movement and posture - was discussed in section 2.3.1; it was shown that directed movement and associated postures towards a conspecific is construed as threatening. A nocturnal animal would not have these threatening devices at its disposal, and to communicate Threat or Aggression, would presumably need to use another means. Chemical communication would not suffice, as it is relatively slow-acting, (section 2.3.3: the only other means are acoustic.

It is striking that in Rhabdomys, all ultrasonic behaviour is directed by subordinates towards dominant animals. The occurrence of ultrasound in association with Approach Elongate, an appeasement display, relates to its absence in the case of Threat: as directed movement towards another animals implies threat, which would elicit intense aggression on the part of the dominant, the approaching subordinate needs a further component to inhibit attack. The use of the aggression-inhibiting ultrasound would therefore seem to say "Don't attack - I am not threatening you."

The analysis of mating behaviour among the hierarchy (section 2.3.2) indicated that it was almost always directed towards a female of equal or lower status: only an alpha male has access to an alpha female, beta males mate with beta or omega females and so on. Directed approach towards an equal or lower status animal does not elicit aggression, , so that the use of aggression-inhibiting ultrasound would be unnecessary.

There is little evidence but much speculation about the mechanism of ultrasound production. Audible cries generally consist of a harmonic series with a formant structure, which can be explained in terms of vibrating vocal cords activated by respiratory air flow, controlled by muscles and modified by vocal tract resonance (Roberts 1972). Ultrasonic calls are usually pure tones subject to rapid frequency and amplitude changes that often occur with no obvious harmonic relations. It is also not unknown for simultaneous harmonically unrelated frequencies to occur (Sales 1972): all these phenomena are difficult to explain in terms of vibrating membranes and muscle action. Audible and ultrasonic cries never occur simultaneously, although one may break in to the other (Sewell 1969) suggesting a physical relationship between the two, under the control of two different mechanisms. The rapid frequency changes that often occur towards the end of a call suggested to Sewell (1969) a wind instrument being "overblown", and led her to propose a whistle-like mechanism for the production of the sound. The fact that ultrasound production is closely associated with respiratory movement, beginning at the onset of expiration, and the close relationship to audible sound, suggested to

Roberts (1972) that this whistle mechanism might be situated in the larynx. The edges of the larynx tend to point upwards (Negus 1949) can can be blown open easily by the expiratory air flow, so that the larynx is in effect acting as a valve. Roberts (1972) believes that fine adjustment of this valve may determine whether the vocal cords vibrate to produce audible sound or whether ultrasound is produced. As yet there is no evidence for this hypothesis.

Although one may study the production of ultrasound and the structure of the calls, one cannot say whether they have an communicative value unless one knows that the animals can in fact perceive sounds of this frequency. This has been done by several workers, starting with Dice and Barto (1952) who used ear movements as a somewhat crude measure of sound perception in Peromyscus. Crawley et al (1965) demonstrated that the laboratory rate could hear frequencies up to 40 kHz; Ralls (1967) found sensitivity to frequencies up to 80 kHz, in Mus and Peromyscus, and Brown (1970) using recordings from the cochlea of three species, Apodemus, Clethrionomys and Meriones, conclusively demonstrated the ability of these animals to hear sounds in the ultrasonic range.

The evidence for the communicative function of ultrasound in Rhabdomys is purely circumstantial. This is unfortunately the case for most work done on ultrasound; even if one is able to play the calls back to the animals, problems arise in determining the recipient's response. A number of methods have been tried: Dice & Barto (1952) used the ear twitch as a sign that the call had been received, while Brown (1970) attempted the more reliable technique of direct electro-physiological measuring from the cochlea. The apparent function of the ultrasonic calls in Rhabdomys as aggression-inhibiting, poses an additional problem - characteristic behaviour is not elicited, but inhibited, by ultrasound. However, these observations described here are certainly interesting, especially the demonstration of the use of ultrasound with a behaviour pattern that has not been found before, and the lack of an ultrasonic component to two categories of behaviour where it is apparently fairly common in other rodent species. This brief study therefore forms a preliminary investigation of an aspect that has been little studied in African rodents, and may provide a basis for further work.

2.5 CHEMICAL COMMUNICATION

2.5.1 Introduction

Although ethology has traditionally stressed visual means of communication, i.e. postural and locomotory displays - perhaps easier for a micro osmic human observer to follow! - recognition of the importance of chemical substances in communication in many species has gained prominence in the last two decades. A chemical substance used for a communicative purpose is a "pheromone", a term coined by Karlson and Lüscher (1959), and which has been defined as a "chemical or mixture of chemicals which is released to the exterior by an organism and which, upon reception by another individual of the same species, stimulates one or more specific reactions". (Shorey 1977). Wilson and Bossert (1963) and Wilson (1963a) divided pheromones into two categories: resease pheromones, which are direct stimulators of behaviour, including a stimulus-response sequence that is mediated entirely by the central nervous system; and primer pheromones, which produce physiological changes, especially to the reproductive and endocrine systems, that are relatively longer in duration. Numerous examples of the effects of primer preromones have been recognised (Parkes and Bruce 1961), such as the Bruce effect, the Lee-Boot effect, the Whitten effect, and lastly the Ropartz effect (Ropartz 1968); all are apparently induced by a substance or substances in the urine of the male.

Release preromones are rather more difficult to investigate. Two reasons for this are apparent: firstly, the complex and flexible nature of mammalian behaviour, which unlike that of insects, on which the most successful work has been done, is not rigid and "pre-programmed" with a certain response always following on from a certain stimulus. Secondly, all indications are that mammalian pheromones are highly complex: to date, no pheromone has yet been fully isolated or identified - the nearest approach to this has been the identification, by the perfume industry, of the essential components of the secretions of the civet Viverra ciretta and the musk deer Moschus moschiferus. Chemical assays of secretions have indicated a vast array of compounds, e.g. Goodrich and Mykytomycz (1972) and Smith et al (cited Beauchamp et al 1976) identified over 30 compounds in the perineal gland secretion of the guinea pig Cavia porcellus Urine alone, which is the basic medium used by mammals (Ewer 1968; Doty 1973) contains "hundreds, or even thousands, of volatile and non-volatile substances (Doty 1973).

The result is that one "pheromone" may serve more than one function. Wilson (1970) has suggested as a reason for this, that the social behaviour of vertebrates and mammals in particular, is "personal", i.e. it is based on recognition of individuals and the maintenance of hierarchies. The term "pheromone" itself is confusing in this context - should it refer to the secretion as a whole or to each active part that has a communicative function? - perhaps greater caution should be exercised in calling mammalian chemical substances preromones.

The functions of "pheromones" in mammals may be subserved under the following headings: identification of individuals, and recognition of social status, etc.; aggression-promoting; dispersion-promoting, and sexual (Shorey 1977). The substance, in the form of urine, faeces, or glandular secretion, is desposited on the ground, on objects in the environment, or possibly even another animal (Ralls 1971). Rhabdomys, in particular the dominant male, exhibits a behaviour pattern, the perineal drag, which could be construed as marking behaviour. Investitation of the "mark" showed a trail of tiny droplets of urine. This type of marking behaviour has been described on numerious occasions in the house mouse Mus musculus.

The preputial gland has been identified as the source of a substance that could have release, or possibly even primer, pheromonal effects in the mouse. It was thus decided to investigate further marking behaviour in Rhabdomys and, in particular, the role of the preputial glands.

It goes without saying that, in order to be effective, the chemical substance or pheromone, has to be perceived by the recipient; this involves some sort of reception and transmission to the central nervous system. Many vertebrates have a dual olfactory system: the "main" olfactory pathway, from the nasal mucosa to the olfactory bulb, and a second system, running from the organ of Jacobson, to the accessary olfactory bulb; both are entirely separate (Winans & Scalia 1970). The function of the latter, or vomeronasal system, has puzzled and fascinated investigators for many years; recently, however, it has been implicated in courtship and mating behaviour (Estes 1975; Powers and Winans 1970). It was thus decided to investigate this aspect of chemical communication as well.

2.5.2 An investigation of marking behaviour and the role of the preputial glands

2.5.2.1 Introduction. The majority of mammals have specialised cutaneous glands that produce odiferous substances (Tembrock 1968; Ewer 1968) and a number of detailed studies of these glands within various taxonomic groups have been made (e.g. Quay 1968; Quay and Tomich 1963; Doty and Kart 1972). These glands are generally modified and hypertrophied sebaceous glands (Quay 1968) and are sensitive to the effects of steroid hormones, in particular the male hormone testosterone. The preputial gland, peculiar to the order Rodentia, is such a hypertrophied sebaceous gland (Brown and Williams 1972a); these are paired structures lying between the skin and the body wall in the abdominal or pubic region, with the ducts passing to the free margin of the prepuce (Brown and Williams 1972b). In the last decade, considerable interest has been shown in the glands, firstly in connection with studies relating reproductive function and adrenocortical activity to population structure (e.g. Christian 1955), and secondly, in the possible role of the gland as a scent organ.

The preputial gland has been recognised and described by workers for many years (e.g. Leydig 1850; Henneberg 1918). Brown and Williams (1972b) in a review of the literature to date, found that the gland is apparently of wide occurrence in cricetid and murid rodents; it appears to be lacking in other rodent groups. It is also present in the female where it is commonly referred to as the preputial gland, as the clitoris in myromorph rodents is relatively large and homologous with the male prepuce; Brown and Williams (1972b) however, recommend the use of the term "clitoral gland" to avoid confusion and ambiguity.

All detailed anatomical and histological studies have been performed on the rat Rattus norvegicus and the mouse Mus musculus. In the rat, (Montagna and Noback 1946a; Brown and Williams 1972b) the glands are flask-like in appearance and lie almost entirely within the prepuce; while in the mouse, their appearance is leaf-like and the glands lie outside the prepuce in the pubic region. In both species the gland is holocrine, with the acinar cells adding to the secretion by their complete breakdown, and tubulo-alveolar (Brown and Williams 1972b).Montagna and Noback (1946a) have drawn an analogy to a bunch of grapes, with the main stem representing the central duct, the lateral stems the lateral ductular acini and the grapes representing the parenchymal acini. The ductular pattern changes continually due to acinar breakdown and formation. The gland as a whole is surrounded by a connective tissue capsule from which fibrous trabeculae pass to subdivide the parenchyma into lobules (Brown and Williams 1972b). Nerves, blood vessels and capillaries are distributed throughout the gland in the stroma (Beaver 1960). The histological appearance of the glands also differs in the rat and mouse: the rat has abundant acinar tissue and thick stroma (Schaffer 1940) and the lumens of the ducts are narrow and branch in a tree-like manner throughout the gland, with only the main central duct being expanded and serving as a reservoir for secretory material; while in the mouse, the stroma and acinar tissue are relatively sparse, and the gland is characterised by widely branching cavernous spaces in which the secretion accumulates.

he secretion of the gland is predominantly lipid in nature; this has been demonstrated by numerous workers (e.g. Walter 1924; Montagna and Noback 1946a; pannese 1954; Brown and Williams 1972a). Granular inclusions in the secretion of the rat gland have been described (Walter 1924; Schafer

1933) and Schafer (1933) Pannese (1954) and Brown and Williams (1972a) have described rhomboidal flattened crystalloids in the central duct of the rat gland. Beaver (1960) on the basis of observations of both lipid droplets and non-lipid granules, has postulated that the gland is dicrine in nature.

There has long been speculation as to the role of the preputial gland as a scent-producing organ. Recent studies appear to confirm this: Bronson and Caroom (1971) and Orsulak and Gawienowski (1972) found that female rats were attracted by homogenates of the male preputial gland; Mugford and Nowell (1971) found that preputial gland homogenates stimulated investigation and aggression in male mice.

On this basis, I have undertaken to investigate the preputial glands in Rhabdomys: their gross morphology, histology and, in particular, possible differences between the social classes and the possible role of the glands in social behaviour and organisation.

2.5.2.2 Materials and Methods.

1. Marking behaviour. Data in this section was collected as part of the observations on behaviour in general.

2. Morphology of the preputial glands. Glands were generally obtained from animals that had died, either as a result of exposure in traps, or as a result of fighting, both from the captive population and from the population on the Cape Flats. In all male animals, their testosterone levels were known, and, in the case of captive animals, details of their social rank and behaviour. The ventral skin over the abdomen was cut, exposing the glands lying in the pubic region just above the prepuce. The glands were removed, measured with callipers, one preserved in 10% buffered neutral tamalin, and the other fixed in Bouins solution. After formalin fixation for at least three days, the tissues were washed in water, and sectioned at 10μ on a freezing microtome; the sections were then stained with Sudan Black IV for lipid. The tissues fixed in Bouins were removed after 3 days, embedded in paraplast, cut at 8μ and stained with haematoxylin and eosin.

3. Response to preputial gland by conspecitics. A number of glands were homogenised, and deposited on surfaces in the cage. Qualitative observations on the reactions of the animals to the homogenates were made.

2.5.2.3 Results.

1. Marking behaviour. The characteristic marking behaviour of Rhabdomys is the "Perineal Drag"; this has been described in section 2.3.1. Briefly, it consists of the animal lowering the posterior part of the body, and dragging the perineal region across the ground surface on an object in the environment, as shown in Figure 2.7. Investigation of the area afterwards shows a trail of tiny droplets.

This behaviour occurs predominantly among the dominant male, occasionally among the beta males, and was also observed on a few occasions in the behaviour of the alpha female.

The behaviour may be unsolicited, or occurring apparently at random or, as was described previously (section 2.3.3) very frequently occurring after an aggressive encounter, and always on the part of the winner of such an encounter. Out of a total of 215 observed chases, by all animals of all classes, perineal drag followed 158 times, the equivalent of 73,49%.

2. Morphology of the preputial glands. External appearance

External appearance: The preputial glands of Rhabdomys lie directly beneath the ventral skin of the abdominal region. If the skin is dissected away around the penis, the separate ducts of each gland can be seen passing posterially to the free margin of the prepuce. In appearance, the glands are creamy-white in colour, flattened and pyriform in shape, thus resembling those of the mouse more so than the rat (Brown and Williams 1972).

Dimensions: The dimensions of the preputial glands are shown in Table 2.9 in relation to sex and status. It can be seen that the dominant male has the largest glands, those of beta males are somewhat

TABLE 2.9 Mass of preputial gland in relation to sex and status.

Note: The figure shown is the mean of the masses of the two glands.

Sex/Status	Gland Mass in mg
Alpha	54,5
Beta	41,2
	39,8
Omega	23,4
	22,5
	21,9
Female	20,6
	22,4

smaller, but nevertheless considerably larger than those of the omegas, who show very little difference from the glands or female animals. Females shown unformly similar and undeveloped glands. The correlation between gland size and testosterone levels is significant (r = 0,71). This confirms many previous reports (Brown and Williams 1972) of the sensitivity of these glands to androgens.

Histology: Surrounding the gland is a capsule of fibrous connective tissue (Figure 2.13).On consideration of the interior, the system of ducts is the most immediately apparent: generally a single main duct, to which numerous smaller branching ducts join, and which are in turn joined by other, smaller ducts. The ducts are lined by a stratified squamous epithelium, which is apparently cornified in the short region of the main duct inwards from its surface opening laterally on the gland surface. The analogy of Montagna and Noback (1946a) comparing the gland structure to a bunch of grapes is descriptive: the main stem represents the central duct, the lateral stems the lateral branching ducts, and the acini, the grapes. The acinar or secretory tissue can be seen in the lobules into which the gland is divided by the branching ducts. The gland is evidently holocrile

FIGURE 2.12. Detail of <u>Rhabdomys</u> preputial gland.
Stain: Haematoxylin and Eosin.

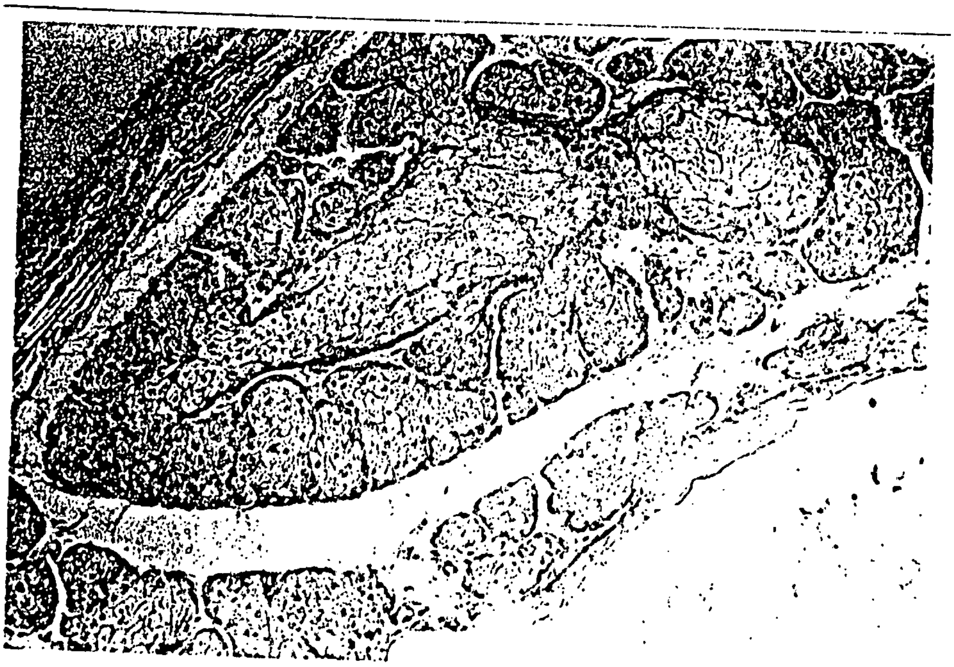


FIGURE 2.13. Detail of *Rhabdomys* preputial gland, showing gradient of cell maturation. Stain: Sudan Black IV.

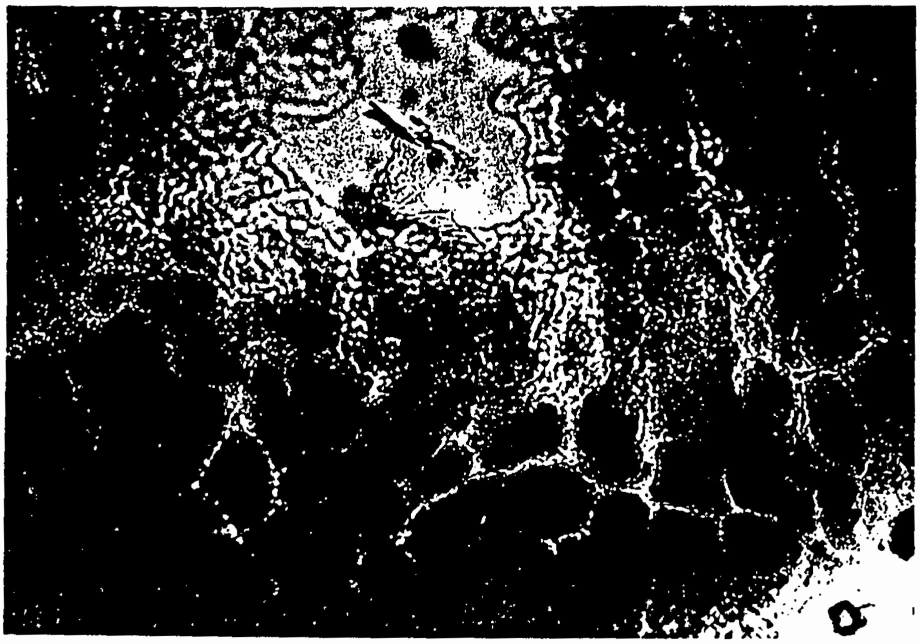


FIGURE 2.14. Detail of alpha male Rhabdomys preputial gland.
Stain: Haematoxylin and Eosin.

FIGURE 2.15. Detail of beta male Rhabdomys preputial gland. Stain: Haematoxylin and Eosin.

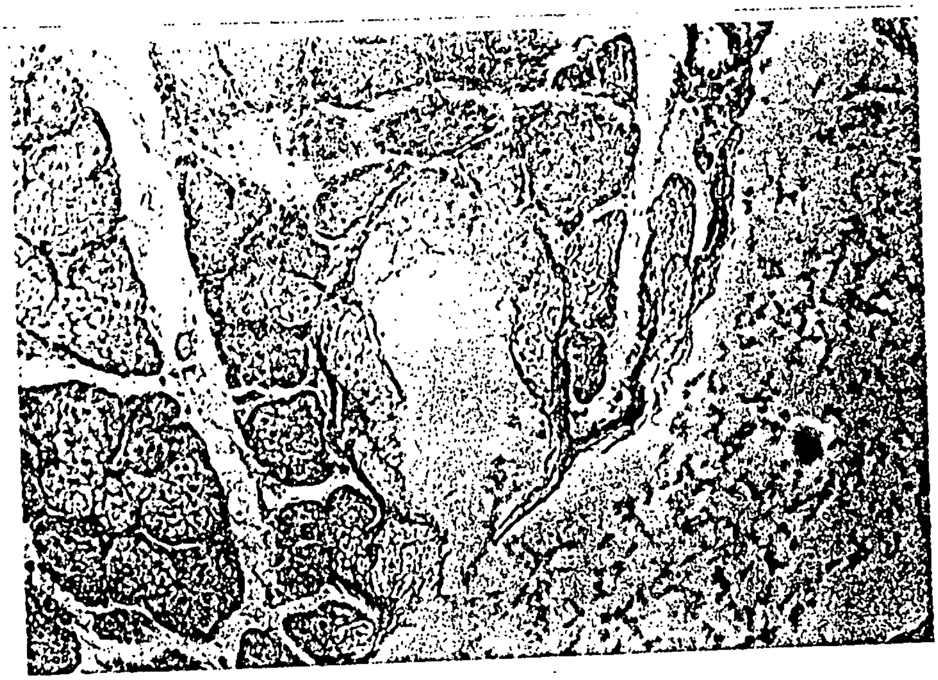
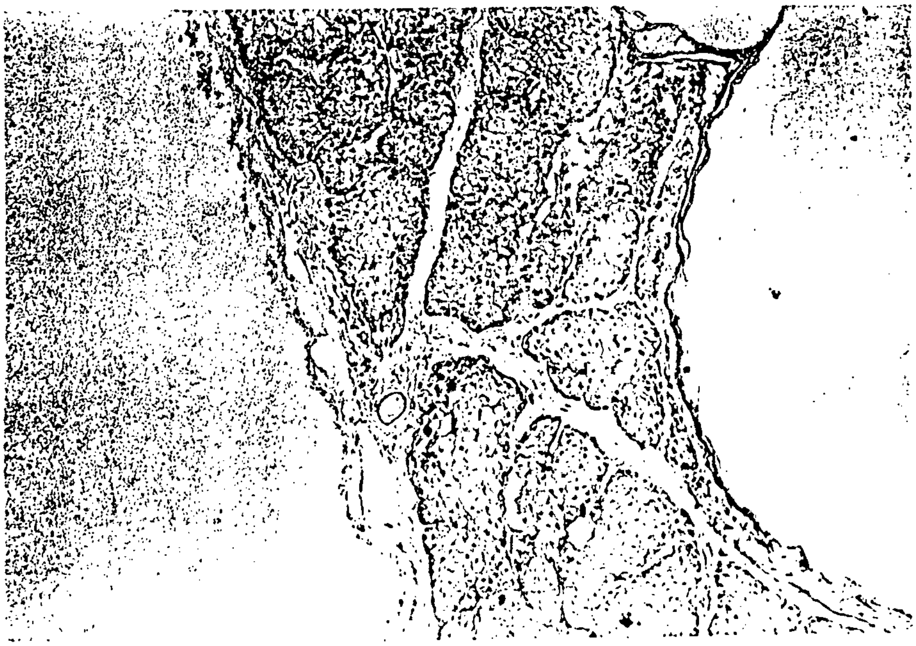


FIGURE 2.16. Detail of omega male <u>Rhabdomys</u> preputial gland. Stain: Haematoxylin and Eosin.

FIGURE 2.17. Detail of female *Rhabdomys* preputial gland. Stain: Haematoxylin and Eosin.



in nature, with the entire cells breaking down both to release, and to form a part of, the secretion. There is a gradient of maturation extending from the immature basal cells on the periphery, to the mature cells towards the centre of the lobule; this is very clearly demonstrated in Figure 2.14. The lipid nature of the secretion is clear from the intensity with which the cells take up the Sudan Black stain. This slide also shows clearly the disintegration process of the cells at maturity: the more peripheral cells are still intact, and their high lipid content is obvious. Progressing towards the centre, one sees the pattern of cellular breakdown, with less and less stain being taken up. This is because the secretion has been released into the space or duct, and was lost on sectioning.

This process of cellular breakdown and secretion is most evident in glands obtained from dominant animals. The slide shown in Figure plus detail is a section from the gland of M2, the original alpha in the captive colony. Clearly, the gland is active, and secreting large amounts of material; the gland in fact, has a highly vesicular appearance.

The gland shown in Figure 2.15 was obtained from a beta male (M10). The gland is less vesicular in appearance, and is apparently not as active as the one shown above. Figures 2.16 & 2.17 were obtained from an omega male and a beta female, respectively. Very little difference is apparent between the two: the cells are closely packed, with little evidence of vesiculation; this is obviously a relatively inactive gland.

3. When a homogenate of the preputial gland of a dominant male was smeared on a stone in the cage, it elicited much sniffing on the part of the inhabitants. While the subordinate males (beta and omega) and females merely showed an interest, the dominant male (M11) proceeded to mark the stone vigorously; the alpha female, F12, was also observed to mark. No specific avoidance of the area was observed on the part of the subordinates.

When a homogenate of a subordinate (omega) preputial gland was used, a certain amount of sniffing was apparent, but not as extensive as above. The marking behaviour of the alpha was not observed. Again, no specific avoidance of the area was shown by any of the animals.

2.5.2.4 Discussion The data presented here indicate that, in spite of being a diurnal creature, Rhabdomys does rely to a certain extent on chemical means of communication. The evidence of marking behaviour in specific situations, the obvious secretory ability of the preputial glands as well as the qualitative observations on behavioural response to the preservation of the gland homogenate stimulus, all point to this. Certainly, it can only be said that these results are preliminary. Ideally an investigation of chemical communication in a species should take the form of a biochemical analysis of the secretion, and identification of the components, and, finally, the presentation of the individual components to conspecifics, and measurement of their response. Such an investigation is both ambitious and time-consuming, and within the framework of this study, was not feasible. However, these results, while they are preliminary, certainly are interesting in their indication that Rhabdomys does make use of chemical means in its communication repertoire.

Morphologically, the preputial glands of Rhabdomys appear to lie somewhere midway between those of the mouse and the rat, as reviewed by Brown and Williams (1972). In external appearance, they are apparently more mouse-like, in their flattened pyriform shape, as opposed to the dense, club-shaped rat gland. Histologically, however, they are neither vesicular as the mouse gland is described, nor as dense as that of the rat, (Brown and Williams 1972). Intensive marking behaviour has been described in the mouse, which ties in with the highly vesicular appearance of the gland, but not so for the rat. On this basis, Rhabdomys appears to lie someway midway between the two, using preputial gland secretion to mark, but apparently not to the same extent as does the mouse. The secretion of the glands passes into the urinary tract, whence it is voided together with the urine; this would account for the trail of urine droplets observed in marking behaviour. This type of marking has also been demonstrated to occur in the mouse. (Desjardins et al 1973; Maruniak et al 1974)

The function of such marking behaviour would presumably be described as dispersion-promoting, or territorial. A second possible function, discussed by Mykytowycz (1965) and Ewer (1968) is familiarisation with the home range; however, the fact that it is essentially only one animal in the colony that marks, would tend to argue against this function as having much significance for the group as a whole. Territorial sexual activity is presumably physiological - a result of heightened testosterone secretion at these times. An increase in marking activity was observed by Mykytowycz (1965) when rabbits engaged in aggressive encounters. Other example are reviewed by Ralls (1975) who states that "animals appear to mark frequently in any situation in which they are both intolerant of and dominant to other members of the same species. Johnson (1973) suggests that marking in conjunction with aggression may play some part in threat display, and thus perhaps in territorial threat. It is, however, important to note that its effect in aggressive encounters has not been determined. The fact that these would often occur after territorial defence would mean that the animal was placing his mark upon his own territory; perhaps this could be the origin of territorial marking. The lack of avoidance of the area around the gland homogenate on the part of the subordinates was possibly a result of its being a strange male odour in a known environment: as previously described, any strange animal elicits attack on the part of all colony members, so that the disembodied odour of a stranger would hardly result in avoidance. It is interesting in this context to note that the territory of the alpha male, or the breeding territories of females for that matter, were not sacrosanct, and invasions by subordinates occurred regularly, with, however, a distinct modification of behaviour: this has been described in detail in a previous section (1.2.4). This phenomenon has been recorded in rabbits (Myers and Poole 1961; Mykytowycz 1965) and in the European hamster by Eibl-Eibesfeldt

(1953) who noted that the marking point, while it probably acted as a warning never appeared to frighten another animal away. As Johnson (1973) has said "It seems probable ... that although scent marks do not cause avoidance, they may signal that an animal is in foreign territory and predispose withdrawal in the presence of the resident animal." It is difficult to say from the response, or lack of it, on the part of the females, whether preputial gland odour could play any part at all in courtship and sexual behaviour: it has been suggested (Beauchamp _et al_ 1976) as the source of the primer pheromones affecting the reproductive activities of the female.

The preputial gland is essentially a sebaceous gland that has become excessively developed (Brown and Williams 1972). The influence of steroid hormones and in particular, the male hormone, testosterone, upon the size and functional capacity of sebaceious glands is well documented: castration results in a decrease in gland size in the rat (Ebling 1963) in side glands of the male shrew (Dryden and Conaway 1967). The ventral gland of the gerbil (Thiessen et al 1968) and many other examples. Administration of testosterone results in enlargement of glands in rats (Ebling 1957, 1963) and mice (Lápierre 1953). Glenn et al (1960) in fact because of the sensitivity of the preputial gland to testosterone, used its weight as a bioassay for androgenic activity. The significant correlation between gland weight and testosterone level is not, therefore, entirely unexpected, and, in fact, confirms previous morphological and behavioural observations (Bronson and Marsden 1973; Müller-Schwartz 1972; Mykytowycz 1968).

From this, it is evident that chemical signals could function in individual recognition (e.g. Müller-Schwarz 1971; Mykytowycz 1970). Individual recognition implies that the "pheromone" of each individual consists of a complex blend of chemicals differing in some way from those of other individuals (Shorey 1977). There is evidence that such blends do occur, e.g. Goodrich and Mykytowycz 1972 on the rabbit _Oryctolagus cuniculus_ found substances to vary qualitatively and quantitatively from individual to individual. Experimental studies, e.g. Bowers and Alexander

(1967), Chanel and Vernet-Maury (1963) and Klakowsky (1961) have shown that house mice Mus musculus are able to distinguish between individuals of even an inbred strain; the same general type of experiment but with less control over specific sensory modalities was performed on rats by Husted and McKenna (1966). Shorey (1977) in a review paper, speculated that levels of dominance are communicated by qualitative or quantitative differences in the blends of chemical constituting the "steromone". The evidence suggests that quantitative differences are the more likely: the dominant individuals of many species, (Johnson 1976) are characterised by larger scent glands, high secretory rates and a higher frequency of marking (Shorey 1977). The close relationship between testosterone levels, dominance, preputial gland size and activity, and marking behaviour would appear to confirm this. The situation is, however, a complex one; as Bronson (1971) has said: "In all probability there is no single pheromonal compound tailored for individual recognition ... olfactory discrimination between individuals is more likely to involve the widest spectrum of odour sources and include variations in both concentration and type of odour."

2.5.3 An Investigation into the Role of the Vomeronasal System

2.5.3.1 Introduction. The vomeronasal organ was first described by the Danish surgeon Jacobson in 1811 - hence its alternative name of "Jacobson's organ". In mammals, the organ is a paired tubular structure, partly lined by sensory epithelium and lying slightly above the floor of the nasal cavity, within the nasal septum, and protected by bone or cartilage (Allison 1953). In the rat, the organ is blind posteriorly and its narrow duct opens anteriorly into the nasal cavity (Allison 1953); there is, however, a great deal of species diversity on this point: in reptiles the duct usually opens into the mouth; reasons for this diversity are not unknown.

From the vomeronasal organ the vomeronasal nerves are directed to the CNS, running in the nasal septum, through the dorsal cribiform plate to synapse in the accessory olfactory bulb, a structure lying posterior and dorsal to the main olfactory bulb, although again there is much species diversity on this point. (McCotter 1912). In 1970 Winans and Scalia reported that, contrary to the general belief at that time, the accessory olfactory bulb does not project into the principle parts of the olfactory cortex, but projects instead to parts of the cortocomedial amygdala that are not reached by axons arising from the main olfactory bulb. Thus the two systems, the olfactory and the vomeronasal, are entirely separate throughout their courses. This fact led Winans and Scalia (1970) to postulate a dual olfactory system, a hypothesis that is supported by other neurological work (Powell et al 1965).

Why a dual olfactory system should exist and what the functions of the vomeronasal system are, remain at present hypothetical, at least in mammals. In reptiles, in which the system is particularly well-developed, it apparently plays a part in the feeding reactions of snakes (Kahmann 1932; Noble and Kumpf 1936; Wilde 1938), in trailing the female during courtship (Noble 1937) and possibly in identifying conspecifics during aggregation (Noble and Clausen 1936). While Jacobson's organ is well developed in most mammal groups, its functions remain obscure. Recently, however, a role for the system in mating behaviour and reproduction has been postulated. Estes (1972) has hypothesised that the organ is used for the detection of oestrus by the male: the "flehmen" behaviour characteristic of many Artiodactyla could very well be a means of introducing the scent into the organ; he has also suggested that the organ might be the receptor associated with primer pheromones in mice.

Indirect evidence for the role of the vomeronasal systems comes from comparisons of studies using complete ablation of the olfactory bulbs (which destroys both the olfactory and the accessory olfactory bulbs) and zinc sulphate treatment of the peripheral receptors (which affects only the olfactory system). For instance, in the rat, Heimare and Larsson (1964) found that bulbectomy produced deficits in mating behaviour, notably an increased latency to ejaculation, while Cain and Paxinos (1974) using $ZnSO_4$ found no deficit in mating behaviour: the males in fact showed increased sniffing and licking of the female's genital area. In mice, bulbectomy completely eliminated mating behaviour (Rowe and Edwards 1972; Rowe and Smith 1972; Whitten 1956); while $ZnSO_4$-treated animals showed no change in mating behaviour (Edwards and Burge 1973; Rowe and Smith 1972). These findings, supported by Powers and Winans (1975) observation that 38% of their hamsters stopped mating altogether after sectioning of the vomeronasal nerves, strongly suggests a role for the system in mating behaviour.

As Jacobson's organ itself is relatively inaccessible for lesion, the few studies that have been carried out on the function of the organ have attempted to section the nerve; Murphy (1976) cites three basic techniques of doing this: firstly, by sectioning within the nasal cavities (Michael and Keverne 1968), secondly inside the cranium as the nerves pass between the two olfactory bulbs (Powers and Winans (1975); and thirdly, inside the cranium under direct vision after one olfactory bulb has been removed (Murphy, unpublished). The technique I have used here is that of lesioning within the nasal cavities. Sexually experienced male Rhabdomys were used, thus conforming to Murphy's (1976) criterion that one must demonstrate that an animal's failure to meet a reponse criterion is due to a sensory rather than a motivational or learning defect. Finally, histological verification of the lesions was carried out.

2.5.3.2 Materials and Methods. The subjects: Adult male Rhabdomys of proven sexual ability were used. Five experimental and five control animals were used.

Anatomy of the vomeronasal system: Dissections were done to locate Jacobson's organ and the course of the vomeronasal nerves from the organ to the accessory olfactory bulb. Following McCotter (1912), the head of the animal was immersed in Muller's Fluid, to which had been added 5% glacial acetic acid; this procedure serves to toughen the nerve fibres and differentiate them from the surrounding tissue. After 24 hours, the head was removed from the fluid and divided just laterial to the medial sagittal plane, so that the nasal septum was left intact. The septum was

carefully dissected to expose Jacobson's organ and the vomeronasal nerves running closely applied to the septum. The course of the nerves is then easily traced back to their passage through the dorsal cribiform plate, between the olfactory bulbs and to the accessory olfactory bulb, lying in a postero-dorsal position to the main lobe.

The lesions: The lesions were done by ablating the nerves as they pass through the nasal cavity. The animal was anaesthetised by Sagatal, and its head anchored in a stereotactic apparatus, the animal lying on a warmed pad to maintain constant body temperature throughout. The skin over the frontal and nasal bones was removed, exposing the suture between the two bones. Two small holes were drilled in the nasal bones, approximately 1 mm (depending on the size of the animal) anterior to the suture between nasal and frontal, and keeping as close to the midline as possible. Using a Lesion-Maker apparatus, an electrode was passed down approximately 3-4 mm (again depending on the size of the animal) to ablate the nerves; the amount of current and the time for which the current was delivered were determined by passing current through egg white, which has a similar consistency to nerve tissue, until the required amount of protein coagulated. The last 2 mm of the electrode was scraped clean of insualting agent, so that current could be delivered to all the nerves simultaneously. Noradrenaline was used to control bleeding, and the skin was sealed using a sterile staple. Control animals were sham-operated, i.e. the same procedure was carried out, but no current was delivered.

The behavioural tests: All tests were conducted within 10 days of the operation; a few days were allowed to elapse after the operation to allow the animal to recover fully. Tests were conducted in glass aquaria (2 x 2 x 1 feet). A female Rhabdomys that had 48 hours previously received a subcutaneous injection of oestrogen to induce oestrus was placed in the aquarium. The control animal was then introduced, and his behaviour was observed for 5 minutes, using a 10 second time base. The same procedure was then followed with the experimental animal. No difference in the behaviour of females towards successive males was observed.

Three behavioural measures were used:

1. Latency to Mount: the time interval from the introduction of the male into the cage until the first mount;
2. Latency to Intromission: the time interval from the first mount (or attempted mount) to intromission;
3. Latency to Ejaculation: the time interval from intromission to ejaculation.

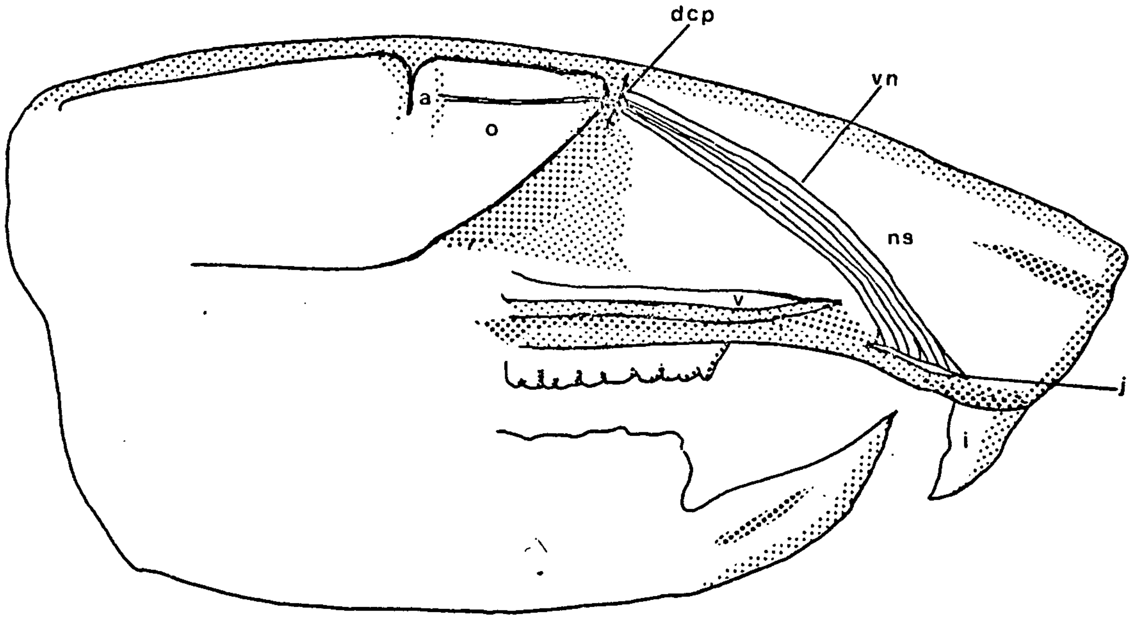
2.5.3.3 Results.

1. Anatomy of the vomeronasal system. Figure 2.18 shows the dissection of the vomeronasal system, showing Jacobson's organ, the course of the vomeronasal nerves through the septum, their passage through the dorsal cribiform plate, and their course between the olfactory bulbs to synapse in the accessory olfactory bulb. The position of Jacobson's organ in *Rhabdomys* is essentially similar to that in the rat (Alberts 1974), with the anterior edge of the organ lying just behind the buccal margin of the upper incisor and extending posteriorly for roughly three quarters the length of the diastema of the upper jaw.

In the rat, only four nerves leave the organ (McCotter 1912); in *Rhabdomys* on the other hand, at least six are seen arising from the dorsal surface of the organ and coursing through the septum in a postero-dorsal direction to the dorsal cribiform plate. The accessory olfactory bulb lies in essentially the same position as that in the rat (McCotter 1912).

2. The behavioural tests. Table 2.10 shows the results of the behavioural tests. It can be seen that in the experimental group, there is a significantly increased latency to mount ($t = 6,92$; $P < 0,01$) and latency to intromission ($t = 5,47$; $P < 0,01$); the latency to ejaculation shows no difference form those of the control group however.

FIGURE 2.18. Sagittal section of *Rhabdomys* head showing the vomeronasal system.



a : accessory olfactory bulb
dcp : dorsal cribiform plate
i : upper incisor
j : Jacobson's organ
ns : nasal septum
o : olfactory bulb
vn : vomeronasal nerves

The histological sections indicated that all the animals used in the experimental group had ablated vomeronasal nerves.

TABLE 2.10 Result of the behavioural tests

(a) Latency to Mount = time from introduction of male to female until mounting occurred.

(b) Latency to intromission = time from first mount until first intromission.

(c) Latency to ejaculation = time from intromission until ejaculation occurred.

(a) Latency to Mount (in seconds)

Exp	Control
270	30
220	90
250	70
210	40
280	50

n = 5 in both groups

Exp $\overline{X}$ = 246 secs. $\sigma = 30$

Cont $\overline{X}$ = 56 secs. $\sigma = 24$

$t = 6,92$

sign. $P < 0,01$

(b) Latency to Intromission

Exp	Control
130	30
140	70
110	40
120	20
140	30

n = 5 in both groups

Exp $\overline{X}$ = 128; $\sigma = 13,04$

Cont $\overline{X}$ = 38; $\sigma = 19,24$

$t = 5,47$;

sign. $P < 0,01$

(c) Latency to Ejaculation

Exp.	Control
10	20
20	15
15	10
25	15
25	25

n = 5 in both groups

Exp $\overline{X}$ = 19 $\sigma = 6,5$

Cont $\overline{X}$ = 17 $\sigma = 5,7$

Non-significant

2.5.3.4 Discussion. The concept of a dual olfactory system is an exciting one; it is also especially challenging in that so little is known of the function or functions of the vomeronasal system. Van Mihalkovics (1898) found no impairment of feeding in the rabbit and cat after bilateral cauterisation of the organ; Broman (1920) postulated that the organ was simply the old water smelling organ of vertebrates that had remained behind after adaptation to terrestrial life; Herrick (1924) hypothesised that the organ was involved with the opening of the posterior nasal aperture and passage of olfactory media from the mouth cavity into the nasal sac. Shortly after this there was an apparent depression in olfactory research, perhaps due to discouragement, e.g. by Papez (1937) that the olfactory areas of the brain were not nearly as extensive as had previously been supposed.

The late fifties and early sixties saw a renewal of interest in olfaction, partly due to the discovery of the role of primer pheromones in the reproduction of mice (e.g. Parkes and Bruce 1961). In recent years there has been considerable speculation as to the role of the vomeronasal system in reproduction: in 1961, Mann stated categorically that "the functions of the organ of Jacobson and the accessory olfactory bulb are related to the release of sexual activity". Estes (1972) has postulated that the organ is used for the detection of oestrus by the male. The first direct evidence for a possible function came from Powers and Winans (1970) who found that the vomeronasal nerve must be sectioned before the mating behaviour of male hamsters could be eliminated by zinc sulphate treatment of the olfactory mucosa; 38% of their hamsters stopped mating altogether after the vomeronasal lesion alone.

While not as dramatic as these findings of Powers and Winans (1970), the present observations are certainly interesting. Clearly, even allowing for the possible inadequacy of the sample size, mating behaviour has been affected by the lesions: the specific effect, that of increased latency to mount, would argue for a role for olfaction in the triggering of sexual behaviour, and may perhaps even implicate a pheromone-like substance. The major problem in the interpretation of the results rests in the lack of control over other sensory modalities: it would certainly be expected that for a diurnal animal such as Rhabdomys vision would play an important part; the lively behaviour of the female Rhabdomys would seem to support this. It would, however, seem unlikely that smell would completely govern sexual behaviour in a diurnal animal; Shorey (1977) in a discussion of sex pheromones, differentiates between those directly releasing behaviour and those that do so indirectly by stimulating aggregation, after which other, perhaps non-olfactory, stimuli take over to control close-range courtship and mating responses. Certainly for a mammal, as opposed to an insect, and especially for a diurnal mammal such as Rhabdomys where vision plays a proportionately greater role in communicative behaviour, one might expect the latter situation; the present findings appear to point in this direction: that olfactory response, mediated by the vomeronasal system, govern the initial attraction of the male to the female.

2.6 DISCUSSION

From these results it is clear that Rhabdomys makes use of a number of channels of communication. Visual communication is particularly well developed, as is evident in the relatively large number of postural and locomotary displays as well as the use of small and subtle postural variations, such as ear and eye position, that may alter the meaning of the display altogether. In comparison to many other species of rodents (Eibl-Eibesfeldt 1958) Rhabdomys has a wide repertoire of visual displays. The reason undoubtedly lies in the fact that Rhabdomys is diurnal: obviously, the perception particularly of subtle postural changes is dependent on the presence of adequate light.

Sociality tends to develop in diurnal rather than nocturnal species: possible reasons for this will be discussed later (see Concluding Discussion). From the fact of sheer proximity, an animal living in close conjunction with others will interact far more with his fellows than one not; also resources must be efficiently parcelled out so that over-exploitation of the environment does not, as far as possible, occur. Both these factors necessitate the development of an ethical social organisation, and, as a consequence, an efficient means of communication to maintain it. The slow chemical signal, conveying as it does, relatively little information, will not suffice. Visual displays, on the other hand, have the supreme advantage of firstly, being able to be switched on and off, and, secondly, by their versatility in having available changes in orientation, posture and movement, or combinations of the three, being capable of conveying nuances of motivational information. The visual patterns used by *Rhabdomys* are both "discrete" - ritualised behaviour patterns such as Approach Elongate or Submission are examples - or "graded". Examples of the latter are the Threat and Defensive behaviour spectra.

Chemical communication is generally regarded as primitive (Wilson 1962) and it might be thought that any such functions observed in *Rhabdomys* are merely the inheritance of an evolutionary past that has now been rendered obsolete. However, it is apparent that *Rhabdomys* in fact does make fair use of chemical signals: the functional capacity of the preputial glands marking behaviour and the indications of the dependence of male sexual behaviour at olfactory cues all point to this. Chemical communication has certain advantages that other channels do not possess - the most obvious is the fact that a chemical signal is continuous and carries on emitting its information, as in a scent mark, in the absence of the signaller. A territory may thus be advertised as such and a considerable amount of time and energy saved in the process. On the other hand, this very continuity may be a disadvantage, in that subtle changes of motivation cannot be conveyed (Morris 1957) and the interpretation of the signals may be slow and subject to error (Marler 1961). The observations on *Rhabdomys* indicate that chemical signals communicate information essentially about physiological states, such as increased preputial gland function in relation to a high titre of androgen, and oestrus. Chemical signals may thus be thought of as forming the basic layer of a multi-layered network of communication: the information conveyed is essentially about status, both male, in terms of preputial gland activity, and female, in terms of oestrus receptivity, and hence ability to breed. These signals may thus function in the spacing of the animals, both as regards territory, in terms of scent marks strategically placed on the ground, and in individual distance, in terms of scent on the animal's body itself: avoidance of dominants by subordinates, and attraction of males to sexually receptive females.

Rhabdomys does not appear to rely at all heavily on acoustic channels of communication. Apart from squealing in pain, tooth chattering as a component of Threat behaviour is the only other audible sound used. The use of ultrasound is highly specialised, and certainly because of its high attenuation in air and particularly in dense vegetation, such as that favoured by Rhabdomys, of limited use, except in close encounters. Here we see it used quite extensively as a component of appeasement displays, which are essentially "visual" in nature.

The subject of communication, especially in relation to sociality and social integration, will be considered in more detail in the Concluding Discussion.

PART II

STUDIES ON RHABDOMYS IN THE FIELD

CHAPTER 3:

DOMINANCE AND SPATIAL RELATIONSHIPS IN A POPULATION OF RHABDOMYS ON THE CAPE FLATS

3.1 INTRODUCTION

> "There is a spatial framework to each population, affected by all neighbouring forces and delicately in balance". (Brown 1966).

Fundamental to the elucidation of spatial relationships is the concept of home range. The concept is not new: it was first used by Seaton (1909) who recognised that: "No wild animal roams at random over the country: each has a home-region, even if it has not an actual home". In 1943 Burt proposed a definition that is generally accepted by all ecologists: the home range is "that area traversed by the individual in its normal activities of food-gathering, mating and caring for the young". While Burt recognised that home ranges could shift in time, it was required that the owner of the range be established, thus excluding the wanderings of young animals, as well as "occasional sallies outside the area, perhaps exploratory in nature" (Burt, 1943). The concept of "territory" was separated from that of home range, the former being defined as "any defended area" (Noble, 1939). In a later paper (Burt 1946) the home range was classified into 3 types: permanent, semi-permanent and seasonal; only the first two apply to small mammals, the latter to large migratory animals.

Since these concepts were formulated, a great deal of information has been gathered on the home ranges of small mammals: shape and size variation both inter- and intraspecific. The emphasis in many of these studies has been on technique and methods of calculation (e.g. Miller 1958; Getz 1961; Brown 1969; Maza et al 1973, and many more); relatively little attention has been paid to possible reasons underlying these variations which Sanderson (1966) has stressed should be the next focus of study: "Biologists should lose some of their preoccupation with shape and size of home range .... emphasis will have to be shifted from the movements themselves to the reasons for the movements". Also Jewell (1966): "It would seem that further attempts to define the qualities of the home range in a formal way are not very useful at the present time when so little is known about home range behaviour. What is required is an understanding of the ways in which an animal makes use of the terrain in which it has established itself".

Rhabdomys is a social animal (Part 1, Chapter 2): the behaviour of the individual members of the Rhadomys society varies as does the behaviour of the society as a whole with changing season. One would therefore expect these variations to be reflected in a free-living society. To this end, a relatively (see methods) isolated population of Rhabdomys on the Cape Flats was chosen for study and a grid set out over the area. The total area of the grids were small (1850^{m2} and 3625^{m2}) but, as the primary aim of the study was the determination of social organization rather than home range size per se, this was not considered to be important.

The aspects considered in this study are as follows:

Whether Rhabdomys preferred certain habitat types on the grid above others and if so, why.

A determination of the social hierarchy by testosterone assay for males and breeding condition for females.

A determination of home range size and position and how this correlates with position in the hierarchy.

Seasonal patterns in home range size and distribution.

A determination of the spatial relationships within the group: whether certain classes of animals are particularly associated or separated and whether these relationships alter with season and breeding condition.

The best technique for collection of home range data is undoubtedly direct observation. However, this is impracticable for studies of small mammals who, if they are not nocturnal, generally live in thick undergrowth. So indirect methods must be used; these can be divided into two classes; trapping and tracking.

Repeated live-trapping yields a series of capture points from which the home range can then be calculated. This was the most common method in many of the earlier studies e.g. Chitty (1937). Such data is often collected as a subsidiary to other studies. There are three disadvantages to this technique: firstly, it may interfere with the animal's movements and behaviour; secondly, and leading on from the first objection, data is accumulated over a relatively long period of time, often weeks or months. Martinsen (1968) has shown that home ranges can vary within a short space of time sometimes as short as 24 hours, so that a lengthy period of data accumulation can introduce an important source of bias into the final assessment. According to Stickel and Warbach (1960): "As the home range is defined as the area over which the animal moves in the course of his regular day-to-day activities, these long-term ranges should not be called home ranges. The distances are increased by shifts in range from month to month as well as by various occasional travels". Lastly, animals differ in their response to traps: (Croncroft and Jeffers, 1961) one may find trap-shy animals that may never enter a trap, or the presence of certain animals may inhibit others from entering traps (Watts 1970). On the whole, tracking techniques are to be preferred.

A variety of tracking techniques has been used; such as the use of natural signs such as faeces or tracks, applicable to large mammals or small mammals in a uniform environment such as sand or snow, e.g. Blair (1951) on the beach mouse and Dice and Howard (1951) for the prairie deermouse in snow; the use of dyes for urine and faeces(New (1958): these do not seem to be very efficient and the physiological effects are unknown; the use of photographic and mechanical devices, e.g. Pearson (1960) and Osterberg (1962); radiotelemetry, a useful technique, but problems arise with its use on small animals as the size and the radio transmitter relative to body size interferes with normal movements (Sanderson 1966); radioactive tracking, e.g. Godfrey (1955) and Miller (1958), the main problem of which is that only a single animal can be marked at any one time, and, lastly, the use of coloured objects led to the animal and picked up in the faeces e.g. glass beads (Sowl) and Minneman 1963); coloured wool (Holisova, 1965); coloured feathers, fur and wool (Randolph 1973). This technique has the advantages of being inexpensive and easy to use as well as lacking in unwanted side-effects, such as might result from the administration and dyes. The material should ideally pass through the gut unchanged, enabling easy identification in the faeces. The great advantage of this method (depending on the number and makes available) of animals to be tracked over a relatively short period of time i.e., the length of time the marker takes to pass through the gut, ranging from 1 - 3 days (Randolph 1973). For these reasons, this latter tracking technique seemed ideal to this study.

Many methods and estimating the home range from recapture data have been proposed. These fall into two categories: the "polygon" and the "probabalistic".

The polygon methods, described and assessed by Stickel (1954) consist of a geographical description based on recaptive points, and include the minimum area method, the boundary strip method, the observed range length and the adjusted range length. These methods, in the words of Jennrich and Turner (1969) have the advantage of "historical prominence, graphical simplicity and .... reasonably good statistical stability". Their great disadvantage is their sample size bias: the value of the home range increases with increasing numbers of recaptures. Stickel (1954) in her assessment of artificial populations, calculated 15 as the minimum number of recaptures necessary for a reasonable estimate of home range some individuals in fact, did not reach their maximum range size after as many as 33 captures. Clearly, methods such as these are impractical if one wishes to assess as many home ranges as possible over as short a time as possible.

The second category comprises the probabalistic methods. At the basis of these is the concept of the "centre of activity" (Hayne 1949), defined as the geographical centre of all points of capture. The probabalistic model can best be understood if one imagines oneself standing at the centre of activity and then moving outwards from it, in any direction. As one progresses, the probability of encountering the animal decreases. One can, in fact, partition the range into concentric rings around the centre of activity: at a certain radius the probability of encounter will be, say, 75%, further away, 50% and so on, until at a certain distance the probability should theoretically reach zero, which should define the limits of the range; in practice, however, the range limit is never specified.

Several authors e.g. Dice and Clark (1953), Harrison (1958), Currie and Bellis (1969) have used the distance from the centre of activity to a point on a concentric probability circle as an index of home range; this is classified as a "univariate" model (Van Winkle 1975).

Calhoun and Casby (1958) proposed a bivariate model: this extends in two dimensions and can therefore be considered in terms of a Cartesian coordinate system.

However, several authors have observed decidedly non-circular home ranges in small mammals e.g. Godfrey (1954) for Microtus; Stumpf and Mohr (1962) for a number of species, and Brown (1969) for Apodemus. Clearly therefore, a more flexible model that will encompass these variations is needed. Van Winkle (1975) in a review of 9 probabalistic home range models, concluded that "the bivariate normal distribution without the restriction of circularity, provided the most general and flexible probabalistic home range model yet proposed, and it seems adequate for characterising the home range of many animals inhabiting homogeneous habitats". Home ranges, therefore, are assumed to be elliptical in shape. The circular home range estimate "seems to be an unfortunate historical accident because .... the assumption upon which [it] is predicted is unnecessary" (Jennrich and Turner 1969). The elliptical home range model can accommodate anything from circular to long thin ranges, and encloses a smaller area than does a circle.

3.2 MATERIALS AND METHODS

Tracking:

Initially investigations were carried out in the laboratory to test the colour fastness, recognisability in the faecal matter and passage of time through the gut of various substances. It was found that brightly coloured feathers - chicken and ostrich feathers obtained from commercially available feather dusters - were the most efficient, as the structure of the finely chopped feather is easily identified in the faeces; the time of passage through the gut was roughly 48 hours.

The bait used was the same as that used for baiting traps: a combination of peanut butter, rolled oats, syrup, oil, candle wax and dried fruit. The feathers were chopped finely and mixed into the bait, having a concentrated mixture so that the maximum amount of marker could be ingested.

For dropping boards, disposable cardboard plates were used. These had the advantage of being light and easy to transport in the field;

their only disadvantage was that some mice seemed to consider them suitable nesting material, so that plates were often gnawed around the edges. However, as most of the faeces were deposited in the centre of the plate this was not considered serious. The plates were anchored to the ground by a piece of heavy wire bent in an inverted U-shape.

A trapping-tracking session was conducted every 6 weeks from February to September 1978. On Monday morning, the traps were set out on the trapping grid (Figure 3.1) at 5m intervals, and were checked on Monday evening. This usually resulted in the capture of about 20 mice, which at that time was the maximum number that could be marked with any efficiency. The traps were taken up and the mice brought back to the laboratory where they were marked (by toe-clipping), weighed, sexed and, in the case of males, a blood sample taken. No blood was taken from juvenile or non-breeding males as these animals show uniformly low levels of testosterone (see Chapter 1). The blood was taken from the sinus beneath the eye, using a heparinised capillary tube; the sample was centrifuged, and the plasma removed and deep-frozen until assayed, by radioimmunoassay, for testosterone. It was expected, on the basis of a pilot experiment run on captive mice (Chapter 1), that the testosterone levels would provide an index of the status of the individual males in the social hierarchy.

The mice were housed for the night with nesting material and individually marked bait. The following morning (Tuesday) they were returned to the field and released at their point of capture. Meanwhile, the cardboard plates had been set out on the tracking grid (Figure 3.1) at 2,5m intervals: these were baited with a small quantity of ordinary bait.

On Thursday morning, the droppings were collected in glass "polytop" bottles, each of which was labelled with the number of the station. A further series of traps was set out on the trapping grid, and the same procedure as before carried through until the second set of droppings was collected on Sunday.

On return to the laboratory the droppings were dried in an oven at 60°C, chopped with a scalpel and examined under the dissecting microscope. Records were kept of each station where a mouse was recorded, as well as the presence of droppings of other small mammal species -- the only possible species were the vlei rat Otomys irroratus and Tatera afra and very small droppings that could have belonged to the pygmy mouse Mus minutoides.

Calculation of Home Range Size.

The elliptical home range model as described by Jennrich and Turner (1969) and Mazwkiewicz (1969, 1971) was used. The details and formulae used for calculation are given in Appendix 1.

The Distribution of Home Ranges with Habitat.

Four habitat submits were differentiated on the grid. A 5 x 5m quadrot was assessed in each submit, using the Zurich-Montpellier method of vegetation survey. Each plant species was assessed as a potential source of cover: this was estimated as "poor", "moderate" or "good".

Four habitat submits were differentiated (Figure 1). Area 1, the largest, contained largely grassy vegetation and some Acacias; Area 2 consisted of Xanthium bushes mixed with Rhus; Area 3 was marshy and underwater in winter, while Area 4 covered an Acacia thicket, with little or no ground cover. As the four habitat submits differed in the amount of food and shelter available for the mice, it was hypothesised that they would prefer certain areas above others. To test this hypothesis, the following method, adapted from Randolph (1977) was used:

The number of tracking stations contained within each area's boundaries was assessed; this figure was then divided by the number of mice available in that particular season, e.g. in the spring, Area 1 contained 119 tracking points, and 10 mice (5 males and 5 females) were caught and tracked during that season, over the entire grid. Therefore, if one considers the males alone: 119 divided by 5 gives a value of 23.8: this is taken as the "expected distribution". The "observed distribution" could then be obtained by calculating the total number of tracking stations in each Area at which mice had deposited droppings; here again, sexes and seasons were kept separate in the analysis. χ^2 was then calculated for each set of data.

The Determination of the Social Hierarchy.

A blood sample was taken from all male animals during the breeding season. The details of this are given in Part 1, Chapter 1. Using the results obtained in Part 1, Chapter 1 as a standard curve, the status of the Cape Flats mice could be determined.

As female Rhabdomys do not form a hierarchy either among themselves or together with the males (Part 1, Chapter 1), but establish and defend territories when breeding, I have merely designated them as "breeding" or "non-breeding". A breeding female was classified as one who is heavily pregnant as determined by palpitation of the abdominal region, or lactating, as determined by the presence of large teats and the secretion of milk when gently squeezed between finger and thumb.

Nearest Neighbour Analysis.

In order to gain some idea of the degree of association of the different classes in the population, whether certain classes are more clumped or more distributed than might be expected, nearest neighbour analysis (Clark and Evans 1954) was applied. This technique, originally developed for vegetation, uses the distance (r) from an individual to its nearest neighbour as the measure of spacing e.g. if one wishes to determine the spatial relationships among a certain class, say, females in winter, one plots the centres of activity of each female mouse recorded for the season on a map of the grid, and, for each mouse, estimates its nearest neighbour. The distance between nearest neighbours is then measured, and the mean "r", $\bar{r}_A$, is calculated for the class as a whole.

The random distribution may then be calculated as follows:

$$\bar{r}_E = \frac{1}{2\sqrt{p}}$$

where: p is the density of individuals (all individuals in the study area) available as nearest neighbours (Clark and Evans 1954).

To compare these two values, the actual and the random distributions, ratio $R = \frac{r_A}{r_E}$ is then calculated. This may vary from a minimum o of 0 for maximum aggregation -- i.e. no distance between home

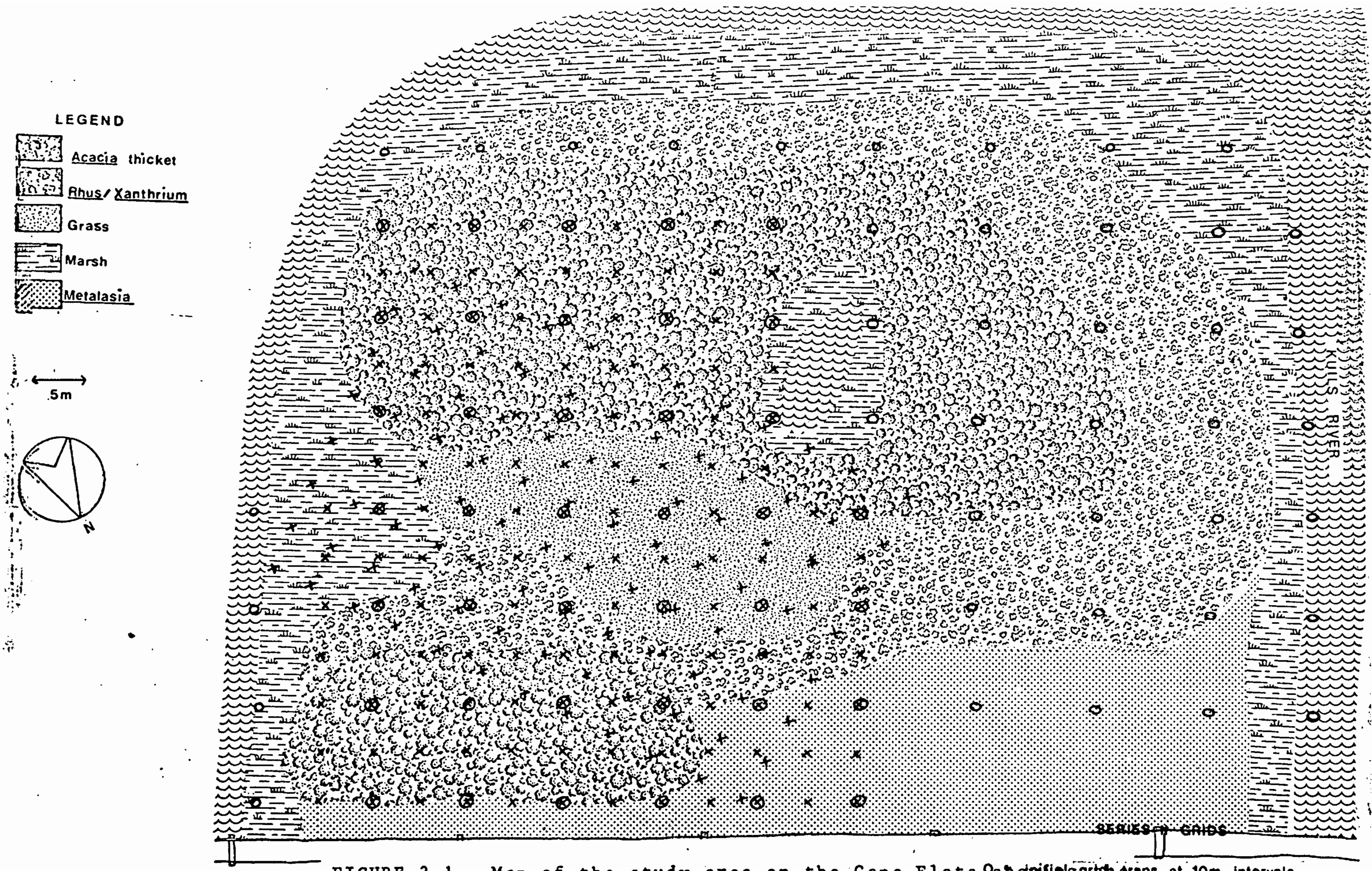


FIGURE 3.1. Map of the study area on the Cape Flats showing the vegetation types and the relative positions of the two grids.

range centres -- through 1 for a random distribution, to a maximum of 2,1491 for a completely uniform distribution, i.e. with the maximum spacing between individuals. (Clark and Evans 1954).

In order to determine whether the difference between $\bar{r}_A$ and $\bar{r}_E$ is significant, the following formula is used:

$$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma\bar{r}_E}$$

where c is the standard variate of the normal curve and $\sigma\bar{r}_E$ is the standard error of $\bar{r}_E$ which is calculated as:

$$\sigma\bar{r}_E = \frac{0,26136}{\sqrt{Np}}$$

where N is the number in the sample and p is the density of individuals.

Second Series of Experiments.

A second series of trapping and tracking studies was instituted in October 1979, largely because it was felt that the grid in the series 1 experiments had been arbitrarily set over a relatively small area without sufficient consideration for possible movements of Rhabdomys outside the grid and also because in the first series testosterone levels were only assessed once for each mouse. In the second series blood samples were taken at each trapping session, thus changes occurring in the status of the mouse could be accurately monitored.

Therefore in series 2, the grid previously used in series 1 was extended to cover the entire area between the Kuils River, the road, and the tributary stream to the river. A 100 x 60m grid was laid out, with traps set singly at 10m intervals. The entire area was trapped for a period of 4 days and nights in October 1979 before the commencement of the breeding season, in order to provide an overall picture of the numbers and distribution of the inhabitants. It was found that, apart from a small group of mice on the banks of the Kuils River, at the South-eastern end of the grid, the majority appeared to inhabit the grassy area and its surrounds on the opposite side of the grid, bordering on the road (Figure 3.1). The study grid was therefore laid out in this part encompassing a total area of roughly 60 x 50m (3625^{m2}).

The discrepancy arises from the fact that the boundaries, especially on the river side, tended to be jagged, due to the presence of water. Traps were set at 5m intervals, and a number of traps were also set 10m apart beyond the grid, except where the presence of the road or stream prohibited; this was done to account for any possible movement of marked mice beyond the confines of the grid.

After the initial overall trapping session, a week was allowed to elapse before commencing the trapping and tracking experiment. Traps were then set for 3 days and two nights; all animals caught were, as in series 1 experiments, removed to the laboratory for processing and feeding of marker bait. The cardboard plates were set out, at 2.5m intervals, on the evening of the third day, and all mice were released at their point of capture on the morning of the following day. All the animals caught received their marker bait at the same time, on the day prior to release. The tracking stations were checked daily for 3 days, after which all plates were removed.

The first trapping and tracking session was conducted in October 1979, at the beginning of the breeding season. Further trapping and tracking sessions were carried out in December 1979, and March 1980, which was towards the end of the breeding season. One trapping session, without the additional tracking of the mice caught, was conducted at the end of January. The purpose of this was to monitor the changes in population size, and the testosterone levels of the resident males.

3.3 RESULTS AND DISCUSSION

3.3.1 The Tracking Record.

3.3.1.1 Series 1 Studies

Out of 5 tracking sessions, a total number of 78 animals were trapped. Of these, 36 were male and 42 female. Five animals died in the traps from heat, all during the summer months; of these 3 were males, two with descended testes and one juvenile, and two females, one perforate and one imperforate. Ten animals were never tracked at all in that their faeces were never picked up; eight of these were females; the remainder of the mice were tracked a total number of

TABLE 3.1(a) THE TRACKING RECORD FOR SERIES 1.

Season	Number Caught	% New	% Captures Tracked	% of Faeces Marked
Summer 1 (February)	39	100	92	77
Summer 2 (March)	22	59	82	85
Autumn (May)	17	35	100	87
Winter (July)	17	23	94	80
Spring (September)	27	52	85	84

Note: (i) Summer 1 and Summer 2: Summer 1 = February sample
Summer 2 = March sample

(ii) Each "season" comprises two tracking sessions: the results have been pooled.

(iii) "90 of faeces marked": the number of faeces containing marker expressed as a percentage of the total number of faeces collected.

TABLE 3.1(b) THE TRACKING RECORD FOR SERIES 2.

Season	Number Caught	% New	% Captures Tracked	% of Faeces Marked
October 1979	20	100	75	72.0
December 1979	23	73.9	65.2	55.0
March 1980	40	54.5	75.7	71.43

89 times. A successful "track" (Randolph 1977) is one in which a mouse is recorded at at least 4 loci (including trap and track points) during a single tracking session. 24 Animals were tracked over more than one tracking session, the maximum being 4 times.

As can be seen from Table 3.1, tracking by marker bait is a highly successful technique. This is indicated by the high percentages of animals successfully tracked (maximum = 100% for Autumn) and the high occurrence of marked droppings (maximum = 90.59% for one of the tracking sessions during summer). It is interesting that the droppings of one animal generally dominated each plate; it was thus common to find the majority of droppings on a plate belonging to a single animal with one or two others. The maximum number of animals recorded at a single track point was 5.

Results indicate that males are slightly more successfully tracked than are females. Out of the 10 animals that were never tracked, only two were males; of the 23 animals with more than 8 recovery loci at any one tracking session, 16 (i.e. 69.5%) were males. This could be an indication of marking behaviour.

Table 3.1a also indicates the percentages of ten animals for each tracking session. These animals are most probably recently matured juveniles; the 6 week interval between trapping sessions is sufficient for a juvenile to attain maturity.

Other possible explanations are, firstly a difference in trap-response among members of the population, that some animals are trap-shy or wary of the traps. This behaviour has been demonstrated by several authors, e.g. Crowcroft and Jeffers (1961) and Watts (1970). However, the high proportion of marked faeces in relation to unmarked would argue against this, as against the second possibility, namely, that the animals are migrants.

3.3.1.2 Series 2 Studies.

Initial Trapping.

Initial trapping, in October 1979 over the entire area between the Kuils River, its tributary stream and the road (Figure 3.1) yielded a total of 36 mice. Investigation of the trap stations at which they were caught showed that they fell into two groups: the first, and the larger, comprising 29 animals, apparently concentrated in the grassy area fairly close to the tributary stream, and the second, smaller group, comprising 7 animals, situated along the banks of the Kuils River, on the opposite side of the grid. The area between these two locations consisted predominantly of dense Acacia thicket with little ground cover; it was shown previously (series 1) that this type of habitat is not favoured by Rhabdomys; this was also confirmed by the sparse catches in this area. Furthermore, the trap stations at which the mice were consistently caught, over the trapping period of 4 days and 4 nights, showed that mice caught in one area were not caught in the other. It was thus decided that the two groups could feasibly be considered separate, and the study grid was concentrated on the first and larger group on the South-western side of the area (Figure 3.1).

Tracking.

In October 1979 a total of 20 mice were recaptured after the initial trapping, fed with marked bait, and released. Of these, 15 were successfully tracked, a success rate of 75%. 11 Of these animals, 5 males and 6 females, qualified by having a minimum of 4 track points recorded, for the home range analysis. 72% Of the faeces collected were marked.

In December, 23 mice were caught; of these only 6 were recaptures. 7 Of the 23 were juveniles, with body weights of 20g and less. 15 Animals were tracked, including 4 of the recaptures from October, and 10, 5 males and 5 females, qualified for the home range analysis. The proportion of marked to unmarked droppings was rather low (55%), indicating that some animals were not captured; it was observed, however, that many unmarked droppings were small, possibly belonging to juveniles.

In March, 1980, 40 mice were caught. Of these 7 were juveniles; many other small juveniles were caught but because of limited markers for the bait, were released. Of the 33 adults, 11 were males, and 22 females; 18 animals were new. Only 10 animals were successfully tracked:

3 males and 7 females. 71.43% Of the droppings collected were marked: of the 28.5%, 50%, judging by their size, belonged to juveniles, leaving only 14.27% of droppings unaccounted for.

No mice from the series 1 studies were ever recaptured during series 2.

It should be mentioned that, because of the design of the study, in which animals were continually being removed, and thus not available for recapture, the size of the population at any one time could not be assessed. However, two facts, firstly, by the end of the trapping session the catch had always fallen to almost zero, and secondly, the high percentages of marker recovered in the droppings (Tables 3.1a and 3.1b), indicate that the majority of the population had been caught.

3.3.2 The Distribution and Home Ranges with Habitat.

The two basic needs for small mammals are a sufficient supply of food and adequate cover. For a diurnal species such as Rhabdomys, the latter becomes especially important. As far as diet is concerned, Rhabdomys if primarily granivorous, and the principal supply of food on the Cape Flats comes from the seeds of the abundant Acacia trees (Shelton 1975); King 1976), with a change to green plant material in the winter months when there are fewer seeds available.

The main floristic features and their characteristics are shown in Table 3.2. It can be seen that the different areas differ both in their shelter and food availability; the Metalasia area appears to be poor in both; the Acacia thicket, while providing ample food, is poor in ground level shelter, and the marshy area, although providing shelter, is deficient in food. The best areas for both food and shelter are therefore the grassy and shrubby (Rhus/Xanthrium) areas.

Tables 3.3(a) and 3.3(b) show the distribution and home ranges, in terms of capture and track points, in relation to habitat. Both Tables show essentially similar trends: a clear avoidance of the Metalasia (only present in the series 2 grid) and Acacia dominated areas throughout the year. Marshy areas, which tend to be inundated in winter, are also avoided in this season.

TABLE 3.2 MAJOR FLORISTIC FEATURES OF THE FOUR HABITAT SUBUNITS.

Major Species	Cover Abundance*	Height (metres)	Shelter Availability	Food Availability
Grassy Area				
Acacia cyclops	2	3	Poor	Yes
Acacia seligna	2	3-4	Moderate	Yes
Rhus tomentosa	2	1	Good	No
Unidentified grass	4	0.5	Good	? Yes
Rhus/Xanthium Area				
Acacia cyclops	2	3	Moderate	Yes
Acacia seligna	2	3	Moderate	Yes
Rhus lucida	2	1	Good	No
Rhus mucranata	3	1	Good	No
Xanthrium strumarium	3	1	Good	No
Marshy Areas				
Chondropetalum tectorum	4	2	Good	?
Xanthrium strumarium	2	1	Good	No
Rumex sp.	2	0.75	Moderate	No
Zantedeschia aethispica	2	0.75	Moderate	No
Acacia thicket				
Acacia cyclops	2	3-4	Moderate	Yes
Acacia seligna	2	3-4	Poor	Yes
Rhus mucionata	2	0.25	Poor	No
Metalasia Area				
Metalasia sp.	1	1	Poor	No

*
Note : For a description of the cover abundance scale, see Appendix.

TABLE 3.3(a) HOME RANGE DISTRIBUTION WITH HABITAT FOR SERIES 1.

	February/March			May			July			September		
MALES	Obs.*	Exp.*	χ^2	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2
Area 1:	53	45,87	1,108	25	18,18	2,588	43	27,17	9,22	37	23,8	7,28
Area 2:	40	36,14	0,412	15	12,36	0,564	12	18,47	2,27	3	13,0	7,69
Area 3:	37	36,14	2,046	16	15,27	0,035	18	18,47	0,012	10	9,75	0,01
Area 4:	9	20,85	6,730	0	10,18	10,18	2	10,87	7,24	2	5,4	2,14
Total:	139	139,0	11,816	56	56,0	13,337	75	75,0	18,739	52	52,0	17,12
	Significant: $p < 0,01$			Significant: $p < 0,01$			Significant: $p < 0,01$			Significant: $p < 0,01$		
FEMALES	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2
Area 1:	51	46,53	0,41	11	10,06	0,08	23	14,49	5,0	26	21,54	0,923
Area 2:	43	36,66	1,096	8	6,8	0,212	7	9,85	0,825	9	11,75	0,64
Area 3:	38	36,66	0,049	7	8,4	0,233	10	9,85	0,002	12	8,81	4,15
Area 4:	9	21,15	6,97	2	5,6	2,314	0	5,8	5,8	0	4,89	4,89
Total:	141	141,0	8,535	31	31,0		40	40,0	11,63	47	47,0	7,612
	Significant: $p < 0,05$			Non-significant			Significant: $p < 0,01$			Significant: $p < 0,01$		

* "observed" = The total number of tracking stations in each area at which a mouse was recorded. If mice were recorded more than once at a particular point, this was counted as the total number of times mice were recorded.

* "expected" = The total number of tracking stations available in a particular area, divided by the total number of mice caught over the whole grid.

TABLE 3.3(b) HOME RANGE DISTRIBUTION WITH HABITAT FOR SERIES 2.

	OCTOBER			DECEMBER			MARCH		
MALES	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2
Open Metalasia	1	7.2	5.31*	0	5.37	5.4*	0	14.33	68.4*
Acacia	8	33.8	19.72*	6	25.4	14.79*	5	67.7	131.0*
Grass	16	9.8	3.87*	18	7.34	15.31*	8	9.8	1.08
Rhus Shrub	10	7.6	0.71	11	5.75	4.79*	10	7.7	1.76
Marsh	0	7.2	7.17*	2	5.375	2.12	7	7.2	0.04
FEMALES	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2	Obs.	Exp.	χ^2
Metalasia	2	4.78	1.62	1	7.17	5.31*	1	6.14	3.7*
Acacia	15	22.5	2.53*	10	33.83	16.78*	9	29.00	57.1*
Grass	17	6.55	16.67*	12	9.83	0.48	31	8.4	72.9*
Rhus Shrub	12	5.11	9.29*	8	7.67	0.015	29	6.00	29.6*
Marsh	6	4.78	0.31	5	7.17	0.657	9	6.1	1.2

* Significant, $p < 0.05$.

The series 2 studies show a distinct preference for the grassy and Rhus/Xanthrium areas at all tracking sessions. The same trend is evident in series 1 in the summer months: in the winter, however, there is an avoidance of the latter area. The reason for this is undoubtedly the dying-down of the Xanthrium bushes which form a sizeable proportion of the cover. This avoidance of this area is accompanied by a preference for grassy areas in the winter. Two reasons for this suggest themselves: firstly, the good ground cover still available in the grassy area, and secondly, the abundance of green plant material which Shelton (1975) and King (1976) found to be an important constituent of the diet at this time of year. This would also partly explain the preference for grassy over marshy areas: the other reason is the accumulation of water in the latter after rain.

It thus appears that in an area such as this where food in the form of Acacia seeds is present, in varying amounts, over almost the entire grid, the availability of shelter becomes the dominant factor affecting the distribution of the mice.

3.3.3 Home Range Utilisation.

Mohr (1974) pointed out that few small mammals use their home ranges to the same extent; rather they make use of runways connecting particular areas. This was confirmed by Blair (1951) and Dice and Howard (1951) in tracking animals in sand and snow respectively. They found that animals used the same route on the outward as on the return journey. Observations on the caged colony of Rhabdomys confirm that this is so for this species (Chapter 1): the mice habitually use the same pathways when moving about. Brown (1966) postulated that the entire community has access to the runways: observations on captive Rhabdomys confirm this: even when a subordinate passes a dominant on a runway he is not challenged.

Although a study of the use of runways on the grid was not undertaken per se, evidence from one station in particular, 11F, indicates the use of runways. This station, situated in marsh in an area of relatively dense cover, happened to fall on what appeared, from its physical characteristics, to be a runway. This observation was supported by the recovery of particularly high numbers of faecal pellets in June 1978, for instance, 13 pellets from 5 individuals were recorded. This station lay within the range of 26 males, the dominant, and later within the range of 45 males, his presumed successor, further evidence that this must have been neutral ground open to all members of the community. This was confirmed from prior observances on the capture colony (Chapter 1) where it was found that the dominant male defended a small area of ground from other members of the colony who were, however, allowed to cross a portion of this area on a set path, a similar situation to that found by Brown (1966) on Apodemus.

Adequate cover when foraging and familiarity with the environment when danger threatens are vitally important for a diurnal rodent. Curry-Lindahl (1956) found in the diurnal bank vole, Clethrionomys glareolus, that the presence of adequate shelter outweighed the presence of food in the choice of a home site namely either a nest or burrow that forms the animals' "headquarters". Runways were used to connect the home sites with the feeding sites. Rhabdomys does not construct elaborate burrows (Choate 1972; Brooks, 1974; and personal observations) but prefers to build nests above ground, although disused burrows of other species, such as Tatera may be used. Nests are of fairly elaborate construction (Chapter 1) and are built in the most sheltered spots available. Shallow burrows not more than 15cm deep may be made with their entrances beneath a thick bush or other very sheltered area.

Due to their inaccessibility, the number and position of nests and home sites was not determined. The only way of doing this is by fine tracking of the animals' movements, either by studying the actual tracks, e.g. Blair (1951), or by radioactive tracking, e.g. Godfrey (1953). Brown (1966) using the latter technique, found that both Clethrionomys and the woodmouse Apodemus had four to five home sites used by a single individual at any one time. Similar results were reported by Blair (1951) for the beach mouse sp., and by Terman (1962) for the prairie deermouse, Peromyscus. Observations on the caged population of Rhabdomys indicate that this is so: the value of the many home sites apparently lies in their usefulness as "bolt-holes" when danger threatens. Home sites may also shift, particularly among females in search of a suitable nest site; Kikkawa (1964) observed that a female Clethrionomys shifted her home site three times in as many months.

Although Rhabdomys does not go below the ground to any appreciable extent, the same cannot be said for utilisation of space above the ground surface: it is an adept climber. I have frequently observed the mice scrambling around in Acacia trees at least 1m from the ground, provided, of course, that there are sufficient low branches or bushes to climb up on. Often they will stretch themselves out on a sunny branch to sunbathe, a behaviour very characteristic of the species (Part 1). Nel and Rautenbach (1975) observed this three-dimensional use of habitat in Rhabdomys in the Kalahari. This implies that the two-dimensional home range can be compressed to a greater extent than would be possible if the species were active in two dimensions only. This factor, together with the quantity of food available on the Cape Flats, will permit very high densities of mice per unit area.

3.3.4 The Social Hierarchy.

"I suggest that one must replace any idea of every mouse with its individual home range in the field with the concept of each individual fitting, or seeking to fit, into a social pattern". (Brown 1966).

The male social hierarchy for the series 1 studies, based on the results of testosterone assays, is shown in Table 3.4(a). It should be pointed out that in this Table and the one following, the ranks assigned to the animals are based on relative,rather than absolute, testosterone levels. The rationale for doing this is discussed in detail later.

The pyramidal structure of the hierarchy, having a single dominant, rather more middle-ranking individuals, and still more low-ranking individuals, corresponds closely with the results obtained for the captive colony (Part1, Chapter 1). The rationale for the use of testosterone as an index of dominance was discussed fully in Part 1, Chapter 1; briefly, stress resulting from social subordination causes an increase in adrenocortical activity, which has the effect of inhibiting production of the male hormone, testosterone (Christian 1956a). The hypothesis continues that a dominant animal experiences the least amount of social

TABLE 3.4(a). THE SOCIAL HIERARCHY, AS DETERMINED BY TESTOSTERONE ASSAY, FOR SERIES 1 TRAPPING STUDY.

Male Number	Body Weight (grams)	Testosterone (n moles/litre)	Assigned Position in Hierarchy
26	61	23.3	Alpha
19	59	10.65	Beta
20	36	11.2	Beta
27	24	10.4	Beta
31	53	13.2	Beta
45	60	10.9	Beta
78	49	9.89	Beta
	Mean of Betas:	10.92; S.D. = 1.2	
30	59	6.46	Omega
32	52	5.49	Omega
42	43	5.77	Omega
46	69	6.66	Omega
51	40	3.62	Omega
52	39	6.6	Omega
55	45	4.89	Omega
75	55	3.94	Omega
76	37	6.58	Omega
	Mean of Omegas:	5.55; S.D. 1.15	

TABLE 3.4(b) THE SOCIAL HIERARCHY, AS DETERMINED BY TESTOSTERONE ASSAY FOR SERIES 2 TRAPPING STUDY.

OCTOBER 1979

ale Number	Body Weight (grams)	Testosterone (n moles/litre)	Assigned Position in Hierarchy
206	54	1.00	-
207	65	1.00	-
208	43	2.40	-
210	44	3.06	-
213	38	0.98	-
216	48	2.36	-
221	45	1.00	-
224	50	1.00	-
225	45	1.16	-

DECEMBER 1979

Male Number	Body Weight (grams)	Testosterone (n moles/litre)	Assigned Position in Hierarchy
261	42	9.60	Alpha
213	60	5.00	Beta
242	41	4.90	Beta
225	68	2.72	Omega
245	41	0.83	Omega
250	36	2.42	Omega
253	34	1.05	Omega
243	31	Undesc. testes	Omega

FEBRUARY 1980

ale Number	Body Weight (grams)	Testosterone (n moles/litre)	Assigned Position in Hierarchy
274	51	5.55	Beta
225	65	3.2	Omega
243	43	1.00	Omega
264	55	1.73	Omega
291	51	2.60	Omega

MARCH 1980

Male Number	Body Weight (grams)	Testosterone (n moles/litre)	Assigned Position in Hierarchy
213	51	14.20	Alpha
243	48	4.65	Beta
280	49	4.68	Beta
291	51	5.10	Beta
293	41	4.51	Beta
295	46	5.40	Beta
250	45	3.02	Omega
206	61	2.45	Omega
284	39	2.03	Omega
292	40	1.50	Omega
294	35	3.58	Omega

stress and therefore has the least inhibition of testosterone production (Christian and Davis 1964).

The data shown in Table 3.4(a) were obtained in the summer months only, during February and March 1978. No data on testosterone levels were collected during the non-breeding season. As this was felt to be a deficiency in the study, it was decided, in the series 2 studies, to trap more frequently - once a month - and monitor the testosterone levels and their possible fluctuations more closely. Table 3.4(b) shows the testosterone levels of all adult males caught between October 1979 and March 1980.

The October 1979 trap fell just before the start of the breeding season: very few of the females were perforate, and none of the males had descended testes. This is reflected in the testosterone levels for this month: all levels are uniformly low. The most striking observation of the testosterone levels during the breeding season - i.e. December 1979, February and March 1980 - is that they are quite considerably lower than those obtained in the series 1 studies, as well as those of the captive colony. At first it was thought that the higher values were merely anomalous beta males, and that the alpha had not been caught; however, when the trend was found to be consistent throughout the three trapping sessions, and the testosterone levels indicated the clear pyramidal structure of one higher than the rest, several at a median position, and rather more very low values, it became apparent that these results were genuine, and not artefactual. The reason behind these consistently lower values is unclear; a possible suggestion is the effect of density of animals per unit area: in both the captive situation and the February/March 1978 trap, densities were very high indeed, while the numbers of animals caught in the summer of 1979-1980 were considerably lower. (Although the captive figures are similar for the two series, it should be remembered that the grid size in the series 1 study was almost a third of the size of that in series 2, meaning the density of mice per unit area was approximately three times greater). It is possible that the close proximity of many animals of both sexes stimulates aggressive and sexual impulses more frequently in the males, who thus maintain a relatively high level of androgen.
In 1979-1980, in a situation of lower density, this stimulation presumably did not occur to the same extent, resulting in consistently lower levels.

Considering the changes in status of males over the six-month period: in October 1979 testosterone levels were uniformly low, and hence the information regarding social position could be gained. The most that can be said is that all these animals were mature adults, having been born the previous summer. No mice from the series 1 studies, (which ended in September 1978) were recaptured.

In December 1979, 12 males were captured: of these 5 were juveniles (4 had body weights less than 16g; the fifth, male 243, weighed 31g but had undescended testes) and were not bled. Of the remaining 7, 1, male 261, could have been an alpha: this was an apparently new animal, having been caught for the first time in December, and not particularly large, weighing only 42g. 2 Possible betas were present, males 213, a recapture from October, and 242, a new animal, weighing 60 and 41g respectively. The remaining 4, males 225 (a recapture from October), 245, 250 and 253, were assigned an omega status.

The trend of far greater numbers of new animals in comparison to recaptures continued in the trapping session conducted in the first week of February 1980, when animals were only trapped and in the case of adult males, bled. In all, 21 males were captured: of these only 5 had fully descended testes. Of these 5, 2 were recaptures: male 225, whose testosterone level indicated that he had maintained his beta status, and male 243, the subadult caught in December and who now appeared to be an omega. Of the 3 new adults, 1, male 274, (body weight 51g) showed beta status; the other 2, males 264 and 291, were apparently omegas. No alpha or more betas were caught. However, on three separate occasions during the trapping, large highly active animals had escaped from processing bags; from experience, highly active animals generally prove to be males. As these animals were not marked, it is not known whether they were in fact the same animal caught on three different occasions, whether he was caught again and marked, or whether more than one animal was involved.

In March 1980, 11 adult males were captured and bled. Of these 6 were recaptures. Male 213, body weight 51g, one of the original captures in October, and previously assigned a beta status, now showed alpha status. The previous alpha male, male 261, was not recaptured after December: it is presumed that he was now dead. It is interesting that male 213 was an old animal, having been born the previous summer, and probably therefore about nine months old, and a previous beta, who had now apparently moved up to the top of the hierarchy as the dominant, This is an exact confirmation of the observations on the captive colony (Part 1).

5 Males, males 243, 280, 291, 293 and 295, appeared to be betas. Of these the last two were new animals; males 280 and 291 recaptures from February. Male 280 escaped from the processing bag after marking and was not recaptured and bled, so his previous status is unknown; male 291 was a previous omega. Male 243 is of interest, in that his career has been followed from a subadult in December, to an omega in February, and a beta in March.

The remaining 5 animals were apparently omegas. Of these, only males 206 and 250 were recaptures, from October and December respectively. It is interesting that while some males, such as those described above, move up through the hierarchy, and may eventually reach alpha position. Some remain as omegas for the whole of their lives. Male 206 is an example of this: an old animal from the previous summer who has maintained his omega status: other examples are males 225 and 250. This was observed in the captive mice as well; one hesitates to authropomorphise and postulate "initiative" and "drive" in mice; perhaps these persistent omegas have just opted out of the rat race!

Female <u>Rhabdomys</u> do not form a similar hierarchy, either among themselves or together with the males, although a female that habitually consorts with the dominant male takes a dominant status herself, equal to that of the male (Part 1, Chapter 1). Generally, however, the females have a separate, more fluid system, and are free to move anywhere in the society. However, when a female approaches parturition, she builds a next and establishes a territory around it. Territorial defence gradually decreases in ferocity until the young mice are reasonably able to take care of themselves. For the purposes of this analysis therefore, females are classified only as "breeding" or "non-breeding". On this basis, for the series 1 studies, 5 breeding and 5 non-breeding females were found in the February/March period; in May, no breeding females qualified for the home range analysis as they were insufficiently tracked, and in the winter and spring traps the majority of females caught were imperforate, and therefore not in breeding condition.

In the series 2 studies, the majority of females in the October 1979 trap were imperforate; although some were just becoming perforate, none appeared to be pregnant: certainly none of the males were in breeding condition. In December, of the 11 females caught, 3 were juveniles, 1 was imperforate, and 4 were pregnant. In February, a further 11 females were caught; of these, 2 were imperforate, 7 perforate, and 2 pregnant. In March, 4 out of 20 were pregnant, while 10 were perforate; the remaining 6, largely juveniles and subadults were imperforate.

3.3.5 Home Range Size.

The home range must supply the requirements of Burt's (1940) definition: "feeding, mating and caring for the young". In other words, it must be large enough to supply sufficient food to satisfy the energy demands of the animal (McNab 1966), to allow the animal to come into contact with members of the opposite sex, and to provide sufficient cover and shelter for the rearing of the young. However, limits are set, firstly by the body size of the animal, which affect the size of the area that can be covered, as well as by the problem of avoiding unnecessary exposure to predators by covering too large an area. By these requirements Rhabdomys, a small mammal in the food and shelter-rich environment of the Cape Flats, might be expected to have a relatively small home range. However, in this study, the interest lies not so much in the absolute size of the home range for the species as in the differences among the social classes and changes with the changing demands of season.

Home range sizes, for the series 1 studies, as determined by the elliptical mathod (Jennrich and Turner 1969) are shown in Table 2.5(a), grouped by season, sex and status. A general trend of changing area of home range with season is apparent: home ranges of winter and spring appear larger than those of autumn and summer. When tested by students' t-test, the differences in range size for males in the breeding and non-breeding seasons is highly significant ($p < 0.001$). A comparison of breeding season vs non-breeding season range sizes for females, however, does not show a significant difference at all, while a comparison of male and female range sizes during the non-breeding season falls just short of significance ($t = 1.474$; tabled $t = 1.761$ for 14 d.f. $p < 0.01$).

Beta and omega males show the difference in the sizes of their home ranges, at any season. The range of the single alpha male, male 26, is relatively small ($72m^2$) in comparison to the range sizes of many of the other males. Unfortunately, he was only caught during the summer period and never again, so no between season comparisons can be made. The smaller home range value could possibly be indicative of the presence of territorial behaviour, which is characteristic of the alpha male. Observations on the caged population (Part 1) reveal that the alpha ranges over the entire area occupied by the colony and is dominant over the rest of the males, but he also maintains and defends a territory into which no other male may venture without attack. The small value of the home range does not necessarily contradict Brown's (1966) statement that the dominian ranges over the entire area of the population nor with the observations on the captive animals: the alpha male spends a large proportion of his time in his territory which, in the case of the caged colony, had an adequate food supply: there is no reason to suppose that this situation would not also apply in the food-rich Cape Flats; thus would not necessitate moving out of the territory in search of food: excursions outside would probably be of an exploratory, or even of a patrolling in the sense of 'seeing what the rest of the "colony" was up to', nature. This agrees with Miller's findings on Apodemus: "The dominants appear to remain located in their favourite positions, even if they move around more freely with some extended trips of exploration". The fact that the home range data for male 26 was accumulated over a short period of time (2 days) might mean that the alpha simply had not moved much out of his territory during this time. The real criterion, however, for determining whether the home range forms the whole, or part, of a territory will be the exclusiveness of the area. This will be dealt with in the following section "Home Range Distribution".

The sizes of the ranges of the breeding females indicate that these animals could very well be territorial. Highly significant differences were found between breeding and non-breeding females ($t = 3.395$; $p < 0.01$) and between breeding females and all status of males for the same season ($t = 2.092$; $p < 0.05$). Breeding territories of females have been described by a number of authors, e.g. Allen (1938); Frank (1957); Shillito (1963); Brown (1966) and many more. Getz (1961) states that *Microtus pennsylvanicus* females showed smaller home ranges in the breeding season and Brooks (1974) describes smaller range length values for female *Rhabdomys* in the Transvaal.

Range sizes for the series 2 studies are shown in Table 3.5(b). Perhaps the most striking observation is that many of the home ranges are larger than those found in series 1, indicating that the grid size in the latter studies was, in fact, too small, justifying the increase in grid size for series 2. In series 2 a larger area was trapped ($3625m^2$ as opposed to $1850m^2$) and the precaution of setting traps on the periphery was also taken. These peripheral traps, set at 10 and 20 metres from the last trap-line, proved unproductive, presumably indicating that mice were not moving out of the grid core area. On this basis it may be considered that the range sizes presented here, for the series 2 studies, are without qualification, the absolute sizes of *Rhabdomys* home ranges for the Cape Flats habitat.

In general, no significant difference was found between the range sizes of males and females between the end of the non-breeding season (October 1979) and early breeding season (December 1979). This contradicts the findings of the series 1 studies where ranges of males in the non-breeding season were found to be significantly larger. Reasons for this apparent difference between range sizes of males and females are speculative; a possible explanation can be based on the observation that the male has a greater tendency to wander and explore than does the female mouse. This phenomenon has been described by Kikkawa (1964) for *Clethrionomys* and *Apodemus*, and Brown (1962) found that the male section of a *Clethrionomys* community needed to wander more freely than the female; the reasons he postulated were the greater inquisitiveness of the male and the possible preoccupation of the females with young. This difference in behaviour could be the result of learning while young: on reaching sexual maturity, the young male leaves the nest, usually as a result of the aggression of the resident adult male, should there be one, and sets off to wander in search of a home site. This phenomenon has been described by numerous authors, e.g. Burt (1949); Howard (1949), Godfrey (1953); Sadleir (1965); Brown (1966) and Christian (1970). The juvenile must find an empty place or die (Andrenartha and Birch (1954)). McCabe and Blanchard (1950) have expressed this quite dramatically: "The young Peromyscus, if the population be near its normal size, is faced with the grim dilemma to find a dwelling-place recently vacated by death or to die". The phenomenon of dispersal by juveniles must be separated from that of dispersal by adults (usually subordinates) as a response to high population density. In both cases, however, the effect is the same: not all the animals can fit themselves into the existing population; many may die but some may survive to colonise new habitats and thus, according to Christian's (1970) hypothesis, form the spearhead of evolution. Certainly these speculations would agree with the previous observations on the caged colony, where young males were observed to leave the parental nest site on attaining maturity, while females remained.

It is possible that attraction to females constitutes the factor that tends to draw the males' wanderings in during the breeding season. This would account for the between-season differences in range size observed in series 1, and could also account for the apparent discrepancy observed between series 1 and 2: the only data for the non-breeding season during the series 2 studies, was collected in the October trapping and tracking session, just before the commencement of the breeding season. As described earlier, although males were not in breeding condition, several females were already perforate, and therefore possibly coming into aestius. This would presumably constitute a force of attraction for the males, thus having the effect of decreasing their range sizes to their equivalent sizes during the breeding season.

For the males, no significant differences were observed either between trapping sessions or between different classes. Male 261, the December alpha, was unfortunately not tracked; the March alpha, male 213, was, but showed no indication of smaller range size. The exceptionally small value for male 291, the omega, in March, is presumably an artefact: a consideration of the distribution of home ranges (see below) shows that his range lay right on the periphery of the grid, alongside the tributary stream. As this was already late summer, much of the stream

TABLE 3.5(a) HOME RANGE SIZES FOR SERIES 1 STUDY. THE UNITS ARE SQUARE METRES.

	FEBRUARY/MARCH			MAY			JULY		SEPTEMBER	
MALES										
Alpha	26	72.75								
Beta	31	116.92		45	58.55		32	163.50	27	90.71
	45	69.70		1	120.70		79	46.08	101	129.25
	71	35.36	(periph)	79	97.95		1	191.34	77	143.44
	$\bar{x}$ =	73.99		78	70.33		84	184.36	79	209.4
	σ =	40.95		85	52.73	(periph)			104	186.03
Omega	30	89.64		90	91.43		$\bar{x}$ =	146.32		
	42	124.65					σ =	67.86	$\bar{x}$ =	151.77
	46	103.24		$\bar{x}$ =	81.94				σ =	46.90
	51	57.86	(periph)	σ =	25.99					
	52	107.46								
	$\bar{x}$ =	90.69								
	σ =	26.61								
FEMALES										
Breeding	23	37.22		29	49.75		82	67.00	102	101.0
	25	19.40		41	95.47		83	69.10	106	207.53
	44	58.17		$\bar{x}$ =	72.61		87	105.87	114	75.9
	47	41.47		σ =	32.32		99	111.55	116	223.62
	29	61.45					$\bar{x}$ =	88.38	$\bar{x}$ =	152.01
	$\bar{x}$ =	43.55					σ =	23.59	σ =	74.39
	σ =	17.04								

TABLE 3.5(b) HOME RANGE SIZES FOR SERIES 2 STUDY. THE UNITS ARE SQUARE METRES.

OCTOBER

MALES	
206	1128.5
208	688.2
213	274.1
224	288.6
225	377.7
232	89.9
Mean =	474.5
σ =	375.6
FEMALES	
203	338.9
204	179.22
211	639.2
212	381.1
221	289.3
223	543.1
237	514.1
Mean =	412.2
σ =	160.6

DECEMBER

MALES		
(Beta)	213	1343.2
	225	475.7
	242	640.1
	245	311.5
	Mean =	692.39
	σ =	454.2
JUVENILE MALES		
	243	177.63
	244	70.68
	Mean =	124.15
FEMALES		
Non-Breeding Females		
	212	791.8
	236	754.2
	248	358.5
	249	774.7
	Mean =	669.8
	σ =	208.1
Breeding Female		
	202	29.1

MARCH

MALES		
Alpha	213	478.3
Beta	243	245.7
Omega	291	30.8 (peripheral)
FEMALES		
Non-Breeding Females		
	268	364.9
	271	495.5
	272	426.9
	300	287.7
	305	288.7
	Mean =	372.7
	σ =	89.9
Breeding Females		
	296	91.1
	299	108.2
	Mean =	99.6
	σ =	12.2

had dried up, exposing more ground than could be utilised. Presumably the range of this animal extended into this area, where no plates had been set, down to the water's edge.

Females show no differences in range size compared to those of the males. However, in agreement with the series 1 findings, the range sizes of breeding females are significantly smaller. The single breeding female in December, femalt 202, showed a very small range ($29.1m^2$, as opposed to $669.8m^2$ for non-breeding females). In March, two breeding females, females 296 and 299,both showed significantly reduced ranges. As discussed previously this could very well be an indication of territorial behaviour.

An interesting feature that was not observed in series 1, is that of range sizes of juvenile animals. As can be seen from the 2 juveniles (both males) tracked in December, the range sizes tend to be smaller than those of adult males. In March, however, due to the large numbers of animals and the restriction of sufficient markers for the bait, adults were fed and tracked in preference to juveniles, so no data is available.

No difference in sizes of home ranges situated in different vegetation types was found; most animals, in fact, tended to have ranges that overlapped several vegetation types and not situated entirely in one.

3.3.6 Home Range Distribution.

Figures 3.2, 3.3, 3.4 and 3.5 show the distribution of home ranges for series 1 studies, for the seasons summer, autumn, winter and spring, respectively. The strongly elliptical nature of many of the home ranges is apparent; indicating the superiority of the elliptical description (Jennrich and Turner 1969) over the purely circular restriction of Calhoun and Casby (1958). It must be emphasised, however, that the centre of activity is a statistical concept and does not necessarily coincide with the home site of the animal.

It is immediately apparent from these home range points that the ranges are clumped. Two reasons for this suggest themselves: firstly a response to habitat,- the majority of the centres of activity lie in

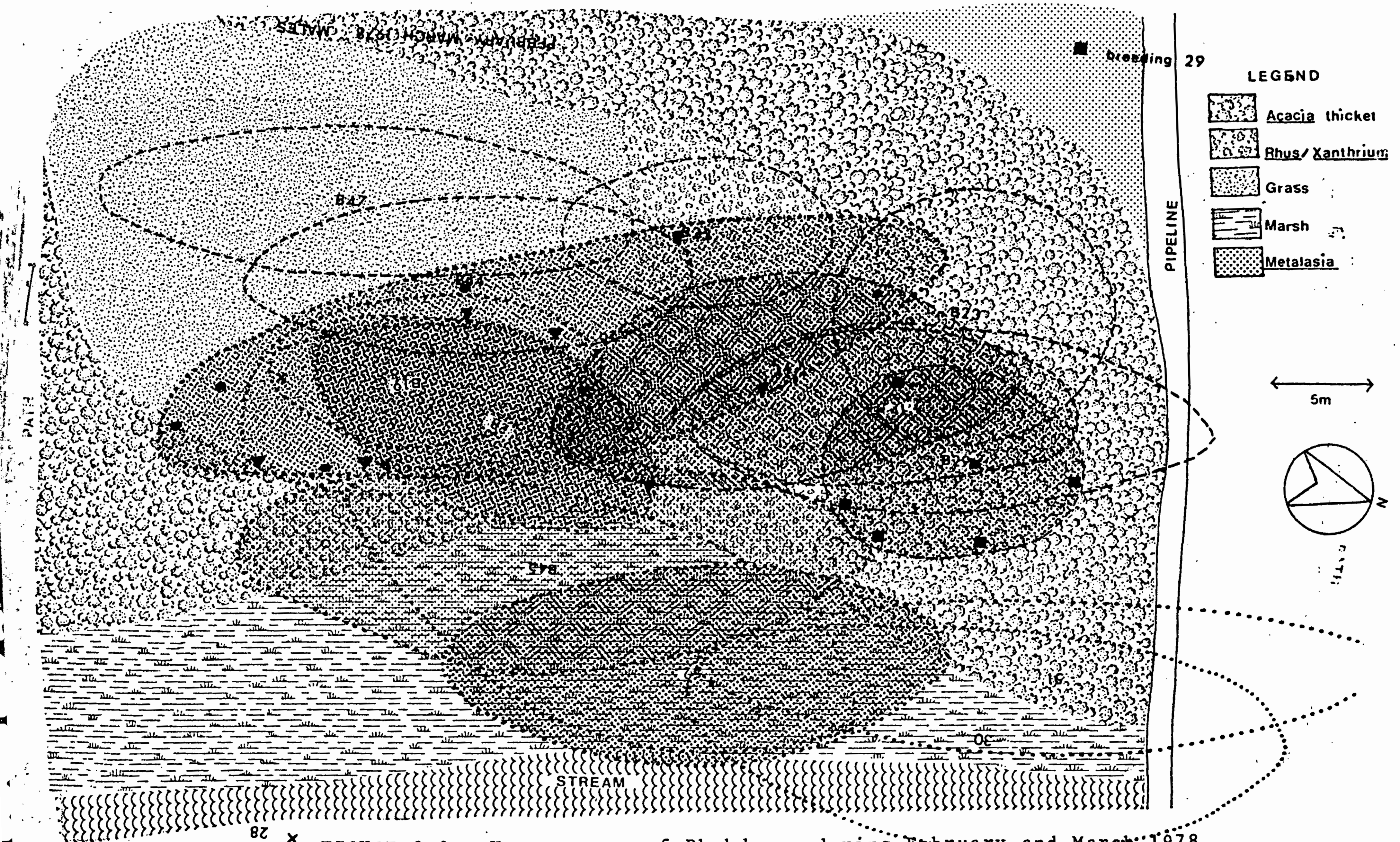


FIGURE 3.2. Home ranges of *Rhabdomys* during February and March 1978. In this and following maps, the actual capture or track points of animals are

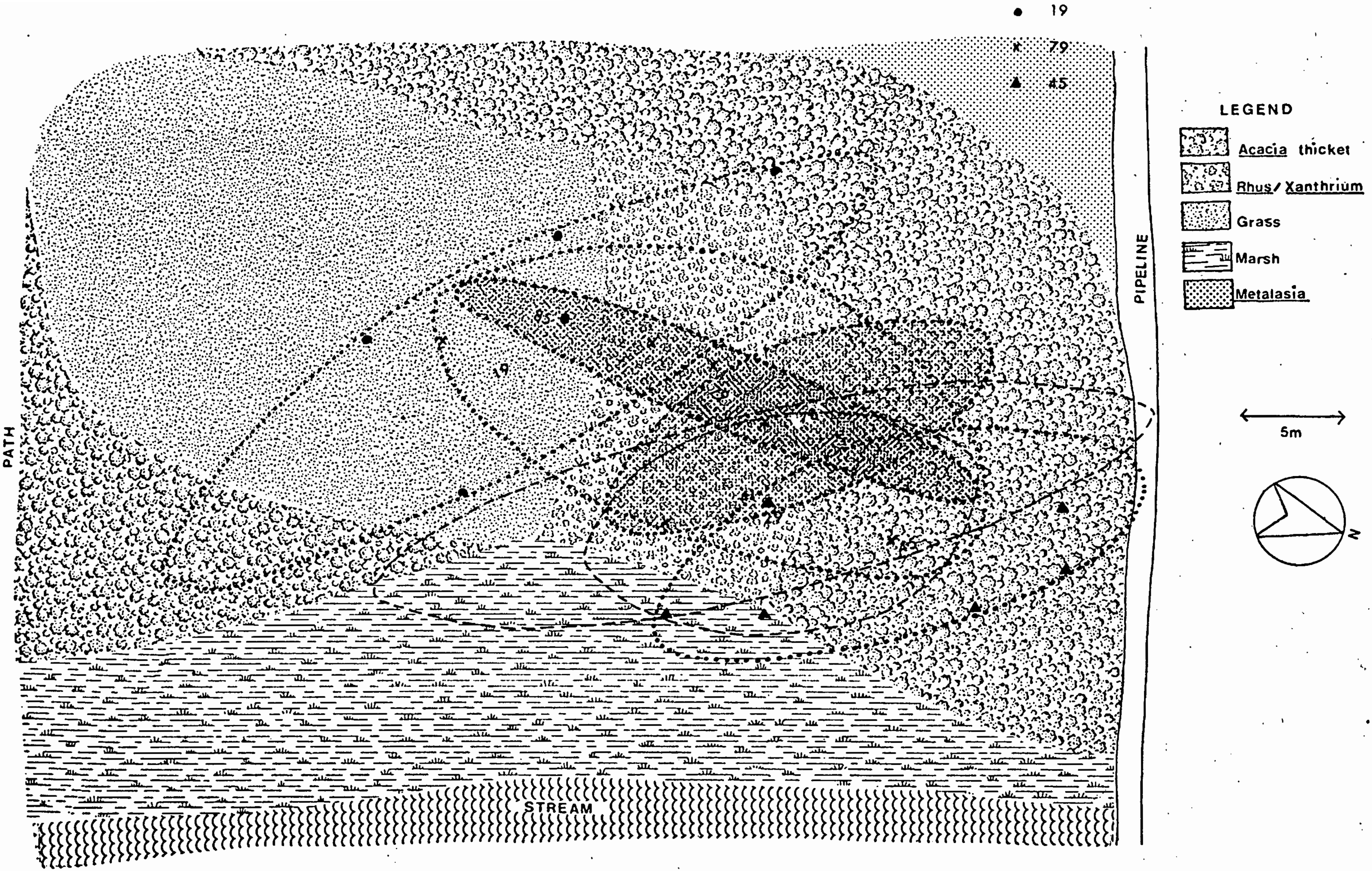


FIGURE 3.3. Home ranges of *Rhabdomys* in May 1978. 1978 FEMALES
MAY 1978 MALES

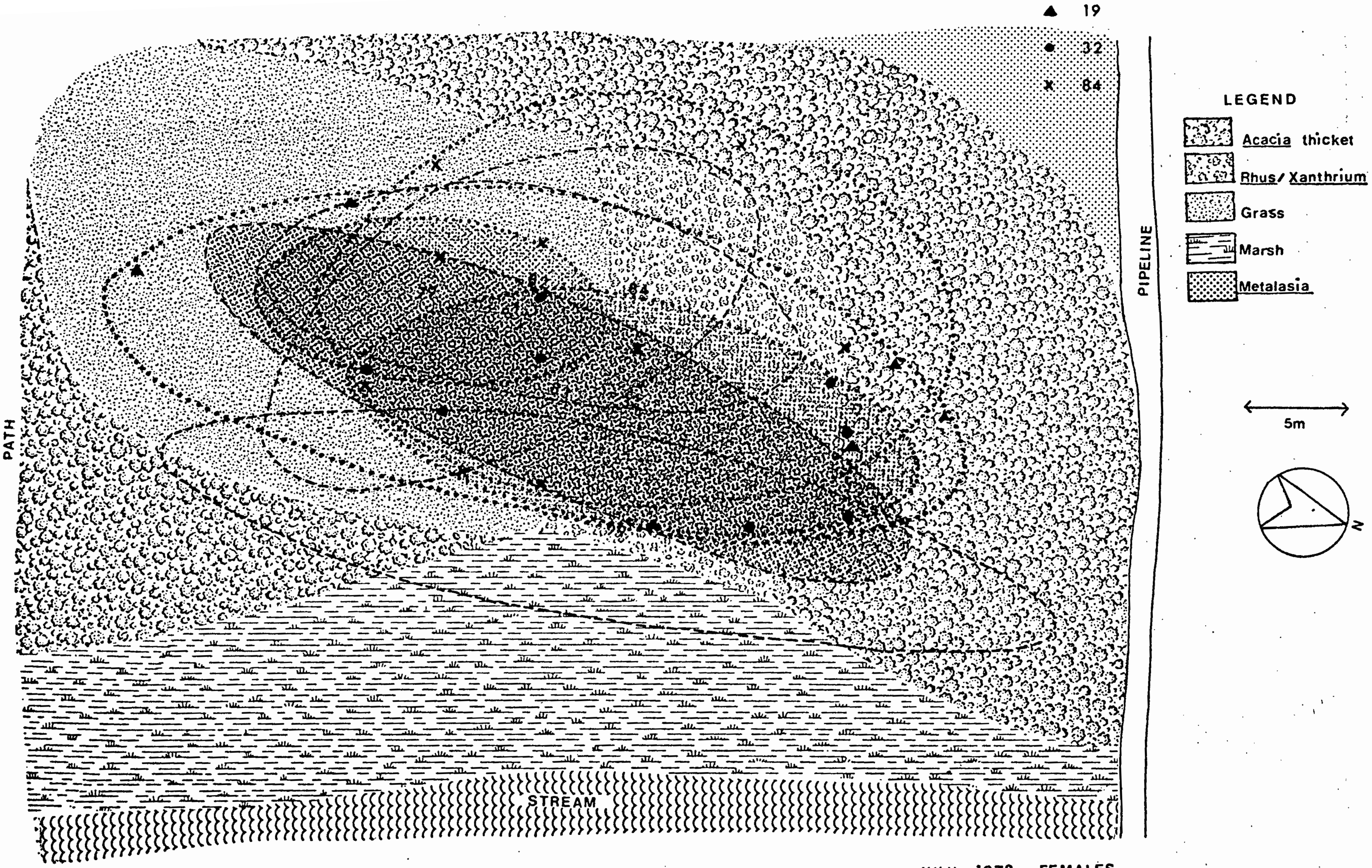


FIGURE 3.4. Home ranges of *Rhabdomys* in July 1978

JULY 1978 FEMALES
JULY 1978 MALES

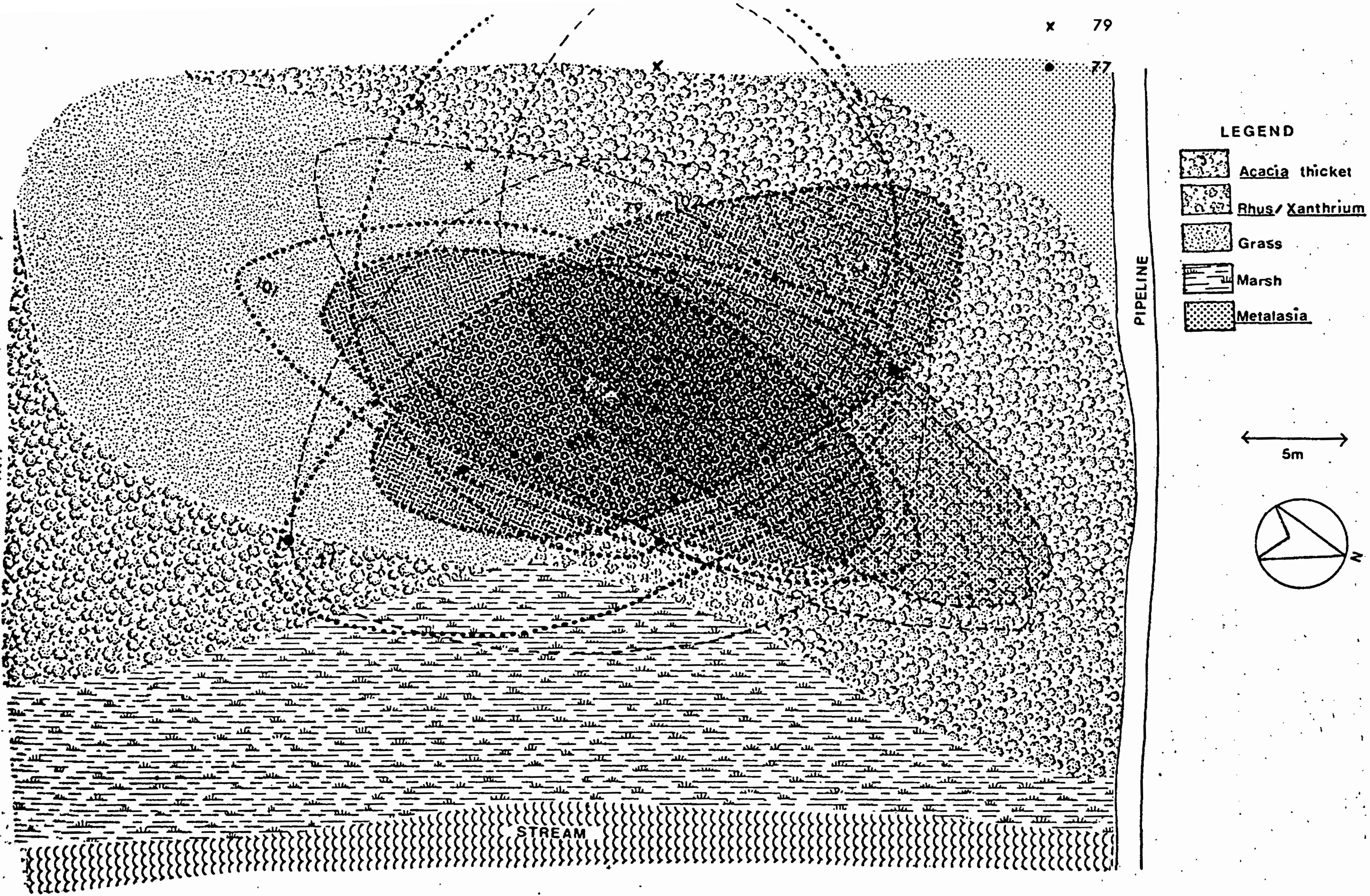


FIGURE 3.5. Home ranges of *Rhabdomys* in September 1978

SEPTEMBER 1979 MALES

SEPTEMBER 1978 FEMALES

the grassy and shrubby areas which, as previously demonstrated, provide the best shelter, and, secondly, social attraction. This might provide a clue as to the evolution of sociality in Rhabdomys: the mice seek areas providing good cover; the enforced concentration and relatively large numbers of individuals in relatively small areas necessitates interaction, and hence the development of a stable social organisation. This agrees with the findings on the caged colony (Part 1) in which large numbers of mice were observed sharing the same small area where shelter was good, while open and partially covered ground remained unused except as a runway. Nel and Rautenbach (1975) observed very similar behaviour in the Kalahari, after finding a dozen or more Rhabdomys sharing the shelter of the same bush.

In the summer months, February 1978 and March 1978, perhaps the most immediately apparent fact is the very large number of animals. As this is the peak of the breeding season, this is not entirely unexpected, but the apparent tolerance of high densities by the mice is interesting. Male home ranges appear similar in size, and are distributed almost wholly within the grassy, Rhus/Xanthrium and marshy areas and not in the relatively open Acacia areas. A point of interest is the fact that much of the home range of the alpha male, male 26, is exclusive; this might be an indication of territorial behaviour. The ranges of the 3 beta males, males 31, 45 and 19, are not exclusive in any way, and in fact overlap quite considerably with those of the omegas. The range of male 61 is, in fact, very small; this is probably an artefact as he was recorded at only 4 stations, the minimum for inclusion in the home range analysis.

The scattered distribution and exclusiveness of female home ranges at this time is immediately apparent, as well as the fact that many are much smaller than those of the males; as described above, this difference is significant. The ranges that are particularly isolated are those of females, 23, 25, 34, 44 and 47. Of these all except female 34 were classed as "breeding"; when the facts are considered together with those of the males, while the ranges of the breeding females are not as dramatically isolated as when females alone are considered. There is nevertheless a part of the range that is exclusive. The fact that none of the ranges of the breeding

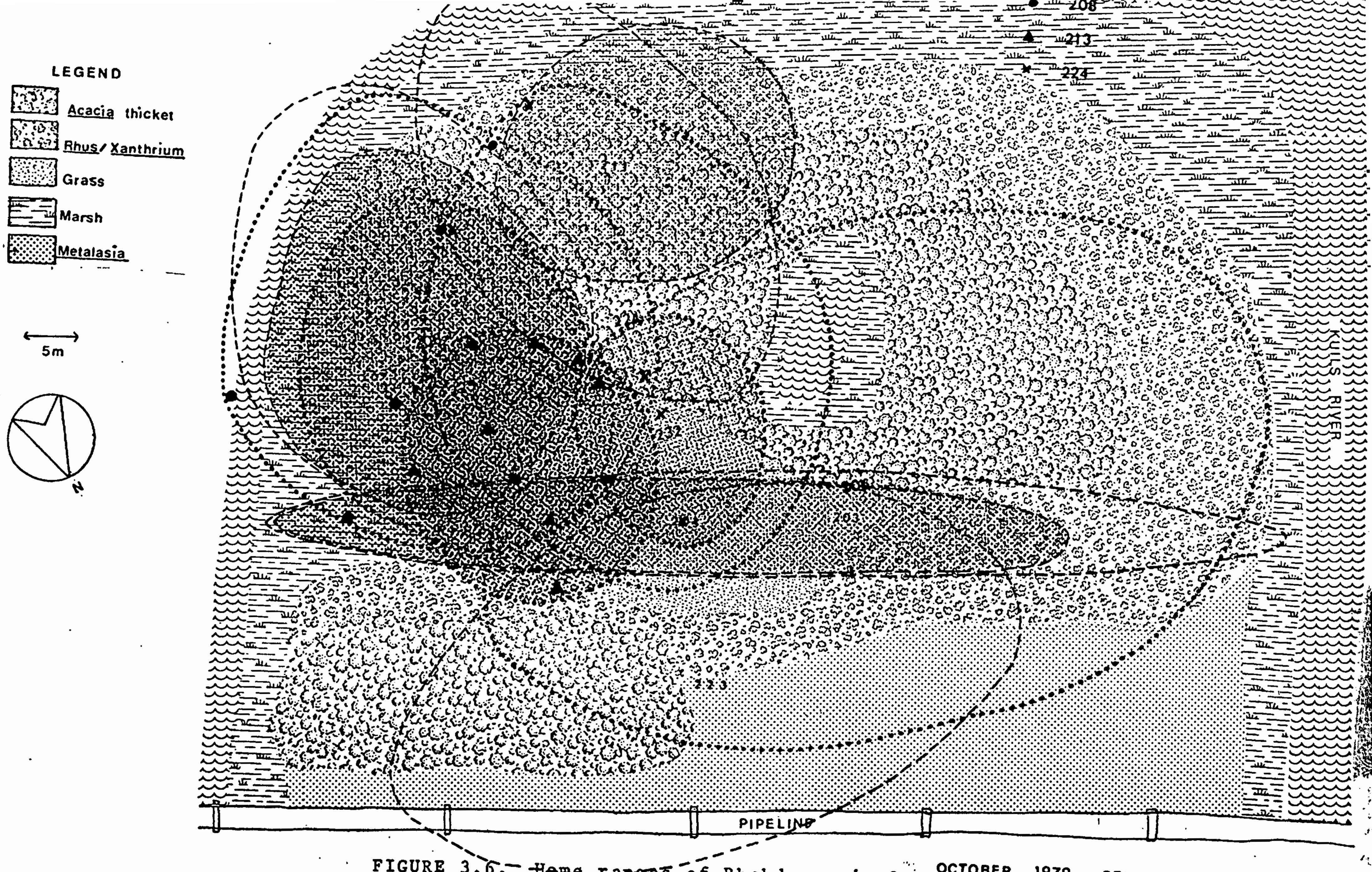


FIGURE 3.6. ~~Home ranges~~ of *Rhabdomys* in October 1979. OCTOBER 1979 MALES FEMALES

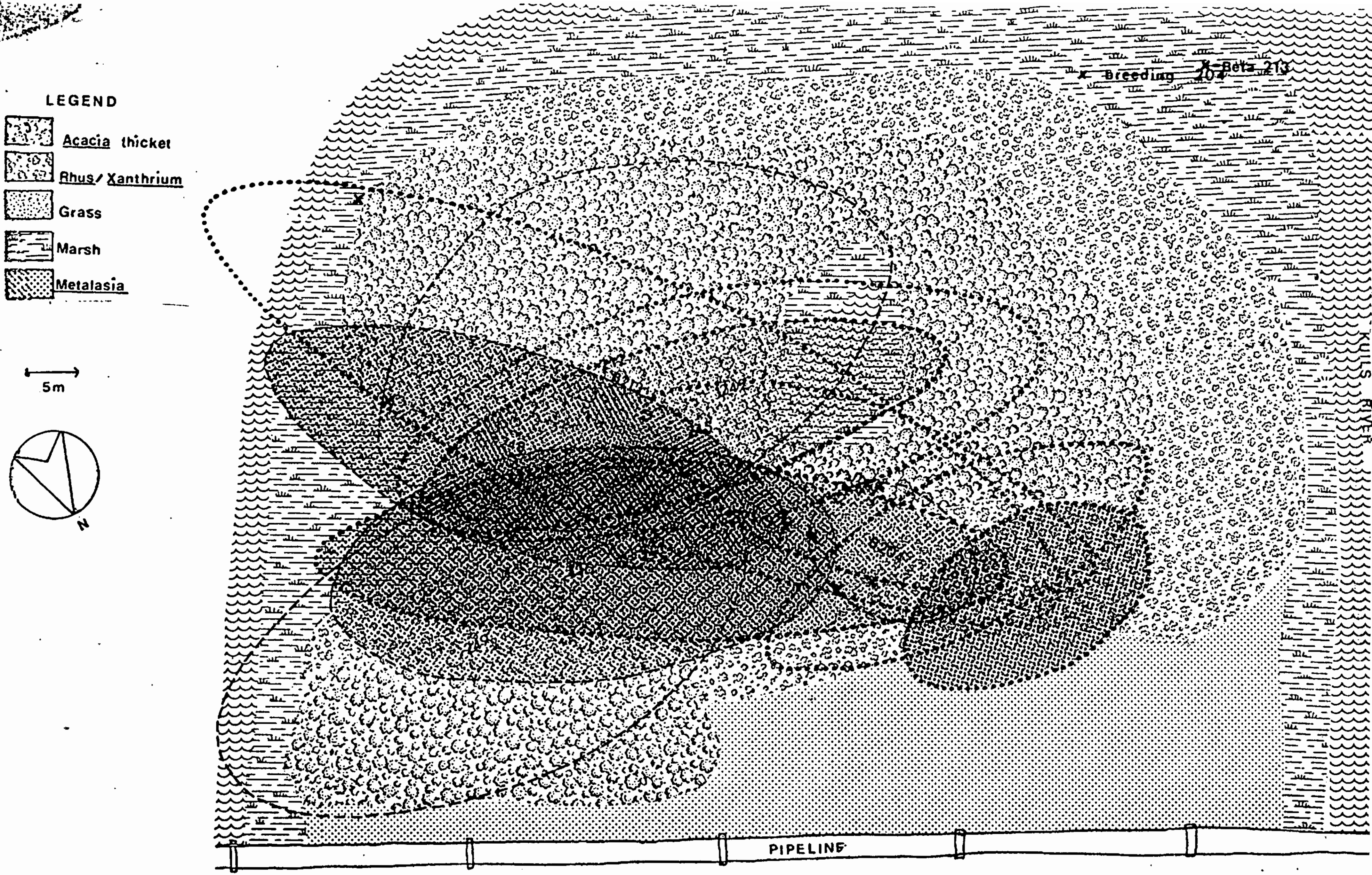


FIGURE 3.7. Home ranges of *Rhabdomys* in December 1979.

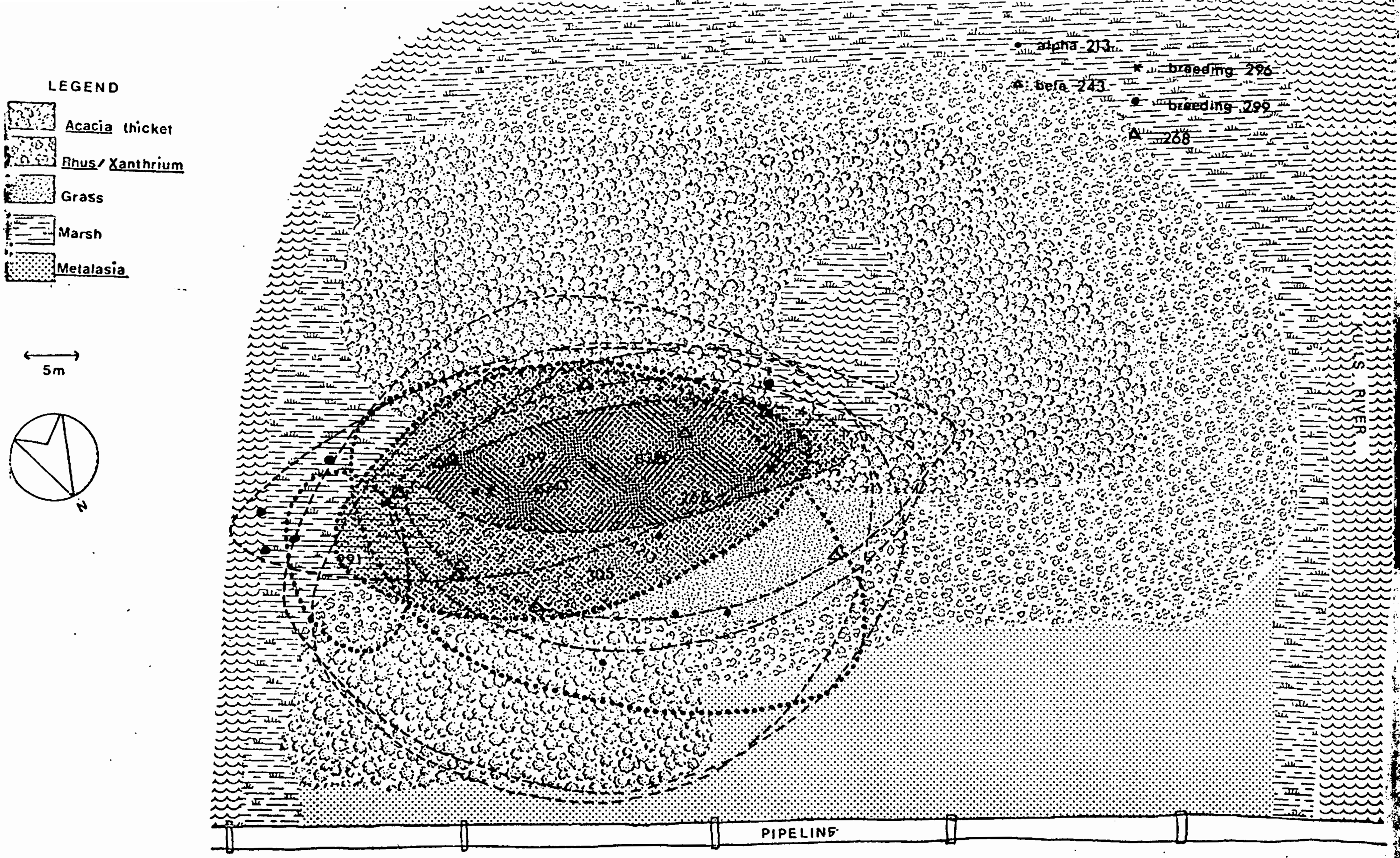


FIGURE 3.8. Home ranges of *Rhabdomys* in March 1980 MARCH MALES FEMALES

females' ranges are fairly widely distributed but overlap considerably with those of the males.

Again, in December, there is considerable overlap of ranges. In agreement with the findings in series 1, the ranges of the 2 beta males, males 213 and 243, are not exclusive, and overlap with those of omega males and females. The main point of interest in these range plots is that of the breeding female, female 202: the home range is obviously very much smaller, and is, in fact, exclusive.

In March only 3 males were tracked. The probable reason for the very small range size of male 291 has already been discussed. A large proportion of male 213, the alpha's range is exclusive: whether this would be the case if more males had been tracked and plotted, is, unfortunately unknown.

The home ranges of the females in March show a great deal of overlap, including those of the 2 breeding females, females 296 and 299. However, when the actual trap or track points are plotted (Figure 3.8) it appears that some of the range is nevertheless exclusive. As stressed before, these home ranges are probability models, statistically including 95% of the animals' activity. This does not mean to say that an animal will utilise the whole ellipse: the actual range may only form part of it. It is interesting, however, that the ranges of the 2 breeding females overlap almost entirely with that of the alpha male, male 213.

3.3.7 Nearest Neighbour Analysis.

The nearest neighbour analysis for both series studies is shown in Tables 3.6(a) and 3.6.(b) respectively. From these, it can be seen that all groups are significantly more clumped than would be expected if randomly distributed: all the R values are less than 1, the value for a random distribution. The principal reason behind this is, I feel, a response to habitat: as the analysis of home range distribution showed, the centres of activity tend to be clumped in areas affording the best shelter. The mere fact that Rhabdomys tolerates the clumping and the high densities that result is an indication that it must have a stable social organisation.

TABLE 3.6(a) NEAREST NEIGHBOUR ANALYSIS FOR SERIES 1. THE UNITS OF R ARE METRES

SUMMER	MALES	BETA M - BETA M	OMEGA M - OMEGA M
No. in sample	8	4	6
No. Nearest Neighbours	7	3	5
R	0.4394	0.2612	0.345
c	3.035	2.565	2.487
Sign	$p < 0.01$	$p < 0.05$	$p < 0.05$

	FEMALES	B-FEMALES - MALES	NB-FEMALES - MALES
No. in sample	9	6	5
No. Neighbours	8	8	8
R	0.488	0.489	0.1626
c	2.938	2.39	4.7987
Sign	$p < 0.01$	$p < 0.05$	$p < 0.01$

WINTER	MALES	FEMALES	MALES - FEMALES	FEMALES - MALES
No. in sample	5	6	5	6
No. Neighbours	4	5	6	5
R	0.2846	0.2041	0.2090	0.1863
c	2.738	3.7295	3.384	3.796
Sign	$p < 0.01$	$p < 0.01$	$p < 0.01$	$p < 0.01$

AUTUMN	MALES	BETA M - BETA M	OMEGA M - OMEGA M
No. in sample	6	3	3
No. Neighbours	5	2	2
R	0.393	0.6117	0.778
c	2.011		
Sign	$p < 0.05$	Non-sign	Non-sign

	FEMALES	MALES - FEMALES	FEMALES - MALES
No. in sample	3	6	3
No. Neighbours	2	3	6
R	0.3907	0.4213	0.342
c	2.019	2.7103	2.52
Sign	$p < 0.05$	$p < 0.01$	$p < 0.05$

TABLE 3.6(a) CONTINUED

SPRING	MALES	FEMALES	MALES - FEMALES	FEMALES - MALES
No. in sample	5	6	5	6
No. Neighbours	4	5	6	5
R	0.3353	0.4507	0.415	0.635
c	2.543	2.101	2.503	1.4384
Sign	$p < 0.05$	$p < 0.05$	$p < 0.05$	Non-sign

TABLE 3.6(b) NEAREST NEIGHBOUR ANALYSIS FOR SERIES 2.

OCTOBER	MALE - MALE	FEMALE - FEMALE	MALE - FEMALE	FEMALE - MALE
No. in sample	5	6	7	6
No. Nearest Neighbours	4	5	7	6
R	0.7921	0.568	0.5789	0.6036
c	0.8894	2.025	2.131	-1.858
Significance	-	$p < 0.05$	$p < 0.05$	-
DECEMBER				
No. in sample	5	5	5	5
No. Nearest Neighbours	4	4	5	5
R	0.5687	0.5468	0.3092	0.3092
c	1.84	1.93	2.95	2.95
Significance	-	-	$p < 0.01$	$p < 0.01$
MARCH				
No. in sample	3	7	7	3
No. Nearest Neighbours	2	6	7	3
R	0.649	0.5782	0.4670	0.7921
c	0.007	0.2479	0.087	0.069
Significance	-	-	-	-

In summer, in February/March 1978, December 1978 and March 1980, there is virtually no difference between males and males and females and females, taken as groups. In series 1 the omega males are slightly, non-significantly less clumped than the beta males. The alpha male is at quite a distance from the main nucleus of the group. Because of the small number of males tracked in March 1980, and the lack of an alpha in December 1979, the classes were not separated in the series 2 studies. Non-breeding females and males are very clumped, indicating attraction and association, whereas the breeding females are further distributed from each other and from other animals; an indication of territorial behaviour.

In Autumn (May 1978, series 1) there is very little difference between all 4 groups, showing that the females are moving towards a non-breeding state: both male-female and female-male groups show slightly higher values than male-male and female-female groups, again indicating attraction and association but this is not as great as in the summer months.

In Winter (July 1978; series 1) the trend appears to be for slightly greater spacing among the males: the other 3 groups are much the same. This may be a reflection of the increase in home range size for the males as described above, and hence a wider distribution of the centres of activity. The females are still associated with the males, but there does not appear to be any greater attraction towards them than to their own sex.

In Spring (September 1978 and October 1979) one finds that, in spite of the restrictions of habitat, the distribution of mice is much more widely spaced. This could be due to the lowered density at the end of the non-breeding season, and before the breeding season commences, when the old and infirm animals have presumably died off. In both series, however, females show close association with mice of both sexes, a trend that is not apparent for the males. Figure 3.5 shows that the ranges of many of the females are still situated in the Rhus/Xanthrium area, which appears to have been largely vacated by the males. This may tie in with the observation of smaller home ranges for the females at this time: perhaps a further indication of females' "faithfulness" to the home site in contrast to the males who tend to wander more.

3.4 CONCLUSIONS.

The study of social organisation of small mammals in a field situation has apparently not been attempted in the past, due, no doubt, to the immense difficulties encountered in determining social relationships and behavioural interactions in a situation where direct ovservation is impossible. One is restricted to studies of animals in captivity, by no means an ideal situation, or simply recording the interrelationships of males and females in the field, without further differentiation, giving no indication of social status or behavioural interaction. The finding that testosterone levels in Rhabdomys are reliably related to social rank is therefore significant, as this can then be used as an index of status in the determination of the social hierarchy and interrelationships. The method does, however, have its drawbacks: firstly, it can only be used during the breeding season, as testosterone levels during the non-breeding season are uniformly low and undifferentiated; and, secondly, the values are apparently not absolute, so that one cannot rely on the use of a standard curve for the determination of the rank of individual animals; the group has to be considered as a whole, and their relative levels assessed. It is suggested, however, that the relative levels are reliable: in all cases, both in captivity and in the field, the same hierarchical social structure, comprising a single alpha, several betas, and rather more omegas, has consistently emerged. On this basis therefore, the use of testosterone as an index of social status appears to be a valuable tool.

The field work has continued many of the findings on the captive colony. Apart from the structure of the hierarchy itself, the changing positions of the mice in the hierarchy are the same: it was observed in captivity that the alpha male was often an older animal that had moved up through the hierarchy, from omega to beta and finally to alpha position. This upward movement was also traced in a younger animal from subadult to omega, to beta leval. Thus these findings confirm the hypothesis that the hierarchy in Rhabdomys is an "age-graded" one: a juvenile that assimilates itself into the system rather than emigrating, assumes omega status; presumably if a beta position falls vacant, it moves up, and so on. It is probable that many of the subadult or nearly matured males emigrate: the inordinate proportion of females-males (2:1) caught, could be an indication of this; the females presumably remain, forming the breeding nucleus of the group. Some males, however, appear never to move from the omega position: this was observed in both the captive and the field situations.

The restricted movements of the breeding females corroborated the findings on the captive colony, where it was observed that the female established a nest and vigorously defended the area around it. Although there are no behavioural observations to support the existence of territorial behaviour in the field. The fact that many of the breeding females' small ranges are exclusive, would indicate that it is a fact occurring. The fact, also, that large portions of the alpha males' ranges were exclusive, could be an indication that they, too, were territorial.

The nearest neighbour analyses confirm the findings on spatial relationships and behavioural interaction that were described in Part 1. Generally, there is a strong association of males and females, particularly during the breeding season. Females appear more tolerant of the proximity of other females than males of their own sex: there is a general male-male avoidance, particularly marked during the breeding season when testosterone levels and hence aggression, are high.

There are a number of findings in the field work that could not be observed in captivity: particularly home range sizes and the distribution of Rhabdomys in relation to habitat. The latter findings that Rhabdomys, in an area of abundant food supply, prefers areas with good ground cover, was indicated in the captivity studies by the observation that the animals always built nests and constructed burrow entrances in places providing very good shelter.

The field studies have therefore, in almost all cases, corroborated the observations on the captive animals; it may thus be concluded that these findings on the social organisation of Rhabdomys, compiled from detailed observations in captivity, and continued by studies in the field, are valid.

CONCLUDING DISCUSSION.

It has been shown in the preceding pages that Rhabdomys is a social animal, and has a well-developed social organisation based upon dominance interrelationships and territoriality.

The importance of the environment on the development and sociality was realised as early as 1906 by Petrucci (cited Crook 1970), who observed that the type of social organisation developed by a species depended on its ecology rather than on its taxonomy. The attractiveness of a group to a salutary animal is ultimately determined by the relative advantage of joining the group, measured by the gain in genetic fitness (Wilson 1975); the advantages conferred on an animal by belonging to a group are threefold, namely, increased efficiency in foraging, defence and reproduction; Wilson(1975) has called these the "prime movers of social evolution". Crook (1970) pointed out that animals that are diurnal and animals living in relatively open environments have a greater tendency to develop sociality than those not. Diurnal animals, by their greater conspicuousness, are more at risk from predation than nocturnal animals under cover of darkness; open environments imply scattered resources - food, shelter and potential males - as well as further risk from predators. Rhabdomys is diurnal and in certain parts of its range, such as the Namib and Kalahari Deserts, (Nel and Rautenbach 1975) inhabits very open environments. It is therefore not surprising that a well-developed social organisation has evolved.

As far as group size is concerned, the lower limits will be set by the interaction of the three prime movers of social evolution described above. The upper limits will be determined by the carrying capacity of the environment, and are much more difficult to discern in field studies than the lower limits. "The more stable the environment and the more evenly distributed the food in time and space, the more nearly group size will approach the maximum (Wilson 1975). The Cape Flats, with its abundant food supply, is capable of supporting very high numbers: David (personal communication) found a minimum of 238 animals per hectare in a peak year. The density of Rhabdomys tends to fluctuate from year to year - in this study, for instance, densities were higher in 1978 than

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in 1979 and 1980. It does not appear that these fluctuations are cyclic in nature (David, personal communication), and are possibly related to changes in food supply: the exact effects of this are uncertain at present.

Once the group has been formed, it is important that a stable social structure be developed: scramble competition for resources and resultant social strife are energetically inefficient and in a group in which each individual knows his place and where fighting and social strife is at a minimum, more energy is available to devote to foraging, defence, and most important, to reproduction. The dominance hierarchy and territoriality, two points on a single continuum, are ways of doing this. As has been shown here, male Rhabdomys form a structured hierarchy while females do not; only the dominant male is territorial; females are territorial only when breeding. The advantage of the dominance hierarchy, or the more descriptive term "peck order" in efficiently parcelling out resources, is obvious, the reason for females not forming a hierarchy somewhat less so; the reason for only the dominant male and breeding females to show territoriality is altogether more obscure. The advantage of territoriality is generally cited as a limitation of population density and apportioning of resources. However, as Williams (1966) has pointed out: "It may be obvious that social spacing can limit populations but that it actually does set the level of density in any particular case would be very hard to demonstrate. Even where such an effect could be demonstrated, the density regulation would not necessarily be the function of social spacing". Certainly the regulation of density does not answer the question of why only the dominant male is territorial. MacArthur (1965) pointed out that pure contest competition for food is energetically less efficient than pure scramble competition; territoriality is a special case of contest competition which the animal need only win once on a relatively ten times, so that the resident expends less energy than if he were forced into confrontation every time; the so-called "dear enemy phenomenon" (Wilson 1975). A territory supplying sufficient food resources is therefore energetically more efficient than a home range, meaning that more energy is available for other activities, particularly reproduction. This argument can be applied to both males and females: the breeding female, therefore, has more time and energy available for suckling and defending her young. The answer as to why only the dominant males should be territorial lies, I believe, in the phenomenon of sexual selection.

Darwin defined sexual selection as, firstly, competition within one sex for members of the opposite sex, and, secondly, differential choice by members of one sex for members of the opposite sex; he pointed out that this usually means males competing with each other for females and females choosing some males rather than others. The female in general, invests proportionately more in her offspring than does the male: she produces fewer and larger sex cells, in contrast to the male who produces vast quantities of small sex cells and is capable of mating with any number of females. Female choice of a male is therefore of vital importance to her, and will therefore be under strong selective pressure. Trivers (1972) cites two bases on which female choice can be made: genetic fitness and parental investment. Females mating with more fit males will produce offspring that are more fit, on the average, than females mating with less fit males: it follows, therefore, that females should be especially responsive to these morphological and behavioural traits of males which reflect their fitness. The dominant male, by virtue of his having defeated the rest to attain his position is presumably the fittest; while the fact that he is territorial might be an additional enhancement, if might feasibly play a part in parental investment: although Rhabdomys is essentially polygamous and promiscuous, with the male playing no part in the upbringing and care of the young, a female might choose to move in with the territorial male and thus afford additional protection for her young. This was observed in the captive colony: there were indications that it could have been so in the field as well. There would thus be strong selective pressure on the males to become territorial and it would be to each male's advantage to prevent all other males from establishing territories and consequently being selected by the females. The male that would most successfully do this would prove the dominant; it is thus probable that the development of the dominance hierarchy among the males is consequent to the development of territoriality. Because the selective force operating is female choice of males and not vice versa, there is no pressure on females either to develop permanent territories (the development of breeding territories has been described above) or a dominance hierarchy.

In conclusion, therefore, it appears that Rhabdomys is a highly social animal, a trait that has presumably evolved in response to the species' ecology, in particular the diurnal activity patterns, which necessitate a closely-knit social organisation as an anti-predator defence mechanism, and appear in particular to have determined the type of communicative displays, especially the strong emphasis on visual communication, that have evolved. All evidence - spatial relationships in captivity, frequencies and types of displays used between different sex and social classes, and, finally, spatial relationships in the field - points towards a highly structured dominance hierarchy among the males, with the development of territoriality in the single dominant male. The argument is advanced that the main selective pressure for the development of this type of social organisation came from sexual selection on the part of the female, leading to the development of territoriality and hence the dominance hierarchy in the males.

SUMMARY

In this study, the social organisation of the striped field-mous Rhabdomys pumilio was investigated. This species is present in very high numbers in the Cape Flats area near Cape Town, where alien Acacias were imported to control the sand dunes and provide an abundant supply of seeds which is Rhabdomys' principal source of food.

A colony of striped mice was established in an outdoor enclosure for behavioural observations over the period of a year. These confirmed the observations of previous workers that Rhabdomys is diurnal, builds nests as well as burrows and shows a highly structured social system based upon a dominance hierarchy in the males, comprising a single dominant, several middle-ranking and rather more low-ranking males. Territorial behaviour was shown only by the dominant male and females shortly before parturition and during lactation. It was found that the testosterone levels of males provided a reliable index of their status; status also appeared to be determined partly by age with young, recently matured males fitting into the subordinate position and gradually moving up the hierarchy. There were exceptions, however, and some males never moved higher than the lowest rank. Females did not exhibit such a hierarchy, although certain females, particularly those in association with the dominant male, showed characteristics of dominance. Analysis of spatial relationships at a neutral site, the feeding site, showed a clear gradient, with the dominant male maintaining the greatest distance between himself and other males.

Investigation of communication between the social classes further supported the existence of a well-structured hierarchy, and showed close association among males and females and animals of equal rank. Rhabdomys appears to rely heavily on visual means of communication, in particular postural and locomotory displays. The use of ultrasonic calls in association with conciliatory displays was observed: the first time this has been observed in a rodent species. Rhabdomys also uses chemical means of communication, and has well-developed preputial

glands which are related to the level of testosterone and are used almost exclusively by the dominant male for territorial marking. An investigation of the accessory olfactory or vomeronasal system was undertaken: this appears to be functional in sexual behaviour.

The second part of the project was an attempt to confirm these findings in the field. Studies were conducted on the Cape Foats in two series: February to September 1978, and October 1979 to March 1980. Testosterone was used as an index of status in the males, and similarly structured hierarchies to that observed in captivity were found. Changes in testosterone and status were monitored over the breeding season in the second series. Animals were tracked using the marked bait technique of Randolph (1973) and home ranges were calculated by the elliptical method of Jennrich and Turner (1969). It was found that home ranges, particularly of males, tended to vary between the seasons; breeding females had significantly smaller and exclusive ranges, while the range of the dominant male showed evidence of exclusivity also. Middle-ranking and subordinate males showed no difference in their range size and distribution; juveniles had smaller ranges. Nearest neighbour analysis showed a close association between males and females which becomes accentuated in the breeding season; males showed mutual avoidance at this time. When the distribution of home ranges with habitat was considered, it was found that Rhabdomys has a distinct preference for areas of good ground cover.

APPENDIX 1.

THE CALCULATION OF ELLIPTICAL HOME RANGE

The calculation of the elliptical home range has been described by Jennrich and Turner (1969) and Mazurkiewicz (1968, 1971). Briefly, the capture points on the grid are assigned Cartesian coordinates; from these, the centre of activity i.e. the mean value of both x and y values may be calculated. The variances of the x and y coordinate --S_{xx} and S_{yy} respectively-- and their covariance, S_{xy} may then be calculated. From the variances the orientation of the ellipse in the coordinate system may be calculated by the formula:

$$\tan 2\theta = \frac{2S_{xy}}{S_{xx} - S_{yy}}$$

where θ is the angle between the major axis of the ellipse and the x axis of the coordinate system.

The area of the home range is then calculated by the formula:

$$\text{Home Range Area} = n\,\pi|S|^{\frac{1}{2}}$$

where: n is a value defining the proportion of capture points within the ellipse, and hence the animal's activity: the "probability" variable. n may have values from 2 to 9. When n = 2, the ellipse encloses 63.2% of the animal's activity (Mazurkiewicz 1969), when n = 6, 95% is enclosed, and when n = 9, the ellipse encloses 99% of activity (Jennrich and Turner 1969). Jennrich and Turner (1969) recommend the use of the value of 6, which is the value that has been used for the present calculations,

$$\text{and } |S| = S_{xx}S_{yy} - S_{xy}^{2}.$$

The lengths of the semimajor (M) and semiminor (m) axes may then be calculated as follows:

Consider a new coordinate system (u,v) with the origin situated at the centre of the animal's home range, and orientated at θ degrees to the original x axis. The covariance $S_{uv} = 0$.

The variances S_{uu} and S_{vv} may be calculated, from trigonometric functions, according to the following formulae:

$$S_{uu} = S_{xx} + S_{xy} \tan \theta$$

$$S_{vv} = S_{yy} - S_{xy} \tan \theta.$$

(Jennrich and Turner 1969).

The lengths of the semimajor and semiminor axes can be calculated from the formulae:

$$M = \sqrt{n.S_{uu}}$$

$$m = \sqrt{n.S_{vv}}$$

where n has the values described above.

APPENDIX 2.

COVER ABUNDANCE SCALE ACCORDING TO THE ZURICH-MONTPELLIER METHOD.

r	Very rare, negligable cover.
+	Present, but not abundant and with a cover value of less than 1 percent.
1	Numerous but covering less than 1 percent of the quadrat area.
2	Very numerous and covering less than 5% of the quadrat area or covering between 5 and 25% of the quadrat area independent of abundance.
3	Covering between 25 and 50% of the quadrat area independent of abundance.
4	Covering between 50 and 75% of the quadrat area independent of abundance.
5	Covering between 75 and 100% of the quadrat area independent of abundance.

NOTE: Only plant species with a cover abundance index of 2 and over were included in Table 3.

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